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CICIMAR

COMPARISON OF THE BODY CONDITION OF CALIFORNIA SEA LION, *Zalophus californianus*, PUPS AMONG ELEVEN GULF OF CALIFORNIA ROOKERIES

by

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To my family, who despite the time and distance, never ceased to encourage me. To Myriam, for her love and faith in me.

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Abstract

The oceanographic conditions which affect primary and secondary production, as well as the feeding habits of California sea lions vary geographically in the Gulf of California. A previous study found that sea lion diet is similar among the southern midriff island rookeries, but different from that of animals at Machos. I investigated whether this pattern of variation coincided with pup body size and body condition during three reproductive seasons (1996-98), because pups get nourishment exclusively from maternal milk energy acquired locally. I compared body size and body condition on a multivariate basis using morphometric characters through discriminant function analysis and principal components, respectively, between sexes and eleven rookeries. I also tested whether several indices of body condition calculated from morphometric relationships, which are frequently used in mammals, were good indicators of sculp volume adjusted for size. In the southern midriff island region, the Rasito, San Esteban, and Roca Blanca rookeries, which lie close to one another (over a 60 km^2 area), pups were among the smallest and had the lowest body condition indices throughout the study. In the northern midriff island region, pups from the Machos rookery were among the largest and had the highest body condition indices during the same period. This is the only rookery found in the narrow Ballenas Channel, where nutrients are readily available for rapid plankton growth due to particularly strong tidal mixing. San Pedro Mártir, just south of San Esteban, and the rest of the rookeries (lying north and south of the midriff island region) had pups whose body size and body condition varied greatly between years. Factors such as prey size, energy content and behaviour, the physiography of the terrestrial habitat and the density of animals feeding in the same area may have been responsible for the observed differences in sea lion pup body condition, because they influence the energy budget of lactating females. Body condition indices commonly used for other mammals were not good indicators of relative sculp volume. The use of the Fulton condition factor (body mass / standard $length^3$) to adjust body mass for size differences, as a measure of muscular and skeletal growth, together with a similar index of sculp depth or volume (residual of the linear regression of one of these variables on standard length), as a measure of energetic reserves, offered a better assessment of sea lion pup body condition. However, variation in the slope of the body mass-body length relationship indicated that the Fulton condition Factor is not an appropriate index for pups older than approximately two months of age. Male pups were larger and about 3% denser than female pups, mainly as a result of females having larger sculp depth or volume relative to their size, suggesting there is a sexual difference in the allocation of maternal energy in their body. Changes in pup body condition and food consumption rates throughout the last 19 years were density-dependent in Cantiles (a colony in the northern gulf), but not in Los Islotes (Bahía de La Paz, in the southern gulf). This may indicate that the sea lion population of Cantiles, in contrast to that of Los Islotes, fluctuated close to its carrying capacity.

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1 INTRODUCTION

1.1 The relationship between environmental variation and population wellbeing

Understanding the interactions between organisms and their environment is a crucial step in the design of natural resource management plans. The current need to manage such resources on a sustainable basis has prompted the development of mechanisms to assess the wellbeing of populations, communities, and eventually, ecosystems (Furness 1982; Sydeman and Allen 1999). Because they are at the top levels of food webs, certain populations of vertebrate animals are sensitive to variations in the quality of their environment (*e.g.* McNab 1980; Litvaitis *et al.* 1986; Fairbanks 1993; Baker *et al.* 1994; Ashley *et al.* 1998). Thus, they are potential indicators of changes in their ecosystems, such as variation in the quantity and quality of the food, the climate, and other physical characteristics. Animals respond to these changes by modifying their physiology, behaviour, and, depending on their magnitude and duration, may affect the population dynamics and the inter- or intra-specific relationships among populations.

One way to measure the effect or result of the interactions between a population and its environment is to estimate changes in population "condition". This concept is still being developed, but it is generally understood as a measure of the wellbeing of a population. Presumably, animals from a population in good condition are thought to be in better nutritional status, and to have lower mortality rates than those from a population in bad condition. Hanks (1981) suggested that, in order to accurately estimate population condition in large mammals, two variables must be considered: (*i*) demographic "vigor", as proposed by Caughley (1977), which uses the growth rate of the population, based on the balance between fecundity and mortality, and (*ii*) physiological condition, or individual energy stores. This is necessary because physiological condition and demographic "vigor" are not necessarily positively related (Hanks 1981), and thus, some of the effects of environmental variation on populations would not be detected by one of these variables alone. For example, a reduction in food availability could immediately affect the physiological condition of certain individuals, but it would have to be stronger and last longer than a certain threshold to affect the survival and fecundity at the population level.

Top predators, such as some marine mammals, have been shown to respond to changes in the abundance and quality of their food, both in terms of physiological condition and demographic "vigor" (Lockyer 1986; Costa *et al.* 1991; DeLong and Antonelis 1991; DeLong *et al.* 1991; Baker and Fowler 1992). Pinnipeds in particular are an attractive model for the study of the relationship between environmental variation and population condition, because in this group, reproduction and lactation are temporally and spatially separated from feeding. Whereas all pinnipeds (except the walrus) reproduce and suckle their pups on land or ice, where they can be relatively easily manipulated, food search and capture are exclusively marine activities. Consequently, the effect of environmental changes on animal populations has been studied more thoroughly in this group of marine mammals than in others (Worthy 1987; Costa *et al.* 1989; Boyd 1991; Trillmich and Ono 1991; Renouf *et al.* 1993; Stewart and Delong 1993; Trillmich 1993).

Sea lions and fur seals together comprise the pinniped family Otariidae, and their life history is fairly homogeneous across species (Bonner 1984; Trillmich 1990). Although they range from subpolar to tropical areas of the Pacific Ocean, they are also found at high latitudes of the Indian and Atlantic oceans (King 1983). They have a polygynous mating system, which, as in other species, is associated with a pronounced sexual dimorphism (Boness 1991). Females are smaller than males at all ages, and during adulthood, they move freely between adult males' territories. During a generally annual reproductive season, pregnant females give birth to a single pup, a few days after arriving at the colony where they were born themselves. Some time after parturition, mothers begin a series of excursions to sea to feed which are separated by periods of time on land or ice to nurse their pup (Bowen 1991; Costa 1991; Trillmich 1990). This foraging-nursing cycle can last anywhere from four months (*e.g. Arctocephalus gazella*, *Callorhinus ursinus*) to three years (*e.g. A. galapagoensis*), depending on the species, and, at least across species, on environmental seasonality and predictability (Gentry *et al.* 1986). However, a recent study pointed out that prey distribution may play a more important role (Francis and Boness 1998).

During the first months of life, pups cannot feed on their own and must rely exclusively on their mother's milk for nutrition (Bowen 1991). Between the third and eighth month of age, once they have reached a certain size and have acquired the appropriate swimming and diving skills (Horning and Trillmich 1997), pups start incorporating solid food to their diet (Costa 1991; Kovacs and Lavigne 1992).

One of the most difficult tasks facing researchers trying to understand the relationship between environmental variability and marine mammal populations is choosing the variables most sensitive to environmental stress. Nevertheless, during the 1982-83 El Niño (EN) event, several researchers documented the effects of a large environmental perturbation on many pinniped populations along the Eastern Pacific (Trillmich and Ono 1991). They concluded that, as a result of a drastic reduction in food availability, mortality rates increased in all year classes and sexes, there were changes in animal distribution, and foraging and maternal attendance behavior (Trillmich *et al.* 1991). The magnitude of these responses showed a latitudinal gradient, being most pronounced at lower latitudes, and pups were more vulnerable than adult animals. In addition, other studies have documented pup mass loss, lowered growth rates, and changes in foraging patterns associated with smaller and more frequent reduction in food availability (Boyd 1984; Costa and Gentry 1986; Worthy 1987; Costa *et al.* 1989; Boyd *et al.* 1991; Lunn and Boyd 1993b; Bowen *et al.* 1994; Trites and Antonelis 1994; Arnould and Boyd 1996; Boyd 1996a). Because pup characteristics are greatly influenced by maternal investment, they may be useful for monitoring habitat quality.

In view of the large decline in Steller sea lion numbers in some parts of Alaska over the last 20 years, several studies have been conducted to determine its proximate and ultimate causes. One of the leading hypothesis is that, unlike the stable population, the declining population may be food stressed (Higgins *et al.* 1988; Merrick *et al.* 1995; Davis *et al.* 1996; Calkins *et al.* 1998). Although the cause of the population decline has not yet been established, the reduction in adult female body size suggests a link between food availability and body condition. This finding highlights the importance of determining the usefulness of body condition measurements for monitoring environmental conditions; a topic that has received considerable attention recently (Laws 1978; Lockyer 1987; Reilly and Fedak 1990; Ryg *et al.* 1990; Beck *et al.* 1993; Renouf *et al.* 1993; Gales *et al.* 1994; Arnould 1995; Hammill *et al.* 1995).

1.2 General ecology of California sea lions

A marine mammal that might be potentially useful for the kind of monitoring purposes described above is the California sea lion (*Zalophus californianus*), which comprises three subspecies. The most abundant of these subspecies, *Z. c. californianus* (Lesson, 1868) (sea lion hereafter), inhabits a relatively large area of the Northeast Pacific Ocean, from British Columbia (50° N) to the Marías islands in Mexico (20° N). In 1983, the total sea lion population was 145,000 (Le Boeuf *et al.* 1983). The Galapagos sea lion, *Z. c. wollebaecki* (Sivertsen, 1953) is less much less abundant with 40,000 individuals (Bonner 1994) inhabiting the Galapagos archipelago, whereas the Japanese sea lion, *Z. c. japonicus* (Peters 1866), is considered extinct, but it inhabited the Sea of Japan and Okhotsk. Most of the sea lion population is found over the continental shelf of the subtropical and temperate regions of California in the United States and on the coasts of Baja California in Mexico. In the latter region there are approximately 100,000 individuals (Le Boeuf *et al.* 1983; Aurioles-Gamboa and Zavala-González 1994), of which 23,000 reproduce on several islands and islets of the Gulf of California (Aurioles-Gamboa and Zavala-González 1994), between 24° and 31° N (Le Boeuf *et al.* 1983). More specifically, 80% of all the animals in the gulf are found north of 28° N, in the region known as the midriff. This distribution pattern responds mainly to the high primary and secondary production levels found in the midriff region, as indexed by pigment concentration and commercial catches of fish on which sea lions are known to prey upon.

Reproduction is an annual event in this species and it begins with the arrival of adult males in May when they establish their territories (Aurioles-Gamboa 1988). Around the same time, the majority of adult females which until then spent most of their time at sea, are more frequently found ashore. A few days after their arrival, pregnant females give birth to a single pup and they stay together for about four days, which is called the perinatal period. In the rookeries of Los Islotes, Rasito and Cantiles, births are most frequent during June. During this time, mothers and pups learn to recognize each other, facilitating their reunion after each foraging trip to sea that lactating females undertake periodically after the perinatal period. These foraging trips average one to three days in duration, at least during the first part of lactation (Heath 1989; García-Aguilar and Aurioles-Gamboa 1997), and are interrupted by one to two day visits to shore to suckle. The foraging-nursing cycle is repeated several times until pups are weaned at about twelve months of age and it is known as the period of maternal attendance. As pups grow older, maternal attendance patterns change as foraging trips become longer, but time spent ashore remains relatively stable (Heath *et al.* 1991). Females become estrous about 27 days postpartum and mating is generally aquatic (Heath 1989). After the egg is fertilized, it remains suspended in the uterus for three months before it attaches to the endometrium. This phenomenon is known as delayed implantation and although it also occurs in other mammals, it is common to all pinnipeds (Boyd 1991).

Unlike adult females and pups, adult males fast throughout the mating season, enabling them to defend their territories through behavioral displays both on land and, to a large extent, in the water. Once the mating season ends during late August, most adult males abandon the rookeries and lead a pelagic existence for the rest of the year. The migratory pattern of these individuals is well documented in the coasts of California and British Columbia, where they appear to travel north during the winter and south during the spring, before the mating season (Fry 1939; Peterson and Bartholomew 1967). There is some evidence indicating some exchange of animals between southern California and Baja California (Bartholomew and Boolootian 1960) and between the Pacific Ocean and the Gulf of California in southern Baja California (Aurioles *et al.* 1983). In contrast, subadult males are more abundant in the rookeries during winter, after the mating season, and the few that are found on land during the summer are segregated from the breeding population in specific beaches (Aurioles 1988). Because lactating females and their pups are tied to the area around rookery for most of the year, they are attractive subjects for monitoring local environmental conditions.

Several oceanographic studies have revealed important spatial and temporal variations in the aquatic habitat of sea lions in the Gulf of California. One of the main sources of such variability is the topography of the ocean bottom because it has a strong influence on water circulation, which in turn affects other physical properties (Maluf 1983). The northern end of the gulf, between the Colorado river delta and the midriff region, is relatively shallow (50-200 m), with the exception of Wagner basin, located south of Rocas Consag island. To the south, this profile is modified by the Delfin basin, north of Ángel de la Guarda island, with depths of more than 900 m. The southern boundary of this basin is the channel between Ángel de la Guarda and the Baja California peninsula, which forms the narrow and deep Salsipuedes basin or Ballenas channel, with depths of 1,400 m. Three more basins are found just south of Ángel de la Guarda island that have depths similar to those of Delfin: San Esteban, Tiburón and San Pedro Mártir. These basins are adjacent to the islands bearing the same name. The deepest depressions of the entire gulf, however, are found south of the midriff region. From north to south, Guaymas is the first one and also the largest, reaching depths of almost 2,000 m. In the same direction, the depth of Carmen, Farallón and Pescadero basins increases (2,700, 3,150 and 3,700 m, respectively).

Surface water circulation in the gulf is relatively isolated from that in the Pacific Ocean because of its geographic position (Maluf 1983). South of midriff islands, water circulation is driven mainly by the wind, which push Eastern Tropical Pacific water northwest into the gulf during the summer and fall, causing upwelling along the eastern coast. During winter and early spring, the winds push the water in the opposite direction and Eastern Tropical Pacific water is limited to the mouth of the gulf. Upwelling is common along the peninsula during this time. In contrast, water circulation is largely a reflection of tidal movements in the midriff region, where surface currents may be up to twenty times faster than in southern areas (Maluf 1983). These conditions give rise to the strongest vertical mixing that can be found in the gulf.

The combination of topographic and hydrographic features sets the stage for the spatial distribution of nutrients, oxygen, and inorganic carbon found in the Gulf of California. Oxygen concentration decreases with depth and reaches a minimum between 500 and 1,100 m (Alvarez-Borrego 1983). This minimum is very clear near the mouth of the gulf and becomes blurred towards the north. The depth range at which the oxygen minimum is found increases in the same direction and may be undetectable north of the midriff region (Alvarez-Borrego and Lara Lara 1991). The concentration of dissolved inorganic carbon is highest at intermediate depths south of the midriff region, whereas no such maximum is present to the north of this area. Ballenas channel has unique properties with respect to these variables mainly as a result of the strong tidal mixing and winds that are found there. In this channel, the concentration of oxygen is relatively high at any depth, the pH is lower, and the concentration of nutrients is higher than anywhere else in the gulf. Furthermore, Badan-Dangon *et al.* (1985) found the lowest sea surface temperatures of the entire gulf throughout the year in Ballenas channel. As expected, these characteristics have a profound influence on the distribution of benthic and pelagic organisms (Alvarez-Borrego 1983).

Phytoplankton concentration near the surface is lowest south of 25° N and highest at the northern extreme of the gulf. However, Alvarez-Borrego and Lara Lara (1991) pointed out that primary productivity may not be so different between both regions if it is integrated over the entire euphotic zone, because the intense vertical mixing in the north results in a reduced euphotic zone, compared to the south. Although no appropriate data are available to describe the spatial distribution of primary production in the gulf, Santamaría-del Ángel *et al.* (1994) used satellite images of sea surface color to estimate the concentration of phytopigments and its differences between different areas throughout eight years. Based on these data, the authors identified 14 regions with different characteristics. In their analysis, Ballenas channel and the northernmost region of the gulf, appeared as distinctive areas, where pigment concentration was relatively high and constant throughout the year. In contrast, the rest of northern area showed marked seasonal variations in this variable.

The geographic pattern described above suggests that the quality of sea lion habitat depends on the location of the rookeries. A concurrent study on the trophic structure of this species among seven rookeries supports this idea (García-Rodríguez 1999). Four different groups of rookeries, which were not strongly associated with the distance between them, were shown to represent different feeding areas. Sea lions from the rookeries of San Pedro Mártir, San Esteban, and Rasito formed one group and fed primarily on mycthophids (Myctophidae) and Pacific sardine (*Sardinops caeruleus*). All of these rookeries are located just south of the midriff islands and lie close to one another (less than 40 km). On the other hand, sea lions from three rookeries in Ángel de la Guarda island (Machos, Cantiles, and Granito) and Lobos, just north of it, showed striking differences in their diet despite being close to one another. Although Cantiles and Lobos formed a single group, where largehead hairtail (*Trichiurus lepturus*) and unidentified midshipman species (*Porichthys spp.*) were important prey for sea lions, Pacific anchoveta (*Cetengraulis mysticetus*) was preyed upon only by animals from Lobos. Another group, comprising only Granito, was characterized by the importance of largehead hairtail and Californian anchovy in the sea lions' diet. In a fourth feeding area represented by Machos, the only rookery in Ballenas channel, sea lions fed predominantly on chub mackerel (*Scomber japonicus*). Additionally, the diversity of species consumed at these rookeries appeared to differ between them and was lowest in Granito and, particularly, in Machos (García-Rodríguez 1999). Aurioles *et al.* (1984) found very different prey species in Los Islotes, in the bay of La Paz, aproximately 400 km south of the midriff islands. Pacific flagfin (*Aulopus bajacali*) and bigeye bass (*Pronotogrammus eos*) are the most frequently consumed species by sea lions in this rookery with very little interannual variability (García-Rodríguez 1995). These findings suggest that the bay of La Paz represents a different feeding area. Unfortunately, no data are available from the rest of the rookeries.

Diet plays an important role in determining an individual's body condition because the size and energy content of prey varies depending on the species and other factors, including the time and energy spent searching, handling, and assimilating each prey item (Stephens and Krebs 1986). In the case of lactating females, one of the results of this energy balance is the growth of their pups because it affects the rate of energy transfer from mother to pup (Gentry 1998). Therefore, sea lion pups' body condition may be useful in assessing habitat quality as a function of birth site.

The rookeries where sea lions reproduce are on a variety of substrates such as pebbles, sand, rock boulders, or rocky terraces, and some are backed by cliffs. The combination of substrate type and the orientation of the rookery affect the temperature, amount of solar radiation, and wind to which the animals are exposed. Limberger *et al.* (1986) showed that these factors have a strong influence on the thermoregulatory abilities of Galapagos fur seal pups. In the Gulf of California, air temperature decreases from south to north during winter, and it increases in the same direction during the summer (Alvarez-Borrego 1983). The average temperature range increases from 6° C in the south, to 18° C at the northern end. Therefore, the physiography of the breeding habitat may affect the animal's energy budget.

The variation in body size and body condition of animals of the same age may be associated with the oceanographic as well as the terrestrial characteristics of the rookery. Newborn body size has been used as an index of maternal effort over the gestation period in grey seals (Kovacs and Lavigne 1986) and in Galapagos (Trillmich 1986) and Antarctic (Boyd and

McCann 1989) fur seals. This variable has been shown to be related to changes in food availability (Costa *et al.* 1989; Boness *et al.* 1991; Lunn and Boyd 1993b) population density (Fowler 1987).

An animal's body condition is a measure of its energy reserves, and the best way to estimate it is through body composition analysis. However, the tecniques involved in this type of analyses are demand considerable time and monery, making it difficult to obtain large samples from small populations. For this reason, other indices have been developed to circumvent this difficulty. Some of these indices are based on morphometric measurements, assuming that they are correlated with direct body composition analyses of the same or related species (Pitcher 1986; Arnould 1995). The variables most commonly used for this purpose in marine mammals are: body mass (Boyd 1984; Castellini and Calkins 1993; Hammill *et al.* 1995), axillary girth to length ratio (American Society of Mammalogists 1967; Castellini and Kooyman 1990) and sculp weight or depth (Lockyer *et al.* 1985; Pitcher 1986; Read 1990; Ryg *et al.* 1990; Beck *et al.* 1993), given that, in these species, most of the total body fat is found the blubber. The methods used to adjust these variables for size differences are diverse, and therefore, an evaluation of the relationships between them should provide a better overview.

In sexually dimorphic species, such as the otariids, it is necessary to examine sexual differences in body condition before attempting make spatial or temporal comparisons between animals. Male pups are more expensive to produce than females pups just because they are born larger (Boyd and McCann 1989). Evidence suggests that in California sea lions, male pups have higher milk intake rates than females, although this may be a result of their larger size (Oftedal *et al.* 1987). Furthermore, at least in one otariid, the allocation of energy from milk constituents varies with the pup sex (Arnould *et al.* 1996a). It is not yet clear whether body condition indices are sensitive to these differences.

1.3 Objetive

The purpose of this study is to compare the body condition of sea lion pups among eleven rookeries of the Gulf of California during three consecutive years (1996-98), using morphometric measurements. I hypothesized that given the heterogeneity in habitat characteristics, the nutritional status of pups depends on the rookery of birth. To test this hypothesis, I studied (i) pup body size and body condition as a function of rookery and sex, (ii) changes in these variables with age, (iii) the relationship between several body condition indices, and (iv) I explored the relationship between pup production, body condition, colony food intake, and sea surface temperature at two rookeries between 1980 and 1999; one in the midriff region, and the other in the bay of La Paz. I expected that pups born in Machos would be among those with the best body condition because the oceanographic conditions in Ballenas channel, where this rookery is located, are conducive to the rapid growth and large abundance of prey species.

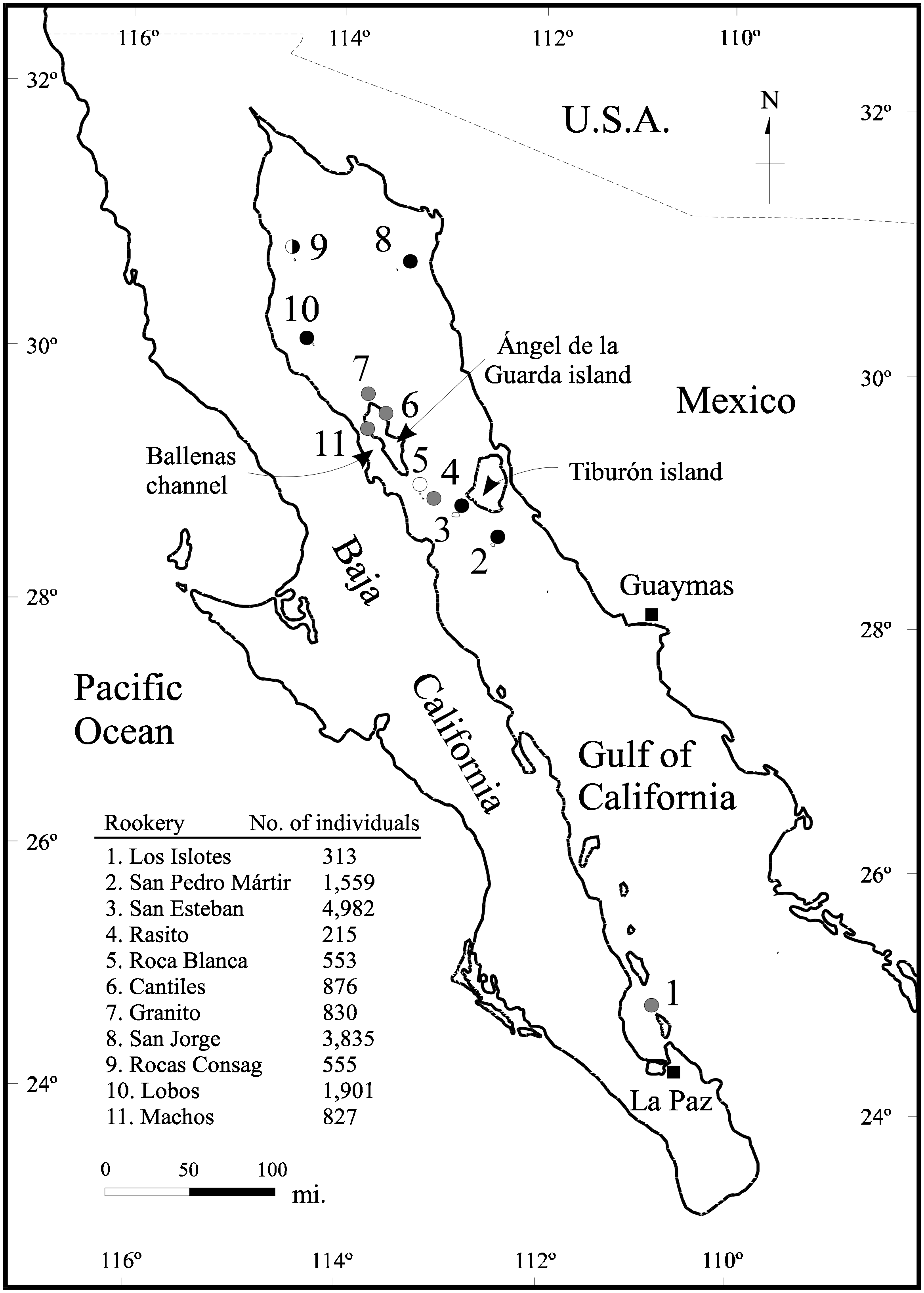
2 METHODS

2.1 Sea lion rookeries of the Gulf of California

This study was part of a larger project aimed at assessing the health status of sea lions in the Gulf of California. It covered the 1996, 1997, and 1998 breeding seasons, during which nine, eleven, and six rookeries were studied, respectively (Figure 1). Five rookeries of the rookeries studied in 1998 (Los Islotes, Rasito, Machos, Granito, and Cantiles) were visited at least one of the previous years. Roca Blanca was visited in 1997 and 1998, while Rocas Consag was visited only in 1997. The rest of the rookeries were visited in 1996 and 1997 (San Pedro Mártir, San Esteban, Lobos and San Jorge). Most of the rookeries are located in and around the midriff region (precise latitude and longitude are shown in Table 1): San Pedro Mártir, San Esteban, Rasito, Roca Blanca, Cantiles, Machos, Granito, and Lobos. San Jorge and Rocas Consag are located near the northern end of the gulf, while Los Islotes is in the bay of La Paz, near the mouth (Figure 1).

Samples were obtained during the same time frame in 1996 and 1998, but during earlier dates in 1997 (Table 1). The temporal difference in sampling periods precluded interannual comparisons, except where noted below. The samples were obtained after most pups in the rookery have been born, which is defined as the period of time when 90% of the total number of births have occured. In Los Islotes (Aurioles and Sinsel 1988), Cantiles (Morales-Vela 1990; Morales-Vela and Aguayo-Lobo 1992), and Rasito (Morales-Vela 1985) this corresponds to the period between the begining of the breeding season and the second week of June. Although no additional data are available to support it, I assumed that this period does not vary among rookeries.

To investigate the relatioship between indices of food abundance in the long term, I used additional information obtained during several years in Cantiles and Los Islotes. This included unpublished pup body mass and standard length data from Cantiles during 1988-89 and 1992-95, provided by M. García-Rivas. The same type of data from Los Islotes, in addition to population censuses from 1980 to 1999 were obtained from both rookeries by Dr. Aurioles-Gamboa and M. García-Aguilar (Marine Mammal Laboratory, CICIMAR-IPN, unpublished data). These data were partially used in several publications (Aurioles *et al.* 1983; Aurioles 1988; Aurioles and Sinsel 1988; Aurioles-Gamboa and Zavala-González 1994). I used this database to generate a time series for each rookery, which included: pup production and body condition, food intake rate, and sea surface temperature during the breeding season.



Rookery	No. of individuals
1. Los Islotes	313
2. San Pedro Mártir	1,559
3. San Esteban	4,982
4. Rasito	215
5. Roca Blanca	553
6. Cantiles	876
7. Granito	830
8. San Jorge	3,835
9. Rocas Consag	555
10. Lobos	1,901
11. Machos	827

Figure 1. Location of sea lion rookeries in the Gulf of California and number of animals counted at each one of them during 1997. Grey, white, black, and black and white circles represent colonies that were studied during 1996-98, 1997-98, and 1997, respectively.

2.2 Relationship between biological and environmental indices of food abundance

I studied the variation in sea surface temperature (SST), the number of adult females on land, the pup production, and food intake rate over almost 20 years at Los Islotes and Cantiles, which, as a whole, may provide better insight into the population condition of these rookeries than each variable independently. SST is known to have an effect on the distribution and reproduction of pelagic organisms which are preyed upon by sea lions (Arntz *et al.* 1991; York 1991; Roemmich and McGowan 1995). The fluctuations in the number of adult females and pup production are associated with food availability (Trillmich and Ono 1991). Food intake rate may reflect the animals' choice to remain near the rookery or to immigrate from other areas to feed nearby. These rookeries are the most extensively studied of the Gulf of California and are thus good subjects for the study of these relations.

SST data from the Gulf of California were obtained from Physical Oceanography Distributed Active Archive Center (PO.DAAC) at the Jet Propulsion Laboratory (JPL 1998). These data were ultimately collected by several NOAA (National Oceanic and Atmospheric Administration) equipped with an AVHRR (Advanced Very High Resolution Radiometer) instrument. The resolution of this instrument was 9 km and the data are monthly average values of daily measurements taken at night during May, June, and July. The data for each rookery was extracted based on estimates of distance to foraging areas in Los Islotes (Durán Lizarraga 1997), which indicate that lactating females forage up to 20 km from the rookery. However, I defined the area of a square with 40 km sides around each rookery because no information is available for other rookeries or on temporal changes, thus making this a more conservative estimate.

The number of animals of each sex and age category were counted by a team of researchers travelling at 10 km $\cdot$ hr^{-1} on a small boat, keeping a distance of 20-30 m from the shore. Counts were made once during July, classifying animals according to age and sex as described in Aurioles *et al.* (1983), Le Boeuf *et al.* (1983), and Aurioles-Gamboa (1988). Briefly, all the animals within viewing distance, with the aid of binoculars when necessary, were counted and divided into five categories: adult male, subadult male, adult female, juvenile, and pup. Adult males are larger than animals from all the other categories, their neck is proportionally larger, and have a fully developed saggital crest in their skull that is visible externally. Subadult males are smaller than adult males, but are larger than animals from other categories, and their neck and saggital crest are not completely developed. Adult females are larger than juveniles and pups, smaller and more slender than adult or subadult males, and may have a suckling pup next to them. They are also recognized by their beige or gray pelage, and their lack of a saggital crest. Juveniles are larger than pups, do not have a saggital crest, and their pelage is similar to that of adult females. Pups are the smallest animals in the population, are born during the reproductive season, have a black pelage, and do not stray far from the shore. Those animals that, for some reason, could not be assigned to any of these categories, were grouped in a sixth category.

This type of census data were obtained from Los Islotes in 1990, 1992, and 1994-99; and from Cantiles in 1981, 1984-91, 1993-98, to document changes in two aspects of the population:

i) the number of adult females and pup productivity, and ii) food intake rate tasa by all animals in the rookery during the reproductive season. Although the number of adult females counted with these methods represents only the fraction of animals on land, they were not multiplied by any factor, because of the difficulties associated with these adjustments. Some of the factors that have not been taken into account in such calculations include interannual differences in fecundity rates and maternal attendance patterns, which may affect the number individuals on land at any given time. Bonnell *et al.* 1978 estimated that approximately 10% of all adult females are out at sea at any given moment during the reproductive season, but there are probably diel, seasonal, and interannual changes that may affect this percentage. I assumed that the errors associated with the estimation of animal numbers remained constant from one reproductive season to the next.

Pup counts are the most reliable because pups stay on the beach and cannot swim far from the rookery (Bowen 1991) and their black pelage easily contrasts with the background, making them easy to see. However, the number of pups may be considerably underestimated in some rookeries, such as Los Islotes, where there are beaches with large boulders. Many pups stay in the small spaces between boulders, where they cannot be spotted from a boat. In some rookeries with these characteristics, up to 50% of the pups may not be counted (Le Boeuf *et al.* 1983; Aurioles-Gamboa 1988). Nevertheless, I did not make any adjustments to the direct counts because absolute estimates of pup production were not indispensable for the temporal analyses involved.

The amount of food that all animals in the colony consume daily ($kg \cdot d^{-1}$) was estimated for both rookeries, under the assumption that adult males fast throughout the breeding season, and that all individuals within each age and sex category weighed the same (Aurioles-Gamboa *et al.* 1997). Based on estimates from other otariid species, I assumed that juveniles and nonlactating females consumed 14% of their body mass; subadult males 8%, and lactating females 10% of their body mass, respectively. Similarly, juveniles were assumed to weigh 40 kg, adult females 80 kg, and subadult males 175 kg. Multiplying each individual's daily food intake by the total number of animals within its category, the daily food intake attributed to that category is obtained. The sum of the values from all categories represents the food intake rate for the rookery.

A body condition index (body masss / standard length^3, see below) to obtain an estimate of pup body condition at each rookery. I assessed the potential association between these four variables at each rookery independently.

2.3 Capture and handling of sea lion pups

Following the census of the rookery, a small camp was built in an appropriate area of the beach where the pups could be kept and measured. The camp consisted of a portable table, two benches, an awning, a tripod and spring scale, equipment for anaesthesia, and a metal tank to measure volume by water displacement. Pups were captured in groups of 4 to 5 individuals trying

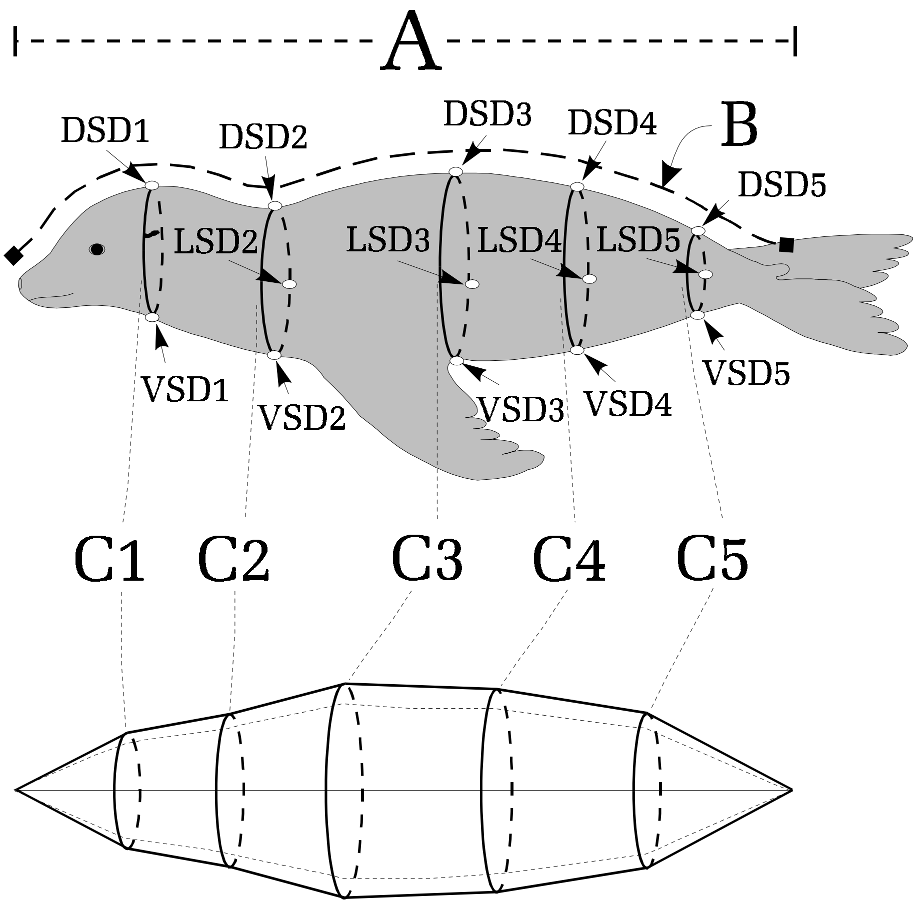


Figure 2. Morphometric variables measured in sea lion pups and geometric model used for the estimation of body volume and sculp volume. Variables A (standard length), B (curvilinear length), and C (girth), were measured in cm. DSD, LSD, and VSD represent dorsal, lateral, and ventral sculp depth measurements, respectively, in cm.

to capture animals that were visually in all states of nutrition seen at the study beach, based on the following criteria: fat pups were comparatively large and their ribs and hip were not visible externally, while malnourished pups had externally visible ribs and hip and their skin folds easily when pinched. Pups are not very agile during the first months of life and do not swim far from the shore, which facilitates this sampling procedure.

To keep their stress to a minimum, animals were kept in the shade inside a small pen partially filled with seawater. Pups were weighed to the nearest 0.25 kg using a spring scale, sexed, and laid ventrally on a portable table where they were manually restrained in 1996 and 1998, and with a 5% isofluorane gaseous mixture in 1997. In all cases, pups were immobilized within three minutes. Following the extraction of three blood samples from the jugular or gluteal vein for biochemical analyses (reported elsewhere), standard length, curvilinear length, girth, and skinfold thickness (Figure 2). The first three variables were measured to the nearest 0.5 cm using a flexible tape measure. In 1996, skinfold thickness was measured to the nearest mm at three ventral and dorsal sites along the body to the nearest mm using an adipometer (Ross Laboratories, Inc.). Skinfold thickness was measured to the nearest 0.5 mm using a skinfold caliper (Lange, Beta Technology Inc.) in 1997 and 1998, but whereas 14 sites were measured in 1997, the average of three repeated measurements over the sternum, was recorded in 1998. I divided skinfold thickness measurements by two, to obtain an index of sculp thickness. The anaesthesia was removed after these measurements were taken, and a unique mark was placed on the dorsal region by clipping a portion of hair. Each pup was placed in the shade inside a net, where they could recover from the effects of the anaesthesia. This process took less than five minutes and once they started vocalizing and walking normally, they were released near the shore. Most pups were seen with their mothers shortly after they were released.

To validate the volume estimates described below, all the pups captured in 1997 were put inside a nylon mesh bag and submerged in a metal tank filled with water, where the amount of water displaced was recorded to the nearest 0.25 l. This procedure was performed after the animals were completely recovered from the effects of the anaesthesia.

Body and sculp volume were estimated for pups captured in 1996 and 1997 using a geometric model consisting of a series of cones and truncated cones (Figure 2). However, the calculations differed slightly between both years because girth and skinfold thickness at positions 1 and 5, and lateral skinfold thickness were not recorded in 1996 (Figure 2). In addition, the distance between each girth measurement was obtained indirectly by multiplying standard length by the fraction that they represented in pups captured in 1997. Therefore, body and sculp volume were estimated using two different models; consisting of either four or six components (Figure 2). Volumes were calculated using the four component model in 1996, and using both models in 1997. Thus, allowing for interannual comparisons without sacrificing the more detailed information obtained in 1997. Paired-sample *t* tests were used to determine the statistical significance of the difference between the estimates from both models. The relationship between the values obtained by each model and those obtained by the water displacement method was tested using simple linear regression analysis. Body and sculp volume could not be estimated in 1998 because only pup body mass, standard length, axillary girth, and sternal skinfold thickness were measured (Figure 2).

The volume of all cones and truncated cones in the geometric model (Figure 2) were added to obtain an estimate of pup body volume. The volume of a cone can be calculated as follows:

$$V_c = \frac{1}{3} (\pi \cdot r^2 \cdot h)$$

where V_c = volume of the cone, r = maximum radius of the cone, and h = height of the cone. This expression was used to calculate the volume of the cones at each end of the model. The volume of a truncated, on the other hand, can be calculated as follows:

$$V_c = \frac{1}{3} \pi h (r_1^2 + r_2^2 + r_1 r_2)$$

where r_1 and r_2 are the large and small radius of the truncated cone. This formula was used to calculate the volume of the truncated cones between the cones at the ends of the model.

Sculp volume was estimated by subtracting the volume of a similar series of internal truncated cones, which represent the lean core volume of the pup, from the volume of the external truncated cones. The cones at the ends of the model were not considered for this calculation because the amount of blubber near the snout and caudal region is negligible (pers. obs.). To calculate the radius of the internal truncated cones, the average of the sculp thickness measurements were subtracted from the radius of the external truncated cones. A similar model was used to calculate blubber content in southern elephant and harbor seals (Gales and Burton, 1987; Rosen and Renouf, 1997, respectively).

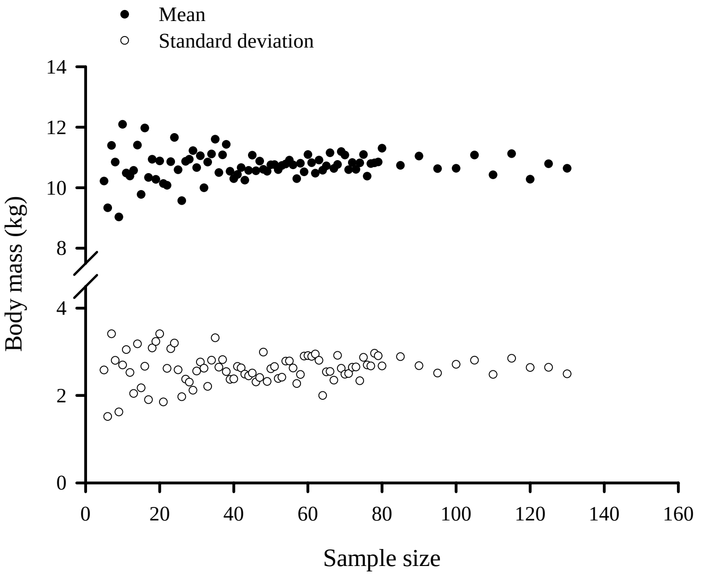


Figure 3. Results of resampling trials performed with measurements from 1,478 sea lion pups captured in the Gulf of California during nine different reproductive seasons.

Resampling trials performed with body mass measurements from 1,478 pups captured at most rookeries of the Gulf of California during 16 reproductive seasons, from 1980 through 1996 (Marine Mammal Laboratory, CICIMAR-IPN, unpublished data) provided an estimate of the number of pups that were needed from each rookery for this study. Random samples of increasing size from the original large database were extracted, and the mean and standard deviation were calculated. As *n* increases, the variation in the mean and standard deviation decreases and stabilizes around a certain value. Most of the variation in pup body mass that may be obtained at a rookery would be sufficiently represented in a sample size that is at least as large as that required to stabilize the variation in these statistics. In the gulf, *n*=40 was large enough to stabilize the variation in the mean and standard deviation (Figure 3). However, this value probably overestimated the necessary sample size because all the variation between rookeries and years was included in the resampling trials.

Although the age of the pups could not be determined precisely, a fraction of the animals had umbilical cord remains which could provide an approximation. Umbilical cord remains usually dissapear by five days of age, and this criterion was used to grossly estimate the age of pups captured in 1997 and 1998 as follows:

i) < 5 days of age: A fresh 3-5 cm section of umbilical cord is still attached to the pup or freshly cut tissue has not yet been shed off.

ii) > 5 days of age: No umbilical cord remains, except for a scar, are visible.

I compared skinfold thickness measurements and the sculp volume index with direct measurements of sculp depth and volume from pups that were dissected soon after their death from natural causes in Los Islotes. To separate the sculp from the rest of the body, an incision was made on the ventral side of the animal, from the neck to just above the anus, and then the sculp was carefully separated from the underlying muscle by cutting in a lateral direction. The sculp was separated in one piece by surrounding the front limbs and cutting around the entire body.

2.4 Estimation of body size differences

Interannual variation

Pup body mass, standard length, and axillary girth were compared among years and the differences were discussed in terms of mean capture date. These were the only variables measured identically throghout the study and, hence, could be used for this purpose. Two-way analysis of variance (rookery and year) was employed to study the variation in these pup characteristics at Machos, Granito, Cantiles, and Rasito. These rookeries were chosen because data were available for the three years. Los Islotes was excluded from this analysis because, in 1996, pups were captured more than 10 days earlier than at the other rookeries. Sample sizes were not large enough to analyze the effects of pup sex, and therefore, the number of pups of each sex at each rookery was randomly adjusted so that they were equal.

Sexual variation

A different design was used to test for sexual differences in pup body size, albeit with the same data as for the previous analysis. For each year independently, all variables were compared among male and female pups using one-way analyses of variance. The coefficient of variation of the these variables was compared among the sexes, to determine potential sexual differences in their variability (Zar 1996).

Variation among rookeries

Pup body size was compared among rookeries on a multivariate basis in 1996 and 1997 using discriminant function analysis. The variables included in this analysis were: body mass, standard length, axillary girth, and sculp depth. As in the previous analyses, the number of pups of each sex within each rookery were randomly equalized. Applying the methods described in Tabachnick and Fidell (1996), data from one male and three female pups in 1996, and from two male and four female pups in 1997, were excluded because they were outliers. The underlying assumptions of homogeneity of variance and normality were assessed by Levene's test and the Shapiro-Wilks statistic, repectively. All the variables were entered simultaneously into the discriminant function analysis, but since there were methodological differences between years, comparisons among rookeries were done separately for each year, using two different approaches. For the first approach, all the rookeries studied each year were included, and for the second, only those rookeries that were studied both years. In the first case, all girth and sculp depth measurements were included, and in the second, only girth and sculp depth measurements 2-4 (Figure 2). However, to avoid introducing multiple correlated variables, the sum of sculp depth measurements was used instead of many single variables. This method also reduced the negative effect of differing variation between sculp depth sites on the assumption of homoscedasticity.

The significance of each discriminant function was assessed by succesive removal of functions and then evaluating the discriminating power of the remaining functions (χ^2 tests). Only those functions that significantly contributed to the discrimination were retained. The relative importance of the variables in establishing differences among rookeries was evaluated by comparing the absolute value of their standardized coefficients (|std. coeff.|) (Campbell and Atchley 1981). The most important variables were compared separately among rookeries using a one-way analysis of variance. Finally, the differences between rookeries were summarized on a dendrogram, produced by cluster analyzing the matrix of squared Mahalanobis distances (D^2) between the centroids of all pairs of rookeries. The unweighted pair group average (UPGMA) method was utilized for linking rookeries.

2.5 Calculation of body condition indices and their variation

Sexual variation

As in other mammals, body mass, body and sculp volume, axillary girth, and sculp depth, were considered to be good indicators of pup nutritional status (Young 1976; Pitcher 1986; Castellini and Kooyman 1990; Read 1990; Castellini *et al.* 1993; Krebs and Singleton 1993; Lunn and Boyd 1993a; Renouf *et al.* 1993; Sweitzer and Berger 1993; Arnould 1995; Hammill *et al.* 1995). However, the effect of body size must be removed from these variables prior to comparing the body condition of animals of different size. One of the commonly used methods for this purpose involves regression and covariance analyses of the relationship between these variables and some independent measure of body size, usually length. Others simply consist of dividing one of these variables by a measure of body size, assuming that the relationship between both variables has a common exponent for all individuals in the population of interest. For this study, the following body condition indices were calculated:

1. $FCF = (BM \cdot 10^5)/SL^3$
2. $GL = (AG \cdot 100)/SL$

where FCF = Fulton condition factor, BM = body mass (kg), SL = standard length (cm), GL = girth to length ratio, and AG = axillary girth (cm). These indices assume that the slope of the relationship between each pair of variables are three and one, respectively, as would be expected if the scaling of body mass and axillary girth on standard length were isometric (Peters 1983). To verify these assumptions and to estimate alternative body condition indices, the following relationships were studied through simple linear regression analysis:

3. BM on SL
4. BM on BV
5. AG on SL
6. BV on SL
7. SD on SL
8. SV on SL

where BV = body volume (l), SD = sculp depth (mm) at its most variable site in the body, following the criterion put forth by Lockyer *et al.* (1985) and used as an index of body condition in other pinnipeds (Ryg *et al.* 1990; Beck *et al.* 1993), and SV = sculp volume (l).

I investigated potential sexual differences in relationships 4-8 using one-way analysis of covariance (Zar 1996), to test for homogeneity of coefficients of regression and intercept. The variables were logarithmically transformed, if it linearized the model. If no significant differences were found, the data from both sexes were pooled and the corresponding regression results presented. The residuals from these regressions were calculated and compared between sexes using analysis of variance. All regressions were estimated by the least squares method, excluding observations more than three SD from the regression line. However, these observations were later included for the calculation of residuals. Because some variables were not measured identically during the study, interannual comparisons of relationships 6 (BV on SL), 7 (SV on SL), and 8 (BM on BV) were limited to 1996 and 1997. Differences in relationship 5 (SD on SL) were determined between 1997 and 1998. Interannual comparisons of relationships 3 (BM on SL) and 4 (AG on SL) were possible among the three years. The significance level (α) for rejecting null hypotheses was set at 0.05.

The relationship between body condition indices based on total body growth and another one, the residual of the regression of sculp volume on standard length, on the other body condition indices described above.

Variation among rookeries

Pup body condition was compared among rookeries using the Fulton condition factor (FCF) and the following indeces of blubber content (IBC): the residuals from the sculp depth on standard length regression (SDR), and the residuals from the sculp volume on standard length regression (SVR), based on the four component (1996 and 1997) and six component geometric models (1997). These comparisons were made using one-way analysis of variance, followed by Tukey's multiple comparisons test for unbalanced designs (Zar 1996). To compare both variables simultaneously among rookeries, each pup was assigned to one of four possible categories, which represent different body condition states, as follows:

State 1: FCF ▲ and SDR ▲
State 2: FCF ▲ and SDR ▼
State 3: FCF ▼ and SDR ▲
State 4: FCF ▼ and SDR ▼

where ▲ = greater than or equal to the yearly average, and ▼ = lower than the yearly average. These states were used as variables and the percentage of pups within each state was compared among rookeries using principal components analysis (Tabachnick and Fidell 1996).

2.6 Changes in body condition indices with age and growth

In the rookery of Los Islotes, several pups were captured, marked, and measured at the begining of the reproductive season in 1994, and 1996-98 (Marine Mammal Laboratory, CICIMAR-IPN, unpublished data) to determine sexual and interannual differences in growth rates and changes in body condition indices with pup age. The pups were serially captured throughout the reproductive season, but whereas body mass, standard length, axillary girth, and sculp depth were measured in 1997 and 1998, only body mass and standard length were measured the previous years. The animals were marked with a unique combination of symbols, approximately 10 by 5 cm, made by clipping their hair in the dorsal region, so that they could be identified later. These symbols are easily recognized and remain with the pups for about three months (pers. obs.).

The relationship between body size measurements, indices of body condition, and relative pup age was analyzed using the Pearson correlation coefficient (r). Growth rates or the rate of change in a variable with respect to age were determined by the slope of the relationship between these variables using simple linear regression techniques.

The body condition of each pup at each capture was determined by the following indices: *FCF*, *GL* and *SDR* (residual of the sculp depth on standard length regression). Because sample assumptions of homoscedasticity and normality could not be met, non-parametric tests were employed for the sexual and interannual comparisons. Differences in growth rates or rates of change with pup age between sexes were determined using the Mann-Whitney test. Interannual differences in these variables were assessed by the Krukal-Wallis test (Zar 1996).

The details of the results from all statistical analyses are presented in the Notes section at the end of this manuscript. To find the relevant details, please refer to the numbers shown in superindex in the text.

3 RESULTS

3.1 Morphometric description of sea lion pups

A total of 625 pups were captured and measured between 1996 and 1998. Table 1 shows the number of pups captured by rookery and year. An interannual comparison of pup body mass, in which only the rookeries that were studied all years, *i.e.* Machos, Cantiles, Granito and Rasito (Table 1), showed that pups were heaviest in 1996, lightest in 1997, and of intermediate weight in 1998 (Table 2). Similarly, pups were longer in 1996 than in the previous years, when pups had about the same length. Although there were no significant differences in axillary girth between pups captured in 1996 and 1998, the girth measurements obtained in 1997 were smaller than in the other years. These comparisons showed that, at least for the four rookeries considered in this analysis, the variation in pup body size could be largely attributed to mean capture date, which was 19, 5, and 18 July, in 1996, 1997, and 1998, respectively. However, the difference in pup body size between 1996 and 1998 was too large for their one day difference in mean capture date.

Standard length, body mass, and axillary girth also varied significantly among these four rookeries[1]; pups from Machos being larger than those from Cantiles or Granito, which in turn were larger than those from Rasito. Body size differences among years and rookeries were not independent of each other, as there was a significant interaction between both factors in the three variables[1]. Pups from all rookeries were smaller in 1997 than in 1996, although only body mass and standard length showed significant differences (Figure 4). Body size differences were not large between 1996 and 1998, but pups from Cantiles, Granito, and Machos were significantly longer in the first year than in the latter. Differences between 1997 and 1998 were even smaller and were significant only for axillary girth measurements in pups from Rasito (Figure 4), where they were larger in the last year. In general, three patterns could be identified: i) relatively large pups in 1996, small in 1997, and of intermediate weight in 1998, which was typical of pups from Machos and Granito; ii) a progressive reduction in pup body size from 1996 to 1998; characterized by pups from Cantiles, and iii) relatively large pups in 1998, small in 1997, and of intermediate weight in 1996, which was observed in pups from Rasito. The interannual changes were, therefore, most strongly affected by the patterns observed in Machos, Granito and Rasito. Although samples were obtained only in 1996 and 1997, pups from Lobos, San Esteban, San Jorge and San Pedro Mártir, were larger in the first year than in the latter. The two rookeries that were studied in 1997 and 1998, Roca Blanca and Los Islotes, had pups significantly larger in 1998.

Girth measurements had its maximum values at position number 3 (*i.e.* axillary girth,

Figure 2), and minimum around the head, neck, and hip (positions 1, 2, and 5, respectively, Figure 2) (Table 3). The distribution of blubber, as measured by skinfold thickness, showed a similar pattern in pups of both sexes and years it was studied. Figure 5 shows such distribution for pups captured in 1997, when it was studied in greater detail. Combining the data from both sexes, sculp depth was maximum at about 50% of standard length,and minimum around the head and hip. This meant that sculp depth was largely proportional to girth. In pups from both years, sculp depth was most variable over the sternum.

Morphometric measurements were obtained from four pups that were dissected soon after death in Los Islotes, bay of La Paz. Sculp weight explained 82% of the variation in the sculp volume index estimated with the geometric model ($P<0.01$). The sculp represented, on average, 24% of pup body mass (range: 18.2-29.5%) (Figure 6).

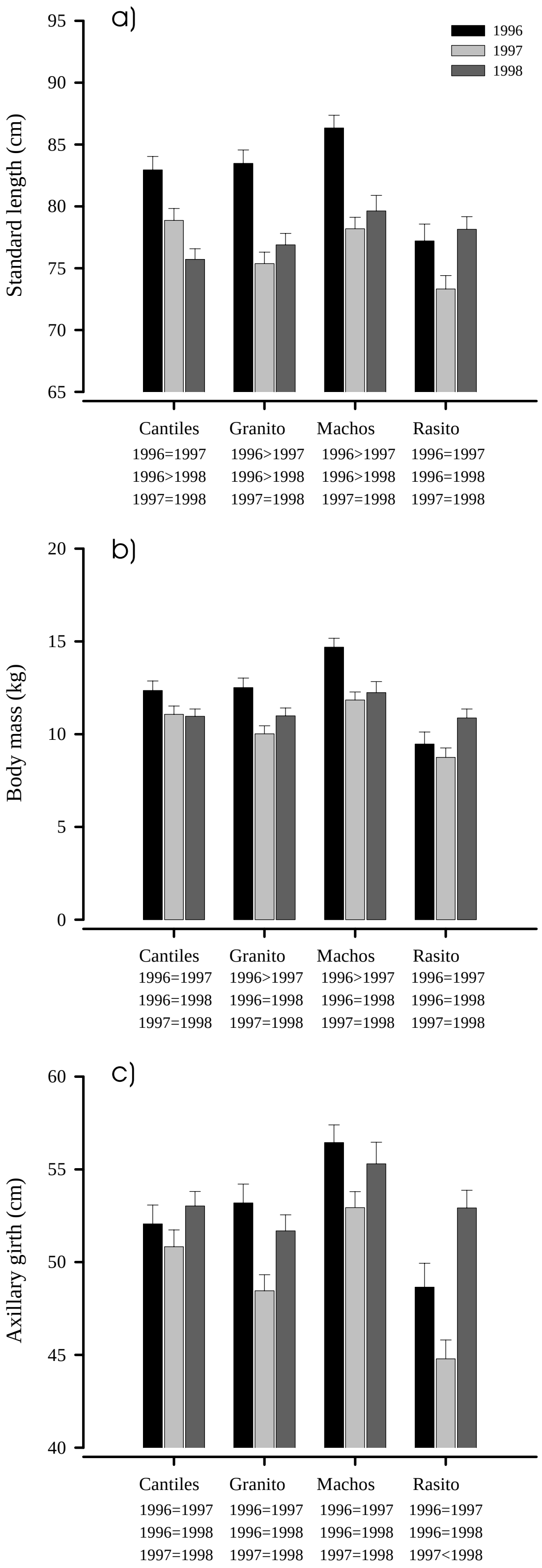


Figure 4. Standard length (a), body mass (b), and axillary girth (c) of sea lion pups from four rookeries during 1996-1998. Results of Tukey multiple comparisons tests are shown below the abcissa.

Table 1. Location of sea lion rookeries, sampling date (d/mo), and number of pups (total, m=males, f=females) captured at each rookery during each year of the study.

Rookery	*n*		
	1996	1997	1998
	179 (103m, 76f)	277 (134m, 143f)	169 (76m, 93f)
1. Los Islotes (ISL)	24 (13m, 11f)	20 (12m, 8f)	29 (21m, 8f)
24° 35' N, 110° 23' W	15/06 and 07/07	26/06	24/07
2. San Pedro Mártir (SPM)	19 (11m, 8f)	27 (10m, 17f)	—
28° 22.5' N, 112° 21' W	24/07	29/06	
3. San Esteban (EST)	25 (13m, 12f)	27 (11m, 16f)	—
28° 40' N, 112° 36' W	17/07	30/06	
4. Rasito (RAS)	11 (5m, 6f)	25 (8m, 17f)	23 (9m, 14f)
28° 49.5' N, 113° 0.5' W	17/07	01/07	21/07
5. Roca Blanca (ROC)	—	28 (15m, 13f)	27 (12m, 15f)
28° 54' N, 113° 26' W		02/07	20/07
6. Los Cantiles (CAN)	20 (12m, 8f)	23 (13m, 10f)	33 (13m, 20f)
29° 29' N, 113° 31.5' W	18/07	05/07	17/07
7. Granito (GRA)	19 (11m, 8f)	26 (11m, 15f)	30 (11m, 19f)
29° 34' N, 113° 33' W	19/07	06/07	16/07
8. San Jorge (JOR)	30 (21m, 9f)	16 (9m, 7f)	—
31° 1' N, 113° 15.5' W	21/07	07/07	
9. Rocas Consag (CON)	—	30 (15m, 15f)	—
31° 7' N, 114° 29.5' W		08/07	
10. Lobos (LOB)	12 (7m, 5f)	30 (16m, 14f)	—
30° 3' N, 114° 29' W	22/07	09/07	
11. Machos (MAC)	19 (10m, 9f)	25 (14m, 11f)	27 (10m, 17f)
29° 21.5' N, 113° 31.5' W	23/07	10/07	17/07

Table 2. Body mass, standard length, and axillary girth (mean ± SE) of sea lion pups from the rookeries of Machos, Cantiles, Granito, and Rasito during 1996-98.

Year	Body mass (kg)	Standard length (cm)	Axillary girth (cm)
1996 (*n*=60)	12.25 ± 0.27	82.48 ± 0.57	52.58 ± 0.54
1997 (*n*=80)	10.42 ± 0.23	76.43 ± 0.49	49.25 ± 0.46
1998 (*n*=78)	11.26 ± 0.24	77.59 ± 0.51	53.23 ± 0.48
ANOVA[†] $F_{2,206}$	13.59*	34.63*	20.72*
Year effect	1996 > 1998 > 1997	1996 > 1998 = 1997	1996 = 1998 > 1997

[†] 2-way ANOVA (rookery x year) indicating differences between rookeries ($F_{3,206}$=10.77, 19.08, 17.70, standard length, body mass, and axillary girth, respectively; $P<0.01$) and rookery x year interaction ($F_{6,206}$=4.75, 2.82, 2.92, standard length, body mass, and axillary girth, respectively; $P<0.02$).

* Significant effect $P < 0.001$.

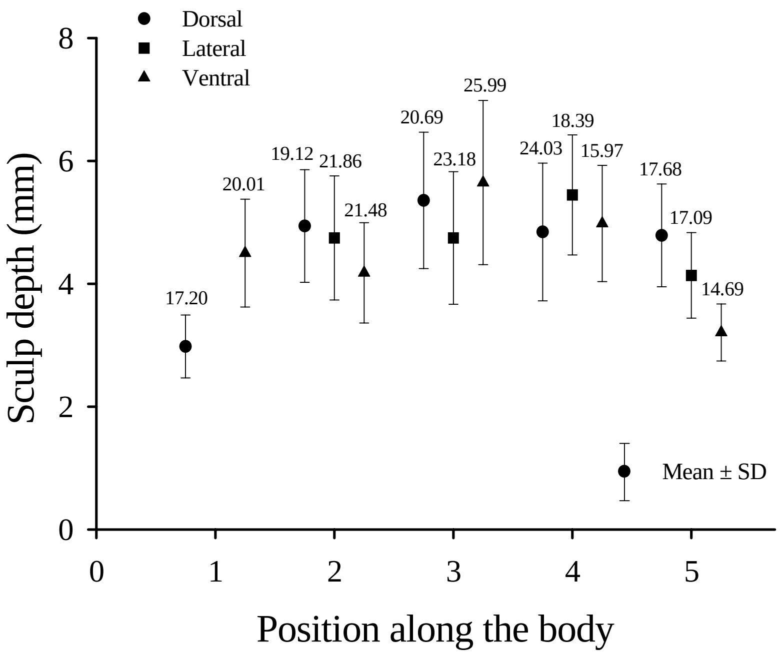


Figure 5. Sculp depth at various positions along the body of sea lion pups, as measured by skinfolds. The number above each error bar is the coefficient of variation. Positions along the body correspond to those in Figure 2.

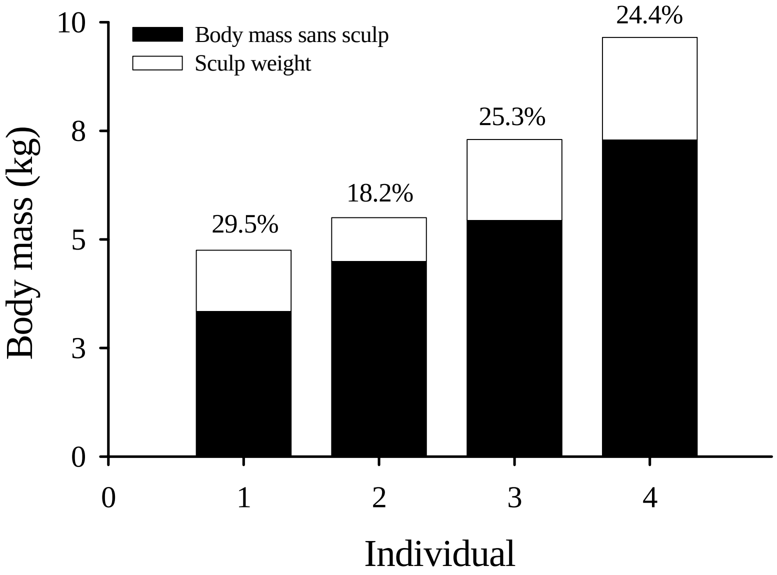


Figure 6. Sculp weight in relation to body mass in four sea lion pups that were dissected soon after death in Los Islotes. The number above each bar represents sculp weight as a percentage of body mass.

3.2 Body size differences among sexes and rookeries

Sexual differences

The data from each year were analyzed separately because there were interannual differences in all variables. Male pups were heavier, longer, and wider than females irrespective of year class (Table 3). Males were, on average, 1.6-2.1 kg (three-year average: 18%) heavier, and 2.0-4.8 cm (average: 6%) larger in their linear dimensions (length and girth) than females. The largest sexual differences were found in girth measurements 4 and 5 (at the level of the umbilicus and hip, respectively), which showed that males were about 8 and 9% larger than females. The body mass, standard length, and girth coefficients of variation had similar values in males and females, but were larger for the first variable than for linear measurements.

Sexual differences were not so pronounced for sculp depth measurements (Table 4). Although males had a thicker sculp than females at all sites, except one, the differences were significant only in 1997 at all the dorsal sites, excluding the head, and at two lateral ones, over the axilla and navel. Significant differences ranged from 0.4 to 1.0 mm (average 15%). The coefficient of variation of these measurements was similar for both sexes, but it was slightly higher in females captured in 1997. In 1996 and 1997, sculp depth was most variable at dorsal site 4 in females, and at ventral site 3 in males (Table 4). However, both sites had similar coefficients of variation in females, so ventral site 3 (*i.e.* over the sternum) was chosen for the regressions described below.

Because interannual differences in body size were largely determined by mean capture date, pups captured in 1997 were probably younger than those captured in other years, because their mean capture date was closer to the available data on the period of maximum birth frequency. Therefore, their body size may approximate that of newborn pups more than the estimates obtained from pups captured in other years.

Male newborn pups (*n*=9) (< 5 d of age) captured at several rookeries of the gulf in 1997 and 1998 weighed (mean ± SE) 9.35 ± 0.35 kg and were 75.11 ± 1.018 cm long. On the other hand, females of similar age (*n*=7) weighed 7.68 ± 0.45 kg and were 71.07 ± 1.29 cm long. Sculp depth over the sternum did not vary among sexes and was 4.7 ± 0.28 mm. All of these measurements were significantly smaller than those of older pups[2].

Table 3. Body mass (kg), standard length, and axillary girth (cm) of sea lion pups from Cantiles, Granito, Machos, and Rasito, during each year of the study. Values are mean ± SE (coef. var.); *n* (machos)= *n* (hembras) = 30 (1996), 40 (1997) and 39 (1998).

Variable[†] and year		Female pups	Male pups	ANOVA *F* Sex effect	*P*
Body mass (kg)					
	1996	11.55 ± 0.45 (21.30)	13.67 ± 0.53 (21.08)	9.38	<0.01*
	1997	9.58 ± 0.28 (18.75)	11.47 ± 0.34 (18.47)	18.47	<0.01*
	1998	10.34 ± 0.24 (14.58)	11.94 ± 0.32 (16.71)	15.89	<0.01*
Standard length (cm)					
	1996	81.32 ± 0.88 (5.96)	84.97 ± 1.00 (6.45)	7.48	<0.01*
	1997	74.54 ± 0.71 (6.01)	78.66 ± 0.70 (5.59)	17.29	<0.01*
	1998	75.91 ± 0.63 (5.18)	78.50 ± 0.63 (4.98)	8.52	<0.01*
Curvilinear length (cm)					
	1996	85.23 ± 0.94 (6.06)	89.68 ± 1.07 (6.56)	9.69	<0.01*
	1997	80.1 ± 0.69 (5.49)	84.89 ± 0.77 (5.76)	21.22	<0.01*
	1998	80.79 ± 0.59 (4.59)	83.73 ± 0.71 (5.31)	10.03	<0.01*
Girth 1 (cm)					
	1997	32.84 ± 0.21 (4.13)	34.46 ± 0.22 (4.10)	27.58	<0.01*
Girth 2 (cm)					
	1996	36.32 ± 0.63 (9.54)	39.07 ± 0.67 (9.45)	8.85	<0.01*
	1997	35.93 ± 0.52 (9.12)	37.95 ± 0.48 (8.01)	8.22	<0.01*
Girth 3 (cm)					
	1996	51.62 ± 0.84 (8.92)	54.60 ± 1.10 (10.99)	4.67	0.034*
	1997	48.21 ± 0.67 (8.85)	50.88 ± 0.69 (8.56)	7.64	<0.01*
	1998	51.60 ± 0.57 (6.85)	54.33 ± 0.62 (7.13)	10.58	<0.01*
Girth 4 (cm)					
	1996	41.98 ± 0.91 (11.93)	45.32 ± 1.15 (13.93)	5.13	0.027*
	1997	45.23 ± 0.72 (10.04)	48.86 ± 0.91 (11.74)	9.89	<0.01*
Girth 5 (cm)					
	1997	28.99 ± 0.39 (8.46)	31.53 ± 0.39 (7.84)	21.25	<0.01*

[†] The numbers next to the variables correspond to those in figure 2. * Significant difference ($P<0.05$).

Table 4. Dorsal (DSD), lateral (LSD), and ventral (VSD) sculp depth (mean ± SE) (coef. var.) of sea lion pups from Cantiles, Granito, Machos and Rasito, by sex and year of study.

Sculp depth measurement† (mm)	Year	Female pups	Male pups	ANOVA *F* Sex effect	*P*
DSD1	1997	3.06 ± 0.10 (20.73)	3.15 ± 0.10 (19.62)	0.45	>0.05
DSD2	1996	4.50 ± 0.16 (19.13)	4.93 ± 0.15 (17.50)	3.79	0.056
	1997	4.93 ± 0.13 (16.03)	5.68 ± 0.14 (15.68)	15.61	<0.01*
DSD3	1996	5.67 ± 0.20 (18.98)	6.12 ± 0.24 (21.33)	2.13	>0.05
	1997	5.04 ± 0.16 (20.62)	5.78 ± 0.17 (18.85)	9.61	<0.01*
DSD4	1996	4.98 ± 0.22 (24.64)	5.49 ± 0.22 (22.35)	2.57	>0.05
	1997	4.46 ± 0.19 (26.19)	5.48 ± 0.20 (23.08)	14.19	<0.01*
DSD5	1997	4.84 ± 0.15 (19.00)	5.26 ± 0.13 (16.10)	4.49	0.037*
LSD2	1997	5.08 ± 0.18 (22.57)	5.31 ± 0.17 (20.16)	0.92	>0.05
LSD3	1997	4.89 ± 0.16 (20.46)	5.39 ± 0.18 (21.35)	4.29	0.041*
LSD4	1997	5.53 ± 0.13 (15.29)	6.19 ± 0.15 (15.20)	11.18	<0.01*
LSD5	1997	4.14 ± 0.12 (18.81)	4.34 ± 0.10 (15.08)	1.55	>0.05
VSD1	1997	4.54 ± 0.14 (19.89)	4.94 ± 0.15 (18.66)	3.84	0.053
VSD2	1996	4.32 ± 0.14 (17.60)	4.45 ± 0.17 (21.20)	0.36	>0.05
	1997	4.29 ± 0.15 (22.02)	4.46 ± 0.15 (20.83)	0.60	>0.05
VSD3	1996	5.71 ± 0.25 (24.35)	5.71 ± 0.26 (25.25)	<0.01	>0.05
	1997	6.10 ± 0.23 (23.53)	6.32 ± 0.24 (23.55)	0.45	>0.05
	1998	5.38 ± 0.17 (20.10)	5.58 ± 0.20 (22.77)	0.55	>0.05
VSD4	1996	5.66 ± 0.18 (17.69)	5.63 ± 0.20 (19.67)	0.01	>0.05
	1997	4.69 ± 0.10 (13.38)	4.88 ± 0.11 (13.72)	1.78	>0.05
VSD5	1997	3.27 ± 0.08 (15.53)	3.29 ± 0.07 (13.41)	0.06	>0.05

† The numbers next to each variable correspond to those in figure 2. * Significant difference ($P<0.05$). Sample sizes are the same as those shown in Table 3.

Differences between rookeries

1996. The discriminant function analysis significantly separated the rookeries, based on pup body morphometry, using two functions[3]. The rookeries' mean scores on each of these functions are shown in Figure 7a. The probability that each pair of rookeries is homogenous (Table 5) showed that San Esteban and Rasito were significantly different from other rookeries and among themselves, particularly in the first function. The other rookeries could not be clearly discerned and formed groups that intersected considerably. For example, Machos could be grouped with San Pedro Mártir, and Lobos, but Lobos, in turn, could be grouped with Cantiles, Granito, and San Jorge. The latter three rookeries formed a homogenous group relatively isolated from the rest, and Lobos was intermediate between these two groups. These observations pointed to the existence of two groups of rookeries and two single isolated rookeries: i) Machos and San Pedro Mártir, ii) Cantiles, Granito, and San Jorge, iii) Rasito, and iv) San Esteban. Groups (i) and (ii) had Lobos in common, although this rookery was more closely linked with group (ii), because the probability that Lobos and Machos (belonging to group (i)) were homogenous was closer to the significance level than were Lobos and any other rookery from group (ii).

The variable that most strongly contributed to the separation of rookeries in the first discriminant function was body mass[4]. There was not a single variable that had a major influence on the second function. Based on each variable's |std. coeff.|, pups from Machos and San Pedro Mártir were the heaviest and widest of all, those from San Esteban were the lightest, but relatively wide, and those from Rasito were light and had the smallest girths.

The cluster analysis gave similar results as the discriminant functions (Figure 7b). Both analyses were most consistent at a linkage distance of 2.0. At this distance, Cantiles, Granito, San Jorge, and Lobos formed one group, Machos and San Pedro Mártir formed

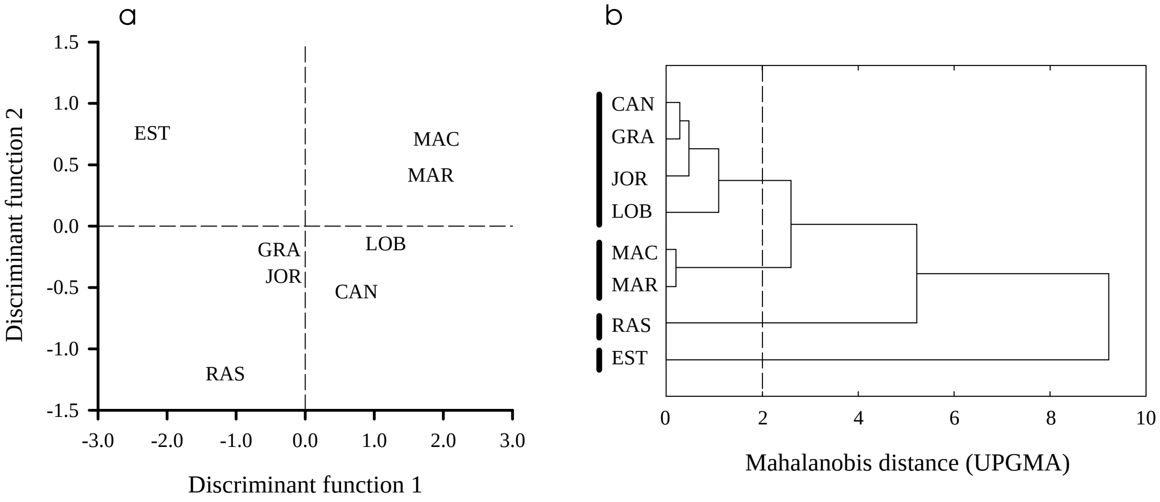


Figure 7. Mean scores of each rookery on two significant discriminant functions (a) and dendrogram (b), summarizing body size differences among sea lion pups from eight rookeries studied in 1996. The ovals in (a) group rookeries whose pups had similar body size (P<0.05), and the dotted line in (b) indicates the distance consistent with the results from disriminant function analysis. The abbreviations for each rookery correspond to those shown in table 1.

another, and Rasito and San Esteban remained isolated. Although a longer linkage distance, for example 4.0, would show the fact that Lobos was statistically similar to the rookeries in the first two groups, it would not be consistent the rookeries' mean scores (Figure 7a) and with the *P* values shown in Table 5.

There were significant differences between rookeries in the variables that most strongly separated them in the discriminant function analysis; pups from Machos and San Pedro Mártir were the largest overall, and those from Rasito were the smallest (Figure 8). However, the multiple comparisons showed more gradual differences between the other rookeries. Nevertheless, two relatively homogenous groups could be discerned; San Jorge, Cantiles, Granito, and Lobos which had pups intermediate in size between those from Machos and Rasito, and San Esteban, which had pups that were as light as those from Rasito, but had high girth 4 and sculp depth values. In fact, girth 4 values from San Esteban pups were comparable to those obtained in Machos and San Pedro Mártir, and is probably the reason for the separation of this rookery in the discriminant function analysis.

Table 5. Probability that pup body size was similar, based on the D^2 statistic, among eight rookeries studied in 1996 and 1997.

	GRA	LOB	MAC	RAS	EST	JOR	MAR
1996							
CAN	0.92	0.35	<0.01*	0.04*	<0.01*	0.81	<0.01*
GRA		0.34	<0.01*	0.03*	<0.01*	0.64	0.02*
LOB			0.05	<0.01*	<0.01*	0.67	0.18
MAC				<0.01*	<0.01*	<0.01*	0.96
RAS					<0.01*	<0.01*	<0.01*
EST						<0.01*	<0.01*
JOR							<0.01*
1997							
CAN	0.05	<0.01*	<0.01*	<0.01*	<0.01*	0.23	<0.01*
GRA		<0.01*	<0.01*	<0.01*	<0.01*	0.12	0.06
LOB			<0.01*	<0.01*	<0.01*	0.76	<0.01*
MAC				<0.01*	<0.01*	<0.01*	<0.01*
RAS					0.24	<0.01*	<0.01*
EST						<0.01*	<0.01*
JOR							<0.01*

Note: The centroids were calculated from the mean values of body mass, standard length, three girth measurements, and the sum of sculp depth measurements at six sites along the body of sea lion pups. * Significant differences ($P<0.05$).

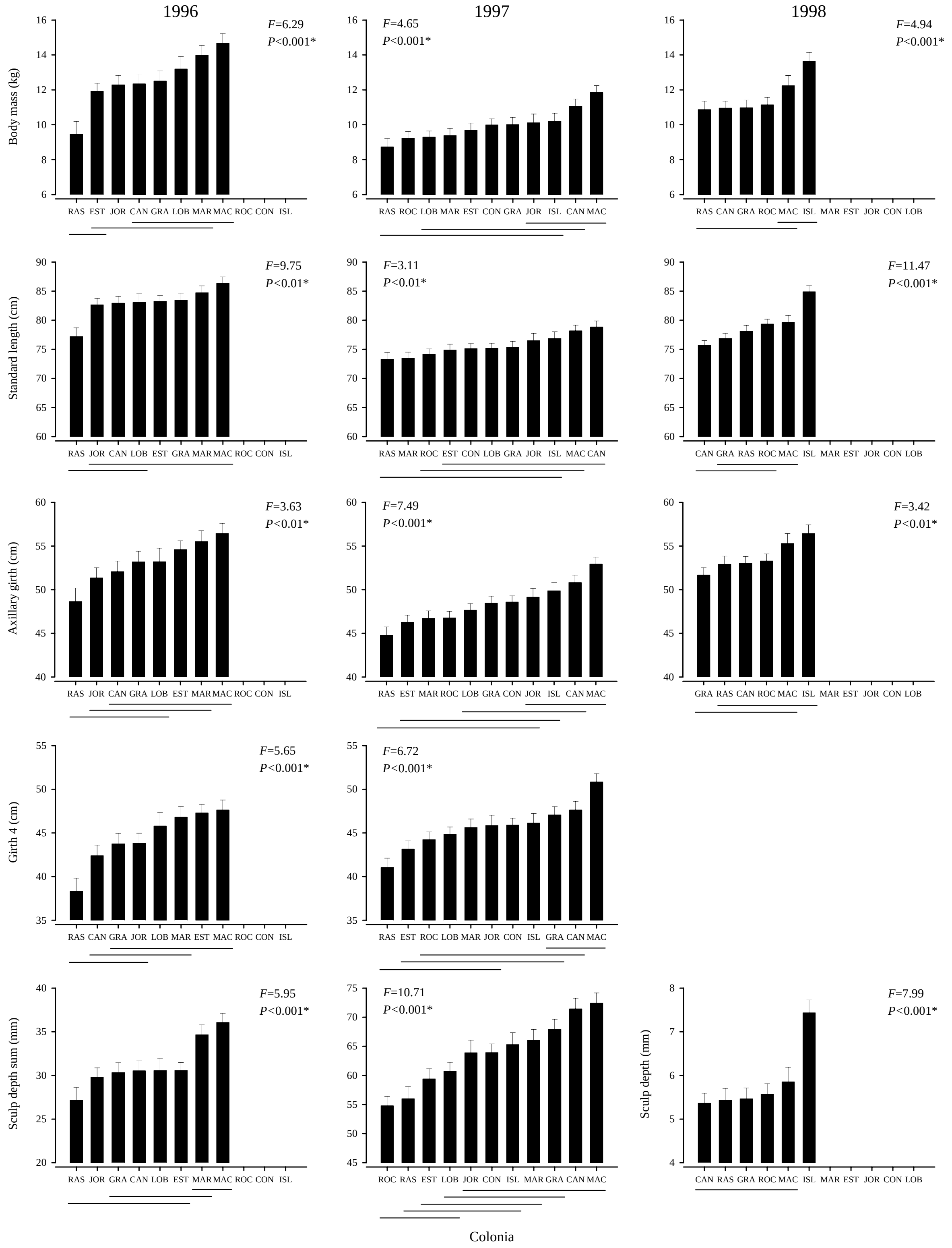


Figure 8. Comparison of morphometric variables that were most important for the determination of body size differences among pups from different rookeries during the 1996-97 reproductive seasons, and all morphometric variables measured in 1998. *F* and *P* values from analysis of variance are also shown, as well as the results from the corresponding Tukey's multiple comparisons tests. For each variable, the lines below each rookery on the abcissa group those that were not significantly different ($P>0.05$) among themselves with respect to that variable. The abbreviation for the rookeries correspond to those shown in Table 1.

1997. The same eight rookeries were significantly separated using three discriminant functions in 1997[5]. The rookeries' mean scores on each of the three functions are shown in Figure 9(a-c). From the probability values shown in Table 5, only Rasito and San Esteban formed a clearly defined group; pups from Machos were not similar to those of any other rookery. Cantiles, Granito, Lobos, San Pedro Mártir, and San Jorge also formed a homogenous group, but two of these rookeries (Lobos and San Pedro Mártir) were not directly linked. Three groups of rookeries could be identified (Figure 9a-c): i) Rasito and San Esteban, ii) Machos, and iii) Cantiles, Granito, Lobos, San Pedro Mártir, and San Jorge.

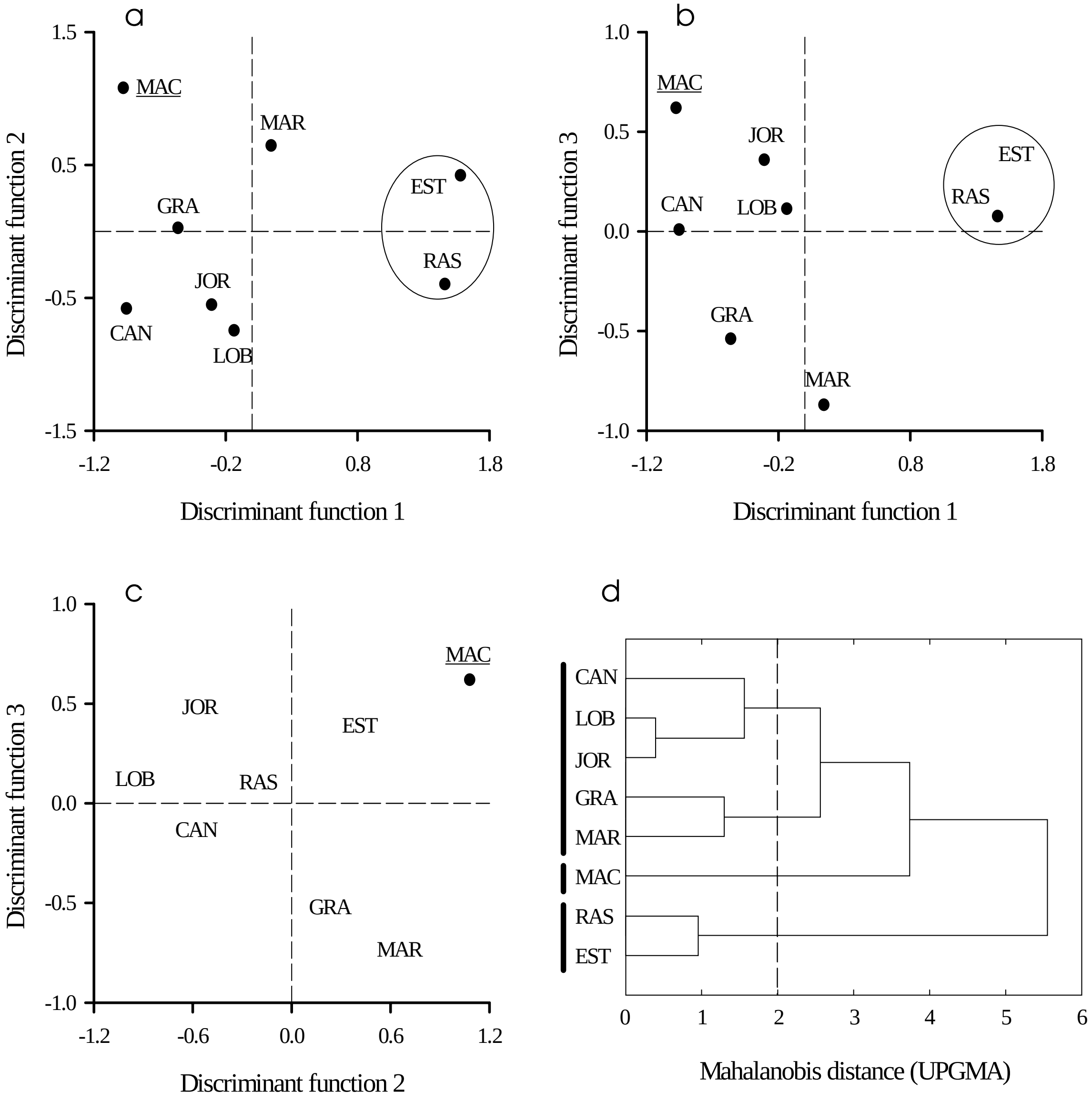


Figure 9. Mean scores of each rookery on two significant discriminant functions (a) and dendrogram (b), summarizing body size differences among sea lion pups from eight rookeries studied in 1997. The ovals in (a), (b), and (c) group rookeries whose pups had similar body size (*P*>0.05). Similarly, underlined rookeries had pups whose body size was significantly different from that of any other rookery. The dotted line in (d) indicates the distance consistent with the results from disriminant function analysis. The abbreviations for each rookery correspond to those shown in Table 1.

Body mass was the variable that most strongly influenced the mean scores of the rookeries on the first two discriminant functions, while the sum of sculp depth measurements did it on the third function[6]. The standard coefficients of the variables did not show a clear break in their values to be able to define the third function, so it was considered to be a combination of sculp depth, axillary girth, and body mass. Accordingly, Rasito and San Esteban had pups which were relatively light, and Machos had heavy pups with thick sculps. The dendrogram produced from the cluster analysis showed identical results at a linkage distance of 2.0 (Figure 9d).

When all the rookeries studied in 1997, and girth measurements 1 and 5 were included in the analysis, five significant discriminant functions were obtained, although only three were useful to adequately separate the rookeries[7]. The rookeries' mean scores on each of the three functions are shown in Figure 10(a-c). The probability that each pair of rookeries is homogenous (Table 6) indicated that Machos and Roca Blanca were not similar to any other rookery or among themselves. Rasito and San Esteban formed a distinct group, and Cantiles, Granito, Lobos, San Jorge, San Pedro Mártir, and Rocas Consagradas formed another. Four groups of rookeries emerged from this analysis (Figures 10a-c): i) Machos, ii) Roca Blanca, iii) Rasito and San Esteban, and iv) Cantiles, Granito, Lobos, San Jorge, San Pedro Mártir, and Rocas Consagradas.

The most important variables for distinguishing rookeries in the first function were body mass and the sum of sculp depth measurements; for the second function, these variables were body mass and axillary girth; and for the third function, these were body mass and standard length[8]. As in the previous years, the standard coefficients varied little among variables, particularly in the second and third functions. Therefore, the second function was considered to be a combination of body mass, axillary girth and girth 5; and the third function a combination of body mass, standard length and girth 2. Based on these observations, pups from Rasito and San Esteban were relatively light and had thin sculps, those from Machos were the largest overall, and those from Roca Blanca compartieron shared the same characteristics with those from Rasito and San Esteban, although they were shorter and their axillary girth measurements were smaller.

At a linkage distance of 4.0, the cluster analysis gave the same results as the discriminant function analysis (Figure 10d).

There were significant differences between rookeries in the variables that most strongly separated them in both discriminant function analyses performed with this year's data (Figure 8). The most remarkable of these differences were observed in body mass and the sum of sculp depth measurements, while pup standard length differences were the smallest. The multiple comparisons tests showed at least three groups of rookeries in any variables, indicating that differences among adjacent means were small. Pups from Machos and Cantiles were consistently found among those with the highest values in all these variables, in comparison with those from Rasito, which were among the smallest. One notable difference from the previous year was the relative size of pups from San Pedro Mártir. Together with

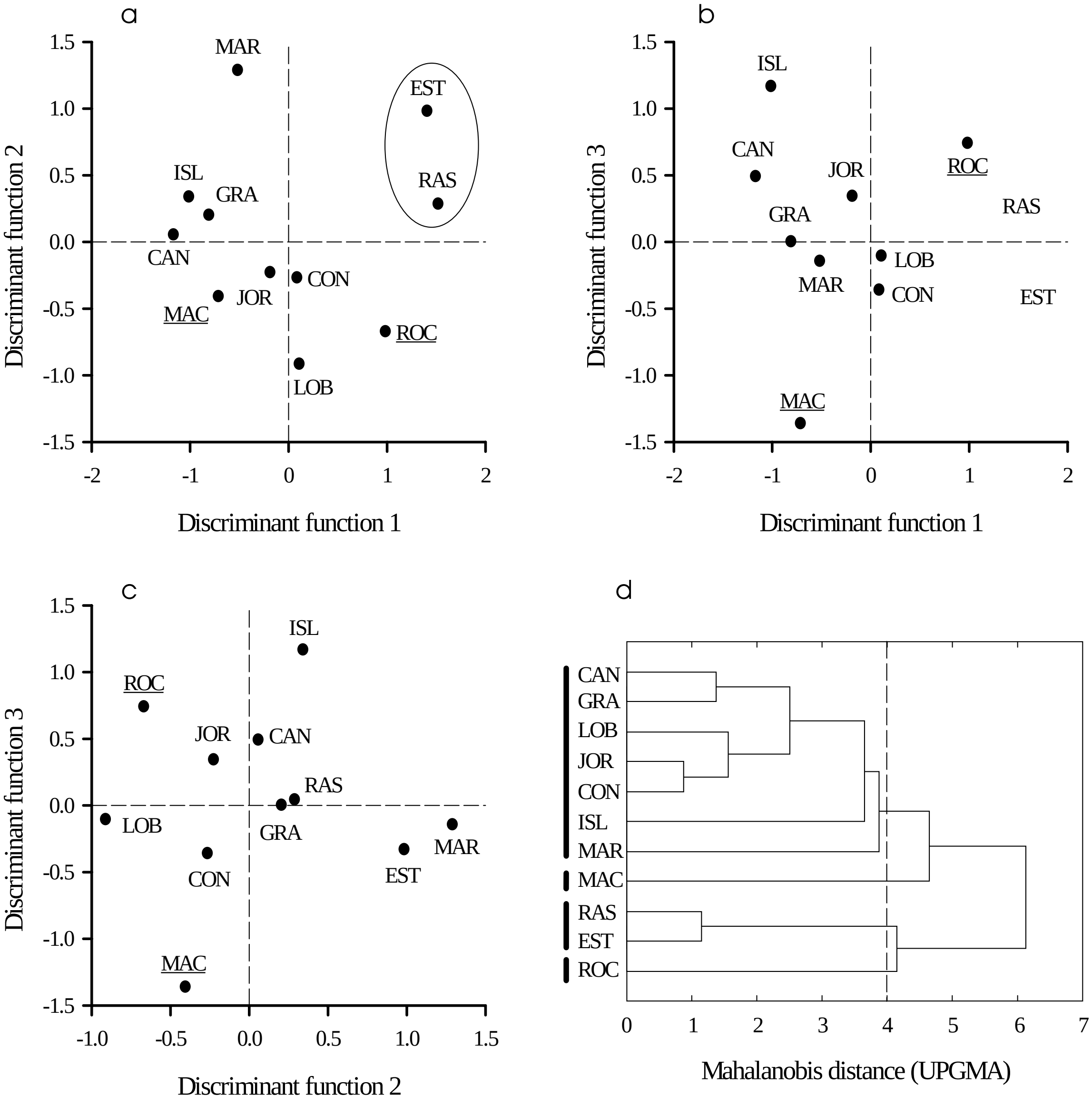


Figure 10. Mean scores of each rookery on two significant discriminant functions (a) and dendrogram (b), summarizing body size differences among sea lion pups from eleven rookeries studied in 1997. The ovals in (a), (b), and (c) group rookeries whose pups had similar body size ($P>0.05$). Similarly, underlined rookeries had pups whose body size was significantly different from that of any other rookery. The dotted line in (d) indicates the distance consistent with the results from disriminant function analysis. The abbreviations for each rookery correspond to those shown in Table 1.

Machos, this rookery had the largest pups in 1996, while in 1997 they were significantly smaller, by all size variables except the sum of sculp depth measurements, than pups from Machos. Another difference was the size of pups from Cantiles, which changed from intermediate to small in size the previous year, to being among the largest in 1997.

Pups from San Esteban were small and though slightly larger than those from Rasito, they were sufficiently similar in size to be linked together in the discriminant function analysis. The similarity between pups of both rookeries was most evident in girth and sum of sculp depth measurements. The relative size of pups from other rookeries depended on the variable in question, *i.e.* the shape of the pups appeared to vary among rookeries. For example, pups from Roca Blanca were as light, short, and wide as those from Rasito and San Esteban, but their sum of sculp depth measurements was the smallest of all, and it was the variable that distinguished these pups from the rest in the discriminant analysis.

Although pups from Cantiles showed more similarities with those from Machos in their body morphometrics, they were easily linked with pups from Granito in the dendrogram (Figure 10d). Machos, however, was isolated in the discriminant analysis because of the high values of girth 4 measurements of pups from this rookery (Figure 8). A similar apparent inconsistency was present in the dendrogram, where San Pedro Mártir pups were grouped with those from other rookeries whose pups were clearly larger. Pups from this rookery had relatively small values in all variables, except for girth 4 and the sum of sculp depth measurements. These two variables (girth 4 and the sum of sculp depth measurements) had obviously a strong influence in the discriminant analysis. In general, San Esteban, Roca Blanca, San Pedro Mártir, Lobos, and Rasito had relatively small pups; San Jorge and Rocas Consagradas had pups of intermediate size; and Machos, Cantiles, Granito, and Los Islotes had large pups.

Table 6. Probability that pup body size was similar, based on the D^2 statistic, among eleven rookeries studied in 1997.

	GRA	LOB	MAC	RAS	EST	JOR	MAR	ISL	ROC	CON
CAN	0.11	<0.01*	<0.01*	<0.01*	<0.01*	0.20	<0.01*	0.05	<0.01*	<0.01*
GRA		<0.01*	<0.01*	<0.01*	<0.01*	0.16	0.05	<0.01*	<0.01*	0.03*
LOB			<0.01*	<0.01*	<0.01*	0.07	<0.01*	<0.01*	<0.01*	0.02*
MAC				<0.01*	<0.01*	<0.01*	<0.01*	<0.01*	<0.01*	<0.01*
RAS					0.29	<0.01*	<0.01*	<0.01*	<0.01*	<0.01*
EST						<0.01*	<0.01*	<0.01*	<0.01*	<0.01*
JOR							<0.01*	0.05	<0.01*	0.48
MAR								<0.01*	<0.01*	<0.01*
ISL									<0.01*	<0.01*
ROC										<0.01*

Note: The centroids were calculated from the mean values of body mass, standard length, five girth measurements, and the sum of sculp depth measurements at 14 sites along the body of sea lion pups. * Significant differences ($P<0.05$).

1998. For this year's data, comparisons among rookeries were done for each variable independently, rather than on a multivariate basis, because only a few variables were measured (body mass, standard length, axillary girth, and sternal sculp depth). Nevertheless, there were significant differences in all these variables, showing that pups from Machos were again among the largest. However, the differences were small and gradual (Figure 8), with the exception of the sum of sculp depth measurements; all the rookeries, except Los Islotes, had pups with similar values in this variable.

Unlike the previous years, pups from Los Islotes were considerably larger than those from Machos. Particularly, they were significantly larger and had a thicker sculp. Similarly, pups from Roca Blanca, which were as small as those from Rasito the previous year, were even larger than those from Granito or Cantiles in 1998, and were almost as large as pups from Machos. In general, pups from Machos and Los Islotes were larger than those from other rookeries, whose pups were of similar size.

In summary, pup body size was largely determined by mean capture date, except in 1998, when pups were small in relation to their mean capture date. Male pups were 18% heavier and approximately 6% longer or wider than female pups. Sculp depth did not vary significantly among sexes. Pup body size varied among rookeries and was mainly due to body mass differences. The interannual variation in body size had a great influence on differences between rookeries, but even considering that, pups from Machos were among the largest and those from Rasito were among the smallest every year. Pups from San Esteban had relatively small pups every year. The other rookeries had pups whose size varied considerably from one year to the next.

3.4 Differences in body condition

Differences between sexes

The slope of the body mass-standard length relationship did not vary among sexes any year[9]. However, in 1996 and 1998, when pups were larger and probably older, male pups were 4% and 3% heavier than female pups of similar length, respectively. These differences were significant, but were too small to be obvious from visual inspection (Figure 11a, c). No such differences were found in 1997, when both the slope and the elevation of the regression line were similar for male and female pups (Figure 11b). The slope of this relationship did not vary among sexes or years, independently or in combination, but its elevation was affected by each of these factors separately[10] (Figure 11d). Keeping standard length constant, body mass increased from 1996 a 1998, showing that pups were, on average, 3% heavier in 1998 than in 1997, which in turn were 3% heavier than in 1996. All these differences were significant. Pooling the data from all years, males were significantly heavier than females of the same

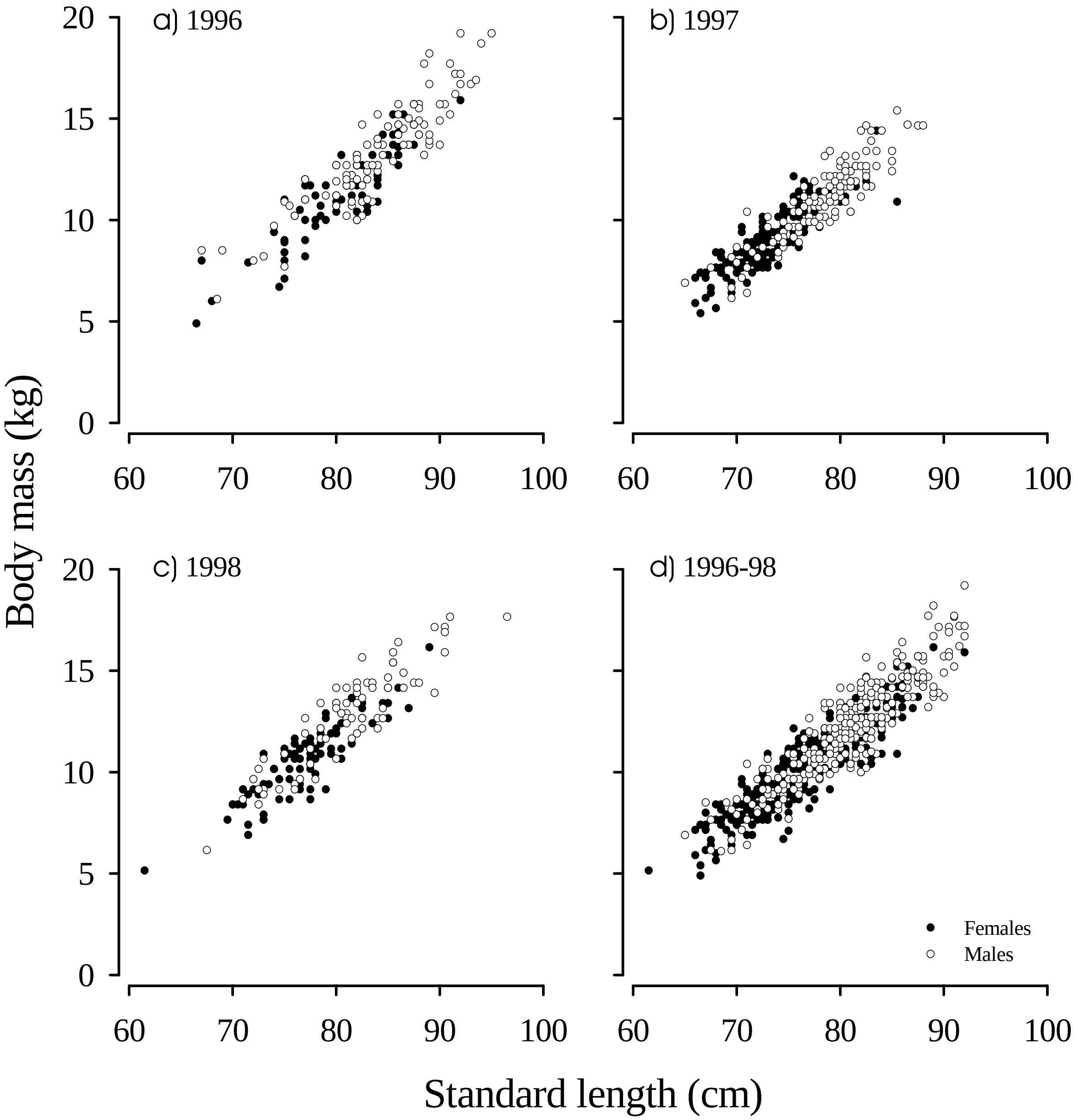


Figure 11. Relationship between sea lion pup body mass and standard length in each of the three years of study.

length. The results from each regression are shown in Table 7.

The slope of this relationship varied from 2.73 to 3.06 and was lower in 1996 and 1998. The value of the slope was significantly different from 3.00 only when the data from all years were pooled[11], and was mainly a result of the low values obtained in 1996 and 1998 for both sexes. Therefore, the scaling of body mass on standard length appeared to be isometric during the first days of life, and allometric after the second month of life. The residuals from this regression were closely related to the Fulton condition factor (*FCF=body mass/standard length*^{3}) for any year and/or sex (r^2 = 0.92-0.97, $P<0.01$). This observation supports the use of FCF as an appropriate index for comparing body mass of pups of different length during the first month of life in a given reproductive season. However, in large samples including animals more than two months of age, it is more appropriate to use the exponent of the relationship, empirically determined, instead of the exponent used in FCF. The value 2.84 ± 0.05, estimated from the pooled data from the three years (Table 7), could be used in such cases, if no additional data are available. For the intra-annual comparisons presented below, FCF was used as a body condition index.

Table 7. Results of the linear regression of body mass (kg) on standard length (cm) (full logarithmic transformation) for each sex and year of the study. Parameters shown are the intercept (*a*), slope (± SE) (*b*), coefficient of determination (r^2), sample size (*n*), and probability (*P*) that *a* or *b* are equal to zero.

Year	Sex	a ($\times 10^{-5}$)	b	r^2	n	P
1996	Males	6.82 ± 3.02	2.75 ± 0.13	0.81	102	<0.01*ab**
	Females	1.67 ± 0.97	3.06 ± 0.20	0.76	75	<0.01*ab**
	Both	2.72 ± 1.04	2.95 ± 0.11	0.81	177	<0.01*ab**
1997	Males	2.61 ± 1.10	2.97 ± 0.13	0.81	131	<0.01*ab**
	Females	3.44 ± 1.59	2.90 ± 0.14	0.74	141	<0.01*ab**
	Both	2.77 ± 0.81	2.96 ± 0.08	0.83	272	<0.01*ab**
1998	Males	7.87 ± 3.88	2.73 ± 0.15	0.81	72	<0.01*ab**
	Females	6.67 ± 3.39	2.76 ± 0.16	0.77	88	<0.01*ab**
	Both	4.83 ± 1.76	2.83 ± 0.10	0.82	160	<0.01*ab**
1996-98	Males	5.68 ± 1.53	2.79 ± 0.07	0.83	305	<0.01*ab**
	Females	6.15 ± 1.79	2.77 ± 0.08	0.80	304	<0.01*ab**
	Both	4.53 ± 0.86	2.84 ± 0.05	0.85	609	<0.01*ab**

* Indicates that the corresponding parameter (*a* or *b*) is significantly different from zero. The model described is $body\ mass = a \times standard\ length^b$.

The slope or the elevation of the axillary girth-standard length relationship did not vary among sexes any year[12]. The results of the regression for each year, with the pooled data from both sexes, are shown in Table 8. The slope of this relationship did not vary among years[13], but was consistently lower than one every year[11]. For any given length, the girth of pups captured in 1998 was approximately 5% and 6% greater than in 1997 and 1996, respectively (Figure 12 and Table 8), suggesting they were in better condition.

The residuals of this regression were closely related to the girth to length ratio (PAL) (r^2 = 0.98-0.99, P<0.01), which indicates that this index may be used for comparing girth among pups of different length. Therefore, PAL was used for the comparisons described below, instead of the residuals.

The amount of variability in sculp depth that is attributable to standard length is small, as shown by the low r^2 values (r^2=0.08-0.46, Table 9). The relationship between these variables was closer in 1997 and 1998, when a more precise instrument to measure sculp depth was used (Figure 13a, c). The slope and elevation of the regression line did not vary among sexes[14] in 1996 and 1998, so data for each of these years were pooled to estimate the parameters of the regression. However, female pups had thicker sculps than males (~11%) of the same length in 1997 (P<0.01) (Figure 13b). This observation was taken cautiously, because the probability that the slope of the relationship was the same for both sexes, was close to the significance level[14], making it difficult to compare the elevation of each regression line. The intercept of the regression line differed from zero in 1997 and 1998, but not in 1996 (Table 9), when the relationship these variables was weakest.

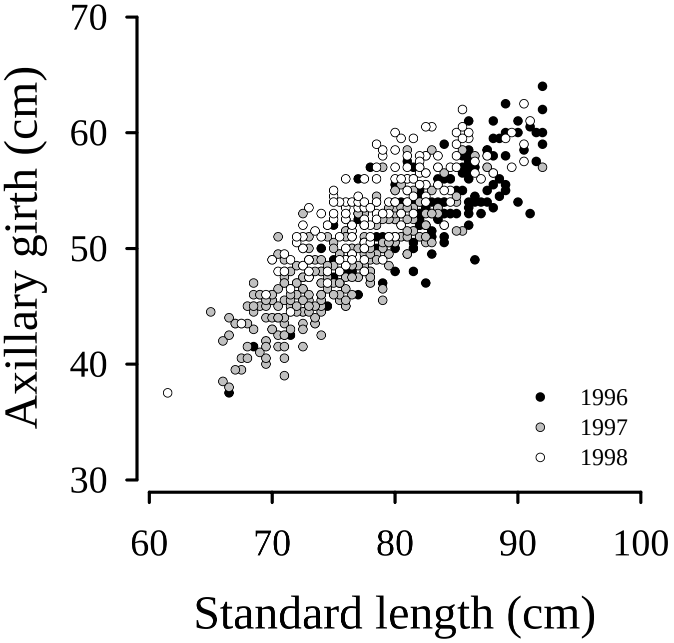


Figure 12. Relationship between sea lion pup axillary girth and standard length in 1996-98.

Table 8. Results of the linear regression of axillary girth (cm) on standard length (cm) for each year of the study. Parameters shown are the intercept (*a*), slope (± SE) (*b*), coefficient of determination (r^2), sample size (*n*), and probability (*P*) that *a* or *b* are equal to zero.

Year	*a*	*b*	r^2	*n*	*P*
1996	-5.83 ± 3.51	0.72 ± 0.04	0.66	150	<0.01*b**
1997	-5.89 ± 2.12	0.72 ± 0.03	0.71	271	<0.01*ab**
1998	2.73 ± 2.77	0.64 ± 0.04	0.68	160	<0.01*b**

* Indicates that the corresponding parameter (*a* or *b*) is significantly different from zero.

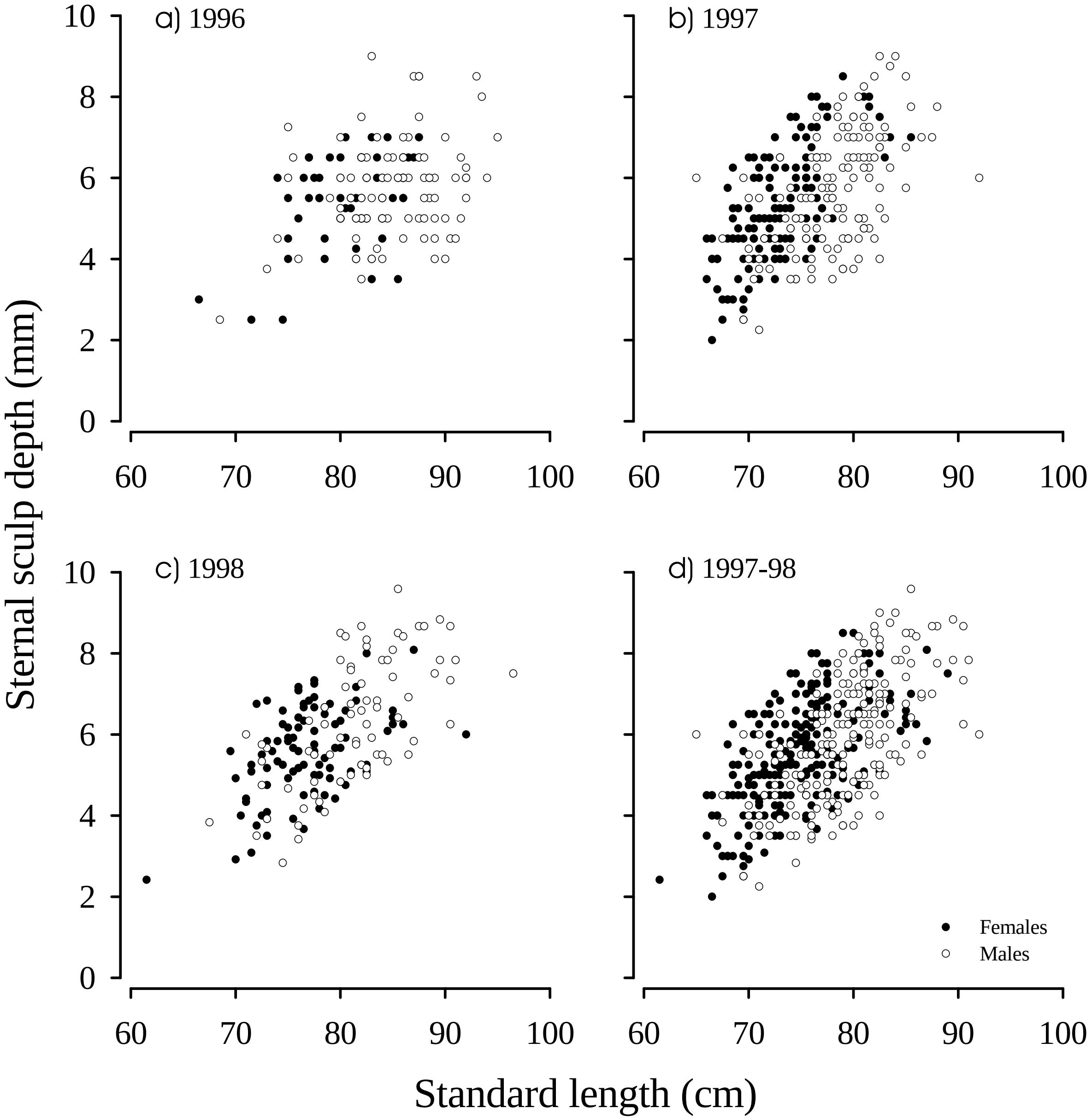


Figure 13. Relationship between sea lion pup sculp depth and standard length in 1996-98.

A study of the simultaneous effects of year (1997 and 1998) and sex on this relationship, revealed that only the sex of the pups had a significant influence[15] (Figure 13d). However, there was interaction between both factors, which was likely to be a result of the sex differences in the slope found in 1997. Therefore, the regression equation with data from both sexes combined for each year was utilized to calculate the residuals that were later compared among sexes and rookeries.

Table 9. Results of the linear regression of sternal sculp depth (mm) on standard length (cm) for each sex and year of the study. Parameters shown are the intercept (*a*), slope (± SE) (*b*), coefficient of determination (r^2), sample size (*n*), and probability (*P*) that *a* or *b* are equal to zero.

Year	Sex	*a*	*b*	r^2	*n*	*P*
1996	Males	-0.37 ± 2.12	0.07 ± 0.03	0.80	90	< 0.01*b**
	Females	-3.01 ± 2.24	0.10 ± 0.03	0.17	64	< 0.01*b**
	Both	-1.23 ± 1.45	0.08 ± 0.02	0.12	154	< 0.01*b**
1997	Males	-8.15 ± 1.88	0.18 ± 0.02	0.28	134	< 0.01*ab**
	Females	-12.49 ± 1.62	0.24 ± 0.02	0.46	142	< 0.01*ab**
	Both	-7.11 ± 1.09	0.17 ± 0.01	0.33	276	< 0.01*ab**
1998	Males	-9.61 ± 2.10	0.20 ± 0.03	0.44	72	< 0.01*ab**
	Females	-5.02 ± 1.80	0.14 ± 0.02	0.28	89	< 0.01*ab**
	Both	-7.02 ± 1.27	0.16 ± 0.02	0.39	161	< 0.01*ab**

* Indicates that the corresponding parameter (*a* or *b*) is significantly different from zero.

Body volume estimates from both geometric models were significantly correlated with body volume estimates from the water displacement method in 1997 (r=0.95, P<0.01), but they underestimated the values obtained by the latter method. As expected, the four component model underestimated water displacement values more than the six component model; 27%, and 16%, respectively. Despite the relative inaccuracy of both methods, they proved to be adequate to study relationships between this and other variables, such as body mass, and standard length, because the correlation between estimates derived from the models and from the water displacement method was strong enough.

The relationship between body volume, derived from the four component model, and standard length did not vary among sexes[16] in 1996 or 1997. Neither sex nor year had a significant effect on the relationship, whether separately or in combination[17] (Figure 14a). The results of the common regression are shown in Table 10. Similar results were found using the six component model in 1997[19], and the pooled regression results are shown in Table 10. In both cases, the slope of the relationship was higher than 3.00, indicating that as pups grew longer, their volume increased disproportionately[11]. The residuals from these regressions were later used as body condition indices. The results obtained using the water displacement method were consistent with those from the geometric models[18], except that the slope of this relationship (2.95 ± 0.10) was not different from 3.00 (P>0.05).

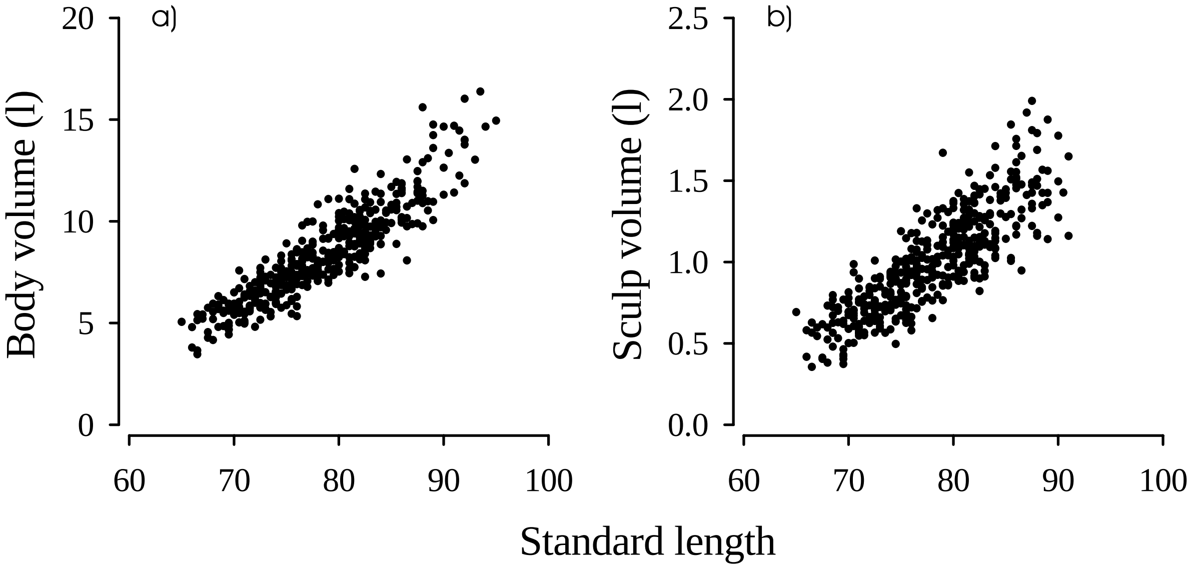


Figure 14. Relationship between sea lion pup body volume (a), sculp volume (b), and standard length in 1996 and 1997. All the volumes were estimated using the four component geometric model (see Figure 2).

Table 10. Results of the linear regression of body volume (l) and sculp volume (l) on standard length (cm) (full logarithmic transformations) in 1996 and 1997. Parameters shown are the intercept (*a*), slope (± SE) (*b*), coefficient of determination (r^2), sample size (*n*), and probability (*P*) that *a* or *b* are equal to zero.

Regression	Geometric model†	*a*	*b*	r^2	*n*	*P*
Body volume on standard length ($BV=a\times SL^b$)	4 comp. 6 comp.	$6.52 \times 10^{-6} \pm 1.66 \times 10^{-6}$ $8.11 \times 10^{-6} \pm 2.64 \times 10^{-6}$	3.22 ± 0.07 3.20 ± 0.09	0.84 0.82	429 276	<0.01*ab** <0.01*ab**
Sculp volume on standard length ($SV=a\times SL^b$)	4 comp. 6 comp.	$1.02 \times 10^{-7} \pm 3.75 \times 10^{-8}$ $9.86 \times 10^{-8} \pm 9.86 \times 10^{-8}$	3.69 ± 0.11 3.74 ± 0.15	0.74 0.68	429 275	<0.01*ab** <0.01*ab**

† Geomtric models correspond to those shown in figure 2. Data from 1996 and 1997 were combined for the four part model, but only data from 1997 was included for the six component model. * Indicates that the corresponding parameter (*a* or *b*) is significantly different from zero.

The relationship between sculp volume, derived from either the four or the six component model, and standard length did not vary among sexes[20, 22] in 1996 or 1997. Additionally, the relationship did not vary among years, independently of the sex of the pups[21] (Figure 14b). The results of the regression with data from both sexes combined for each model are shown in Table 10; the residuals from these regressions were later used as body condition indices. The slope of the relationship showed stronger positive allometry than that found in the scaling of body volume on standard length[11], which suggested that pups accumulated disproportionately larger amounts of blubber than would be expected from their growth in volume.

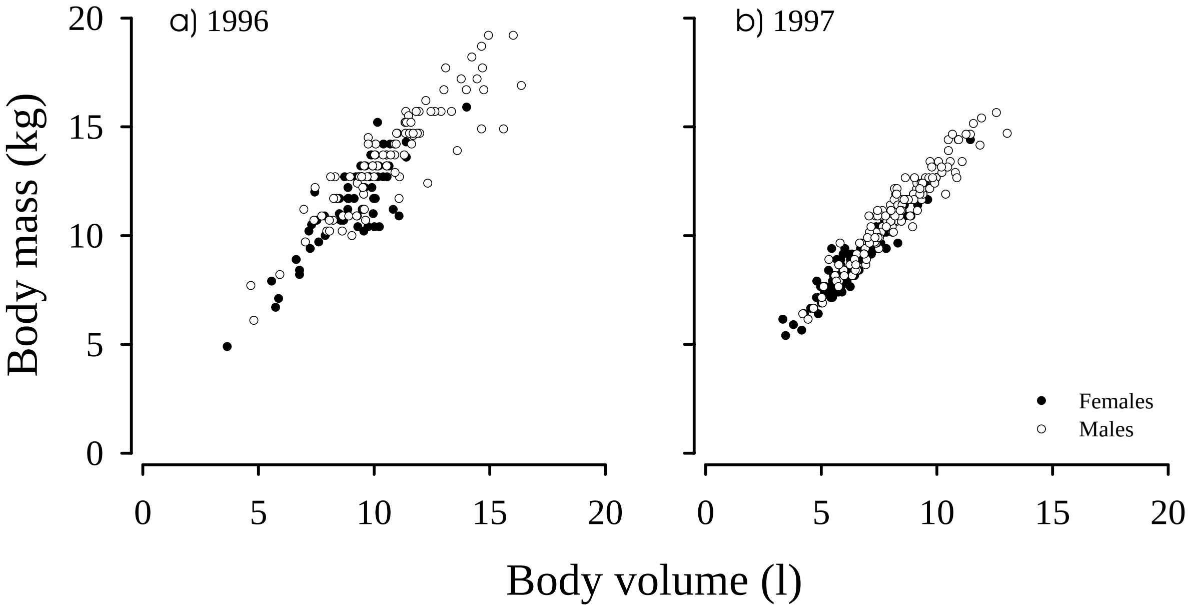


Figure 15. Relationship between sea lion pup body mass and body volume in a) 1996 and b) 1997.

The slope of the relationship between body mass and body volume, derived from either geometric model, did not vary among males and females[23, 24] in 1996 or 1997. In both years, males, however, were ~4% heavier than females of the same volume. The results of the regression for each sex and year are shown in Table 11. These variables were the most strongly related, as demonstrated by the high r^2 values, particularly in 1997 (Table 11). An analysis of interannual variations in this relationship, using the four component body volume model, indicated that the slope was higher in 1997 than in 1996[25]. However, this result may have been affected by the higher variability around the regression line found in 1996 in relation to 1997, as shown by the higher r^2 values for that year (Table 11).

The slope of the relationship, using the four component model, showed a positive allometry in the scaling of body mass on body volume[11] in 1997. No evidence of allometry was found in 1996 or using body volume estimates from the six component geometric model in 1997. Figure 15(a, b) shows the relationship between these variables (four component model of body volume) for each sex and year of study.

The analysis of the relationship between body mass and body volume, calculated by the water displacement method, lead to the same conclusion; only the elevation of the regression line differed among sexes[26] in 1997. In this case, males were ~2% heavier than females of the same volume. Contrary to the results obtained using the geometric models, this relationship showed negative allometry[11], suggesting that as pups grew more voluminous, their body mass did not increase proportionately (slope=0.931 ± 0.013).

Table 11. Results of the linear regression of body mass (kg) on body volume (l) for each sex and year of study. Parameters shown are the intercept (*a*), slope (± SE) (*b*), coefficient of determination (r^2), sample size (*n*), and probability (*P*) that *a* or *b* are equal to zero.

Year	Sex	Geometric model†	*a*	*b*	r^2	*n*	$P^‡$
1996	Males	4 comp.	3.48 ± 0.53	0.95 ± 0.05	0.81	90	< 0.01ab*
	Females	4 comp.	1.90 ± 0.76	1.06 ± 0.08	0.72	65	< 0.01ab*
	Both	4 comp.	2.61 ± 0.41	1.01 ± 0.04	0.80	155	< 0.01ab*
1997	Males	4 comp.	2.04 ± 0.24	1.09 ± 0.03	0.92	232	< 0.01ab*
		6 comp.	1.50 ± 0.25	1.01 ± 0.03	0.92	232	< 0.01ab*
	Females	4 comp.	1.78 ± 0.19	1.09 ± 0.03	0.91	265	< 0.01ab*
		6 comp.	1.42 ± 0.17	1.00 ± 0.02	0.93	265	< 0.01ab*
	Both	4 comp.	1.65 ± 0.14	1.12 ± 0.02	0.94	274	< 0.01ab*
		6 comp.	1.22 ± 0.13	1.03 ± 0.02	0.94	274	< 0.01ab*

† Geomtric models correspond to those shown in figure 2. * Indicates that the corresponding parameter (*a* or *b*) is significantly different from zero.

Table 12. Regression equations and corresponding statistics for the linear relationship between sculp volume adjusted for standard length on other body condition indices. Parameters shown are the intercept (*a*), slope (± SE) (*b*), coefficient of determination (r^2), sample size (*n*), probability (*P*) that *a* or *b* are equal to zero and the standard error of the estimation (*SEE*).

Regression equation	Year	Geometric model†	r^2	*n*	*P*	*SEE*
SVR = 0.52(*FCF*) - 1.15	1996-97	4 comp.	0.38	432	<0.01*	0.14
SVR = 0.66(*FCF*) - 1.50	1997	6 comp.	0.55	276	<0.01*	0.12
SVR = 0.026(*GL*) - 1.66	1996-97	4 comp.	0.34	430	<0.01*	0.14
SVR = 0.031(*GL*) - 1.97	1997	6 comp.	0.42	276	<0.01*	0.13
SVR = 0.13(*SDR*) - 0.009	1996	4 comp.	0.54	155	<0.01*	0.14
SVR = 0.10(*SDR*) + 0.040	1997	4 comp.	0.61	276	<0.01*	0.09
SVR = 0.12(*SDR*) + 0.060	1997	6 comp.	0.64	274	<0.01*	0.10
SVR = 0.015 - 0.022(*BMR*)	1996-97	4 comp.	0.009	432	<0.05*	0.17
SVR = 0.022 - 0.020(*BMR*)	1997	6 comp.	<0.001	275	>0.05	0.17
SVR = 0.13(*BVR*) + 0.018	1996-97	4 comp.	0.49	432	<0.01*	0.12
SVR = 0.17(*BVR*) + 0.020	1997	6 comp.	0.64	277	<0.01*	0.11

† Indicates what geometric model was used for the estimation of the corresponding volume (see figure 2). * Indicates that the regression coefficient was significantly different from zero ($P<0.05$). SVR = residual from the regression of sculp volume (l) on standard length (cm), FCF = Fulton condition factor (body mass (kg)*10^5 / standard length^3, GL = (axillary girth (cm)*100 / standard length, and SDR, BMR, and BVR are the residuals from the regression of sternal sculp depth (mm) on standard length, body mass on body volume (l), and body volume on standard length, respectively.

To analyze the relationship between several indices of body condition (FCF, GL, SDR, BMR, and BVR) and an index of the relative sculp volume (SVR), data from both sexes were pooled. All the indices were significantly related to SVR (Table 12), with the exception of BMR (residuals from the body mass on body volume regression) using the six component geometric model of body volume. In fact, regardless of which geometric model of body volume was used, BMR was the index most weakly related to SVR. The percent of the variability in SVR attributable to these indices was, in general, quite low (0.009-0.64%), although it was somewhat higher when the six component model of sculp volume was used. The indices that were best related to SVR were SDR (residual from the sternal sculp depth on standard length regression) and BVR (residual from the body volume on standard length regression).

In each of the three years of study, there were no significant differences among sexes in most body condition indeces (Table 13). Differences in FCF reached the significance level in 1996. Both in 1996 and 1998, males had slightly higher values in this index than females; consistent with the sexual differences found in the body mass-length relationship. No sexual differences were found in GL, SVR, or BVR. The sexual difference in body condition indices were found in BMR in 1996 and 1997, and SDR in 1997. Males had higher values in BMR than females in 1996 and 1997, while the opposite was true for the SDR index in 1997. These observations were consistent with the results from covariance analyses; males were heavier than females of the same length in 1996 and 1998, when the pups were older than than those captured in 1997. Additionally, males were denser than females in 1996 and 1997, regardless of age.

Four pups that had died from natural causes in Los Islotes, and measured soon after death had FCF values of 1.33, 1.60, 1.73, and 2.33, respectively. All of these pups, except the last one, were found to have little blubber (sternal sculp depth: 2.67-4.75 mm) in relation to other pups, so they probably died of starvation.

Table 13. Differences in body condition indices (mean ± SE) between male and female sea lion pups during the three years of the study.

Body condition index[†]		Females (1996 *n*=65; 1997 *n*=143; 1998 *n*=89)	Males (1996 *n*=90; 1997 *n*=134; 1998 *n*=72)	ANOVA *F* Sex effect	*P*[‡]
1996					
FCF		2.17 ± 0.03	2.22 ± 0.02	3.96	0.05
GL		63.81 ± 0.52	64.41 ± 0.43	0.80	0.37
SDR		0.25 ± 0.13	0.17 ± 0.12	0.20	0.67
SVR (4 comp.)		-0.02 ± 0.02	-0.01 ± 0.02	0.08	0.78
BMR (4 comp.)		-0.25 ± 0.14	0.17 ± 0.12	5.40	0.02*
BVR (4 comp.)		-0.16 ± 0.12	-0.008 ± 0.13	0.65	0.42
1997					
FCF		2.28 ± 0.02	2.28 ± 0.02	0.02	0.89
GL		63.57 ± 0.33	64.21 ± 0.28	2.20	0.14
SDR		-0.05 ± 0.09	-0.55 ± 0.11	13.35	<0.001*
SVR	(4 comp.)	0.02 ± 0.01	0.007 ± 0.02	0.26	0.61
	(6 comp.)	0.03 ± 0.01	0.01 ± 0.02	0.92	0.34
BMR	(4 comp.)	-0.07 ± 0.05	0.13 ± 0.05	8.31	<0.01*
	(6 comp.)	-0.03 ± 0.04	0.12 ± 0.05	4.59	0.03*
BVR	(4 comp.)	-0.02 ± 0.06	0.02 ± 0.08	0.15	0.70
	(6 comp.)	-0.006 ± 0.06	0.02 ± 0.08	0.06	0.81
1998					
FCF		2.31 ± 0.02	2.36 ± 0.02	2.30	0.13
GL		67.77 ± 0.34	67.97 ± 0.36	0.16	0.69
SDR		0.38 ± 0.10	0.27 ± 0.14	0.41	0.52

[†] FCF = Fulton condition factor (body mass (kg)*10^5 / standard length^3, GL = (axillary girth (cm)*100 / standard length, and SDR, SVR, BMR, and BVR are the residuals from the regression of sternal sculp depth (mm) on standard length, sculp volume (l) on standard length, body mass on body volume (l), and body volume on standard length, respectively. The geometric model to estimate the corresponding volume is shown in parenthesis (see figure 2).

* Significant difference ($P<0.05$).

Differences between rookeries

Because there were no sexual differences among sexes in FCF or SVR (from the four component geometric model of sculp volume in 1996 and 1997), data from both sexes were combined to compare body condition among rookeries. To facilitate comparisons among years, the SDR index was also used, but due to the sexual differences found in this index in 1997, the number of pups of each sex was randomly adjusted within each rookery, to minimize the effect of this factor.

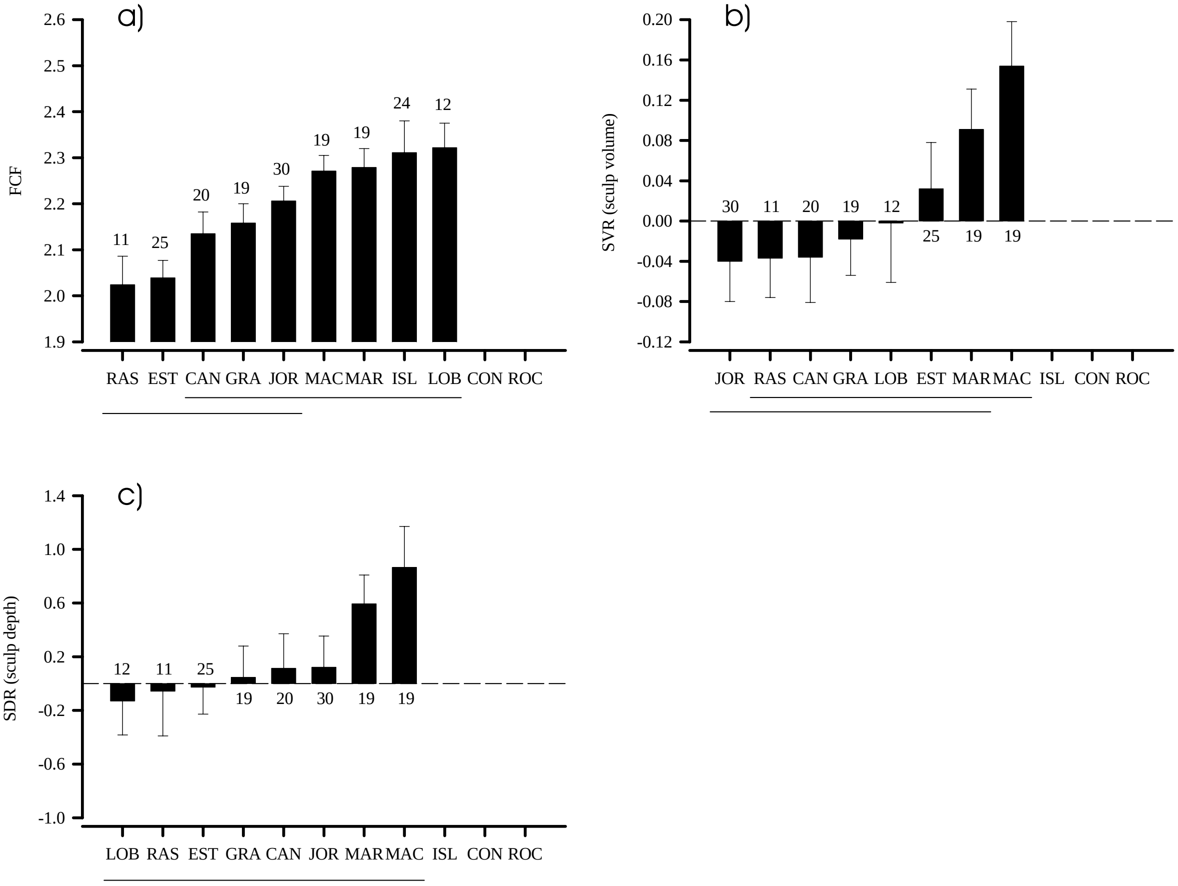


Figure 16. Fulton condition factor (FCF) (a), sculp volume index (SVR, b), and sculp depth index (SDR, c) of sea lion pups from eight rookeries of the Gulf of California in 1996. SVR and SDR were calculated as the residual from the regression of sculp volume (four component model) on standard length, and of sternal sculp depth on standard length, respectively. The lines below the abcissa join those rookeries whose means were not significantly different among themselves, as shown by Tukey's multiple comparisons tests. The values shown are the mean ± SE. The dotted lines indicate where zero is on the abcissa; the numbers above or below the abcissa are the sample sizes. The abbreviations for the rookeries correspond to those in Table 1.

1996. There were significant differences in FCF and an index of blubber content, SVR, among rookeries[27]. No such differences were found in another index of blubber content, SDR. The multiple comparisons tests reavealed two homogenous groups of rookeries with different FCF values for their pups (Figure 16a). These groups overlapped considerably, which indicated that the differences among rookeries were not large, but small and gradual. At the extremes of the FCF distribution were pups from Lobos and Los Islotes with the highest values, and those from Rasito and San Esteban with the lowest. Pups from Machos and San Pedro Mártir had FCF values almost as high as those from Lobos and Los Islotes, but they were not significantly higher than those of pups from other rookeries. A similar observation was made at the lower extreme of the distribution for pups from Cantiles and Granito with respect to those from Rasito and San Esteban (Figure 16a).

The comparisons of SVR revealed two groups of rookeries. Pups from Machos had the highest values in this index, and San Jorge the lowest (Figure 16b). The SVR of pups from

San Esteban and San Pedro Mártir approached that of those from Machos, but again, it could not be distinguished from those of other rookeries. Pups from Rasito, Cantiles, Granito and Lobos had low SVR values that were close to those obtained from San Jorge, though not significantly lower than those obtained from other rookeries. Los Islotes was not included in this analysis data were not available to calculate this index. Although no significant differences in the SDR index were found among rookeries, the values showed the same pattern described above (Figure 16c).

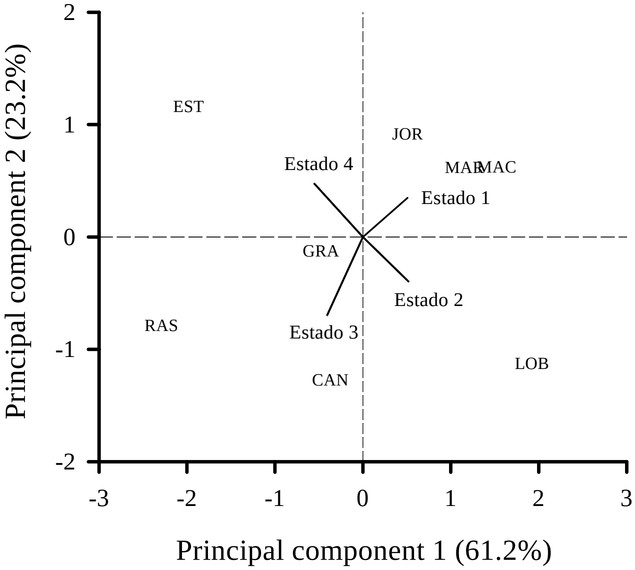


Figure 17. Centroids of eight rookeries on two principal components extracted in 1996. The percent of variance extracted by each component is shown in parenthesis. Before performing the analysis, the pups were classified into four mutually exclusive body condition states: a pup was considered to belong to state 1 if both the Fulton condition factor (FCF) and blubber content index (IBC, based on sternal sculp depth) were higher than or equal to the yearly average; to state 2 if FCF ≥ and IBC < the yearly average; to state 3 if FCF < and IBC ≥ the yearly average; and to state 4 if both FCF and IBC were lower than the yearly average. These body condition states were later entered as variables into the principal components analysis. The correlation of each state with the components are shown by the lines that intersect at 0,0. The abbreviations for the rookeries correspond to those shown in Table 1.

The yearly FCF and SDR average values were 2.195 and 0.204, respectively, and these were used as a references to assign in each pup to one of four possible body condition states, in order to combine both indices. Two principal components were obtained from principal components analysis, which accounted for 84.4% of all the variance. The first component was useful in separating Rasito and San Esteban from the rest of the rookeries. Pups from these rookeries fell in the State 4 category (FCF and SDR < yearly average) (Figure 17). To a lesser extent, this component was also useful in separating Lobos, on the one hand, and Machos and San Pedro Mártir on the other. Pups from Lobos were mainly in the State 2 category (FCF ≥ and SDR < yearly average), while those from Machos and San Pedro Mártir were mainly in the State 1 category (FCF and SDR ≥ yearly average). The second principal component was useful in separating Cantiles from other rookeries, and pups from this rookery were predominantly in the State 3 category. San Jorge and Granito could not be adequately separated because pups from these rookeries belonged to each of the four States to a similar extent.

1997. The FCF index was significantly different among the rookeries this year of study[27]. However, the multiple comparisons tests suggested that the differences between pairs of rookeries with adjacent values were small and not significant. Nevertheless, there were three homogenous groups of rookeries with different FCF values. Pups from Machos had the highest mean FCF values, and were significantly different from those of pups from Lobos, which had the lowest mean values (Figure 18a). San Pedro Mártir and Rocas Consag had FCF values similar to those of Machos, but were not significantly different from those of other rookeries with lower mean values. At the lower extreme of the distribution, Rasito, Los Islotes, Roca Blanca, San Jorge, and Cantiles had FCF values similar to Lobos, but not significantly different from rookeries with higher mean values.

The SVR index (four component model) was also significantly different among these rookeries[27]. Tukey's multiple comparisons tests showed that there were three groups of rookeries with different mean SVR values. Again, these groups overlapped partially and the

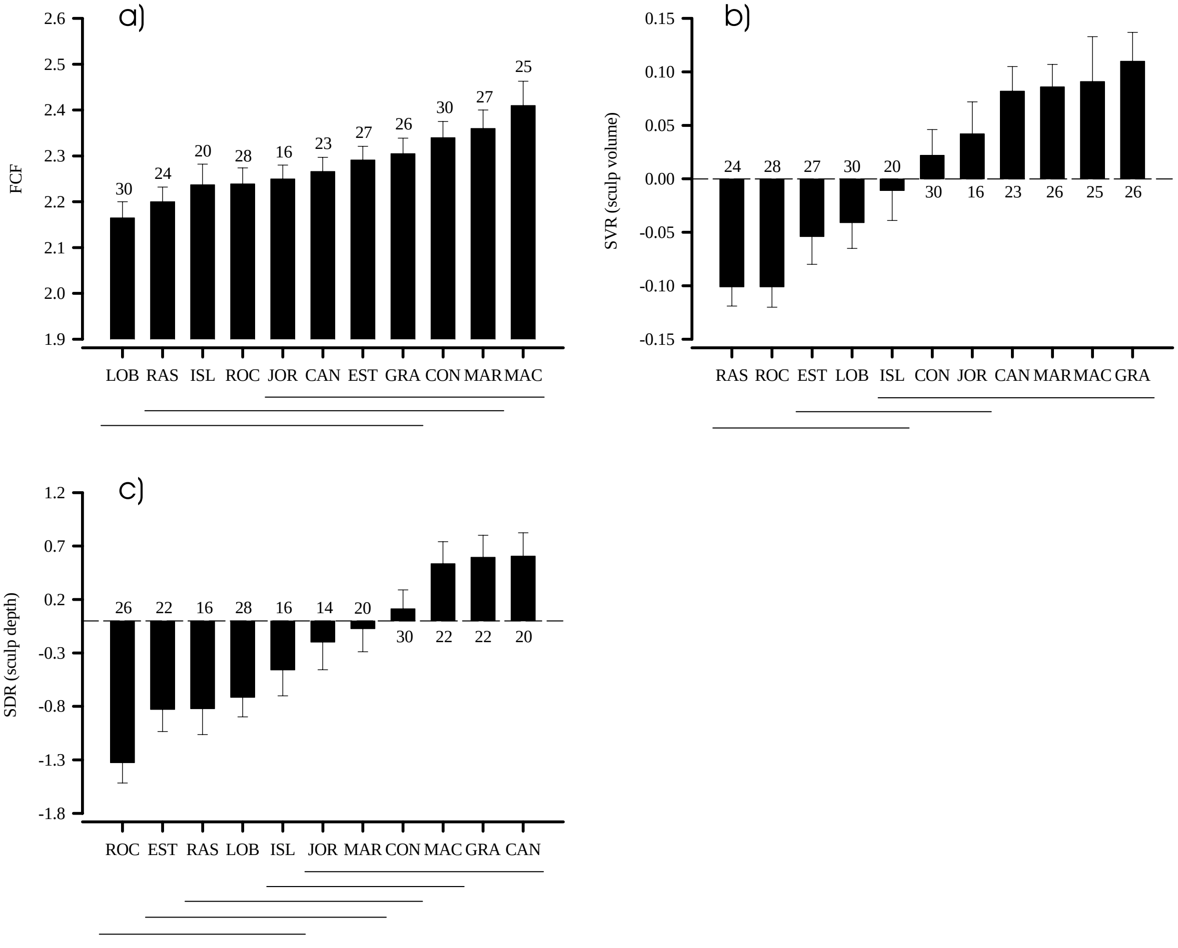


Figure 18. Fulton condition factor (FCF, a), sculp volume index (SVR, b), and sculp depth index (SDR, c) of sea lion pups from eleven rookeries of the Gulf of California in 1997. SVR and SDR were calculated as the residual from the regression of sculp volume (four component model) on standard length, and of sternal sculp depth on standard length, respectively. The lines below the abcissa join those rookeries whose means were not significantly different among themselves, as shown by Tukey's multiple comparisons tests. The values shown are the mean ± SE. The dotted lines indicate where zero is on the abcissa; the numbers above or below the abcissa are the sample sizes. The abbreviations for the rookeries correspond to those in Table 1.

differences between rookeries with adjacent mean SVR values were not significant. Nevertheless, Granito and Machos had the highest mean values, which were significantly different from those of Rasito and Roca Blanca, which had the lowest mean values (Figure 18b). Other colonies with relatively low SVR values were Roca Blanca, San Esteban, and Lobos. Similarly, other colonies with high SVR values were San Pedro Mártir, Cantiles, and San Jorge. The variation in the SVR index using the six component model showed significant differences among rookeries[29] and displayed a pattern identical to the four component model.

The SDR index also showed significant differences among rookeries[30]. There were five groups of colonies with different mean SDR values. Cantiles and Granito had the highest values of this index and were significantly different from those of pups from Roca Blanca (Figure 18c). In general, the multiple comparisons tests gave similar results as the ones obtained using the SVR index.

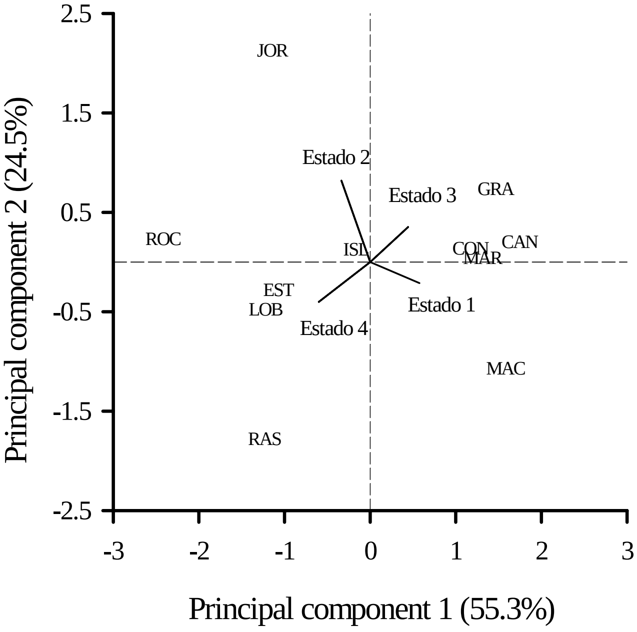


Figure 19. Centroids of eleven rookeries on two principal components extracted in 1997. The percent of variance extracted by each component is shown in parenthesis. Before performing the analysis, the pups were classified into four mutually exclusive body condition states: a pup was considered to belong to state 1 if both the Fulton condition factor (FCF) and blubber content index (IBC, based on sternal sculp depth) were higher than or equal to the yearly average; to state 2 if FCF ≥ and IBC < the yearly average; to state 3 if FCF < and IBC ≥ the yearly average; and to state 4 if both FCF and IBC were lower than the yearly average. These body condition states were later entered as variables into the principal components analysis. The correlation of each state with the components are shown by the lines that intersect at 0,0. The abbreviations for the rookeries correspond to those shown in Table 1.

The average FCF for the eleven rookeries studied in 1997 was 2.280, and the average SDR was -0.291. These values were used to classify pups into the four possible body condition states. The principal components analysis performed with this sample produced two principal components which accounted for 79.8% of the variance (Figure 19). The first component adequately separated those rookeries that had pups that were mainly in State 4 (FCF and SDR < yearly average): Rasito, Lobos, San Esteban. Pups from Roca Blanca were also mainly associated with State 4, but there was an important proportion of pups in State 2. To a lesser extent, this component was useful to isolate pups from Machos, which had a majority of pups belonging to the State 1 category (FCF and SDR ≥ yearly average). The second principal component was almost exclusively sensitive to pups belonging to State 2 (FCF ≥ and SDR < yearly average), and thus successfully separated pups from San Jorge. The centroid of the values for Los Islotes was very close to zero in both principal components, meaning that there was a similar proportion of pups in all body condition states. Rocas Consag, San Pedro Mártir, and Cantiles had a preporenderance of pups in State 1, and a lower

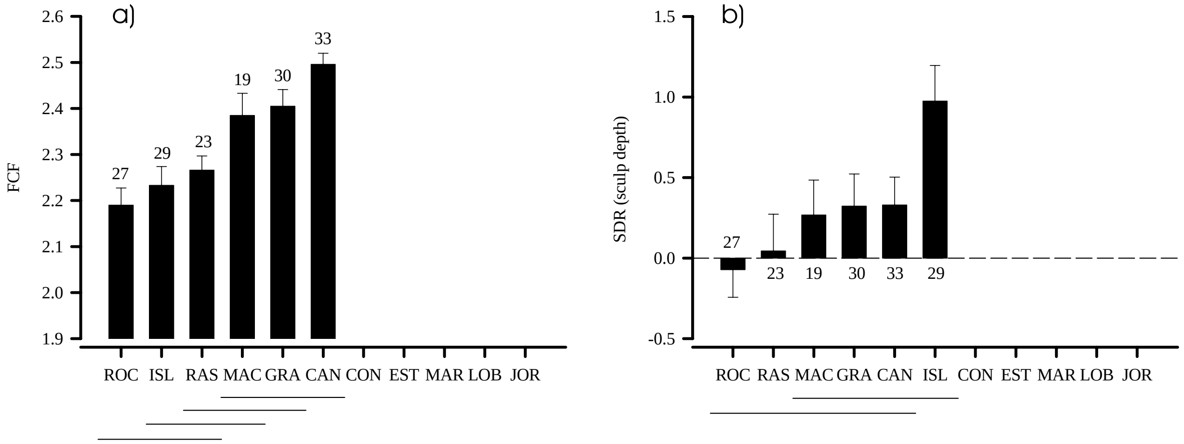


Figure 20. Fulton condition factor (FCF, a) and a sculp depth index (SDR, b) of sea lion pups from six rookeries of the Gulf of California in 1998. The index of blubber content was calculated as the residual from the regression of sternal sculp depth on standard length. The lines below the abcissa join those rookeries whose means were not significantly different among themselves, as shown by Tukey's multiple comparisons tests. The values shown are the mean ± SE. The dotted lines indicate where zero is on the abcissa; the numbers above or below the abcissa are the sample sizes. The abbreviations for the rookeries correspond to those in Table 1.

proportion of pups in State 3 (FCF < and SDR ≥ yearly average). Granito se caracterizó por tener porcentajes altos e idénticos de crías en los estados 1 and 3.

1998. Both FCF and SDR were significantly different among rookeries in 1998[27], but as in the previous years, the comparisons tests revealed overlap between with respect to both indices. Cantiles and Roca Blanca were the colonies with the highest and lowest mean FCF values, respectively (Figure 20a). Machos and Granito had FCF values similar to Cantiles, but formed a homogenous group with the other rookeries, which had lower FCF values. Similarly, Los Islotes and Rasito had FCF values equivalent to those of Roca Blanca. The SDR of pups from Los Islotes was the highest and was significantly different from that of pups from Roca Blanca, which was the lowest (Figure 20b). The rest of the rookeries had mean SDR values which lied between these extremes, and were not significantly different among themselves.

The mean FCF and SDR values for 1998 were 2.334 and 0.329, respectively. The principal components analysis performed with this sample and the four body condition states produced two components that accounted for 98.9% of the variance (Figure 21). The first component adequately separated the colonies that had a predominance of pups in the State 2 (FCF ≥ and SDR < yearly average) or the State 1 (FCF and SDR ≥ yearly average) categories: Cantiles and Granito. It also separated Roca Blanca, Machos and Rasito, which had a large fraction of pups in the State 4 category (FCF and SDR < yearly average), although Machos and Rasito had a larger proportion of pups in other categories than Roca Blanca. The second component clearly separated Los Islotes, which was characterized by pups in State 3 (FCF < and SDR ≥ yearly average).

The interannual changes in FCF and SDR indices of pups from the four rookeries that were visited all three years of study (Figure 22) showed that all of them, except Machos, increased their FCF index, which may explain why the differences between Machos and the other rookeries were not so pronounced in 1998, compared to the previous years. The SDR index was more variable, but there was a negative trend in Machos, bringing the values of pups from this rookery down and closer to those of pups from other colonies.

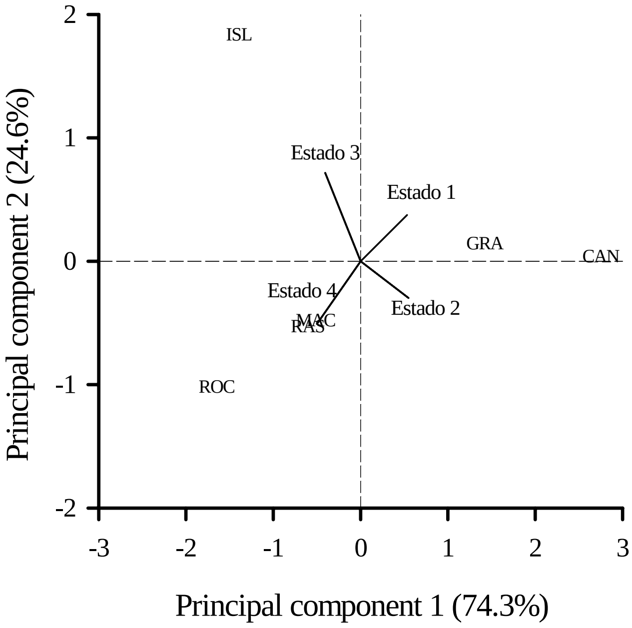


Figure 21. Centroids of six rookeries on two principal components extracted in 1998. The percent of variance extracted by each component is shown in parenthesis. Before performing the analysis, the pups were classified into four mutually exclusive body condition states: a pup was considered to belong to state 1 if both the Fulton condition factor (FCF) and blubber content index (IBC, based on sternal sculp depth) were higher than or equal to the yearly average; to state 2 if FCF ≥ and IBC < the yearly average; to state 3 if FCF < and IBC ≥ the yearly average; and to state 4 if both FCF and IBC were lower than the yearly average. These body condition states were later entered as variables into the principal components analysis. The correlation of each state with the components are shown by the lines that intersect at 0,0. The abbreviations for the rookeries correspond to those shown in Table 1.

In summary, males were approximately 3% heavier than females of the same length or volume after they reached one month of age. At least during 1997, the sculp depth of males was smaller than that of females of the same length. The FCF index is useful for comparing body mass in relation to length among rookeries only for pups of similar age and the samples are collected over a short period of time (less than 15 days) and during one reproductive season. The residuals of the regression of sculp volume or depth on standard length complement the FCF index by providing a measure of blubber content, and thus allowing for a better evaluation of pup body condition in sea lions. Pups from Machos had the highest body condition indices during the three years of study, while those from Rasito and Roca Blanca had the lowest. The FCF of pups from Lobos and San Esteban was highly variable among years, while their SDR index remained low during the same period. Pups from San Pedro Mártir had high FCF values, but their SDR values were more variable during the study period. Pups from San Jorge had average FCF and SDR values during the two years it was studied (1996 and 1997). Pups from other rookeries had indices which varied considerably from one year to the next, and did not show a consistent pattern.

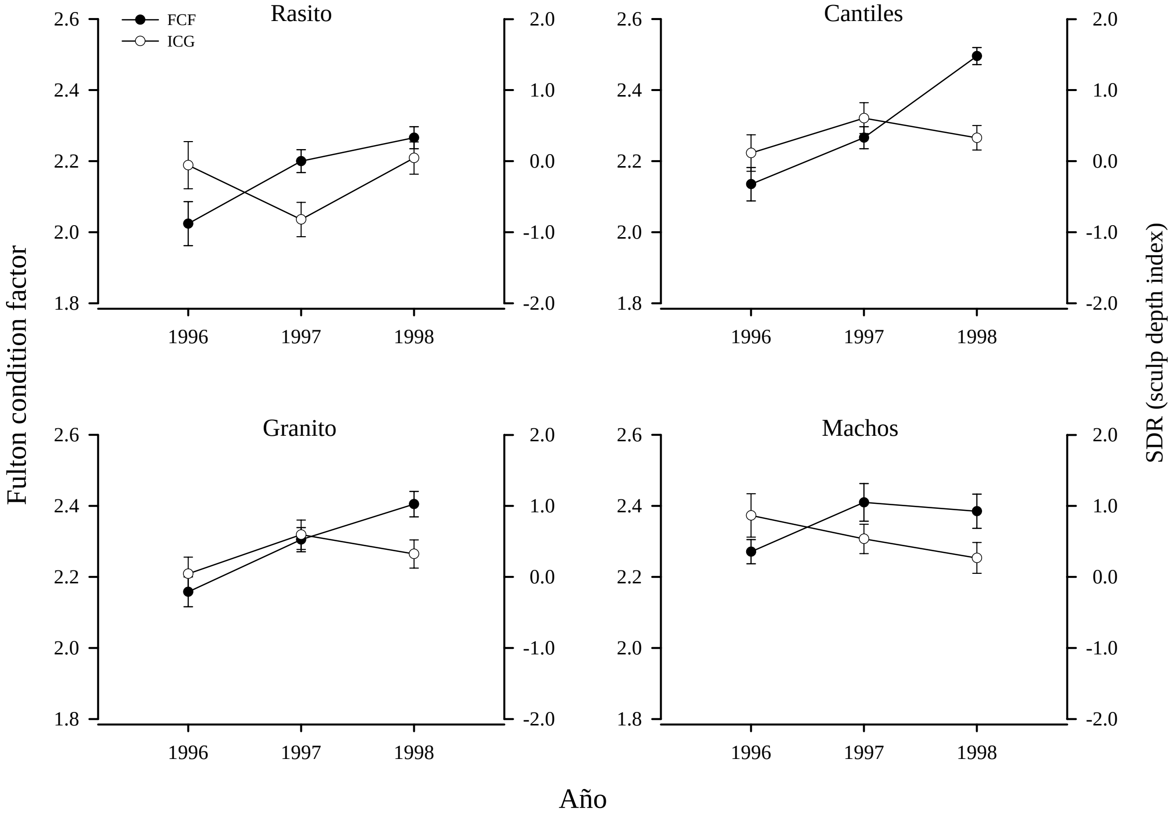


Figure 22. Interannual changes in sea lion pup body condition, as indicated by the Fulton condition factor and the residuals of the sternal sculp depth on standard length regression, in four rookeries of the Gulf of California during 1996-98.

3.4 Growth and age differences in body condition

During the summers of 1994 and 1996-1998, 44 male pups and 17 female pups were captured repeatedly throughout the reproductive season in Los Islotes. In 1994 and 1996, only body mass and standard length data were obtained, while all the variables shown in Figure 2 were obtained in 1997. In 1998, body mass, standard length, axillary girth, and sternal sculp depth were measured (Figure 2). Such methodological differences did not allow for the investigation of changes in some of the variables and condition indices as pups grew in size for the samples taken before 1997.

Body mass growth rate did not vary significantly among years or sexes[28] in 1994 and 1996-1998, so the data were pooled. Figure 23a shows the changes in body mass for individual pups throughout the reproductive season. Pups grew at an average of 0.150 ± 0.0074 kg · day^{-1} (n=61). Similarly, standard length and sternal sculp depth growth rates did not vary significantly among year or sexes in 1997 and 1998, so these data were also pooled (Figure 23b, d). Pups grew at an average of 0.27 ± 0.016 cm · day^{-1} in standard length and 0.081 ± 0.0064 mm · day^{-1} in sternal sculp depth (n=28, both cases). Axillary girth growth rate, however, did vary among sexes, but not among years. Male and female pups grew at an average of 0.28 ± 0.014 (n=23) and 0.21 ± 0.021 (n=5) cm · day^{-1}, respectively (Figure 23c).

The GL and SDR indices were positively related to pup age in 1997 and 1998 (P<0.05) (Figure 24). This relationship held when data from both years were pooled. The FCF index was positively related to pup age only in 1998 (P<0.05), and held when data from both years were pooled. In general, body condition indices appeared to increase as pups grew older. This pattern was most evident in 1998.

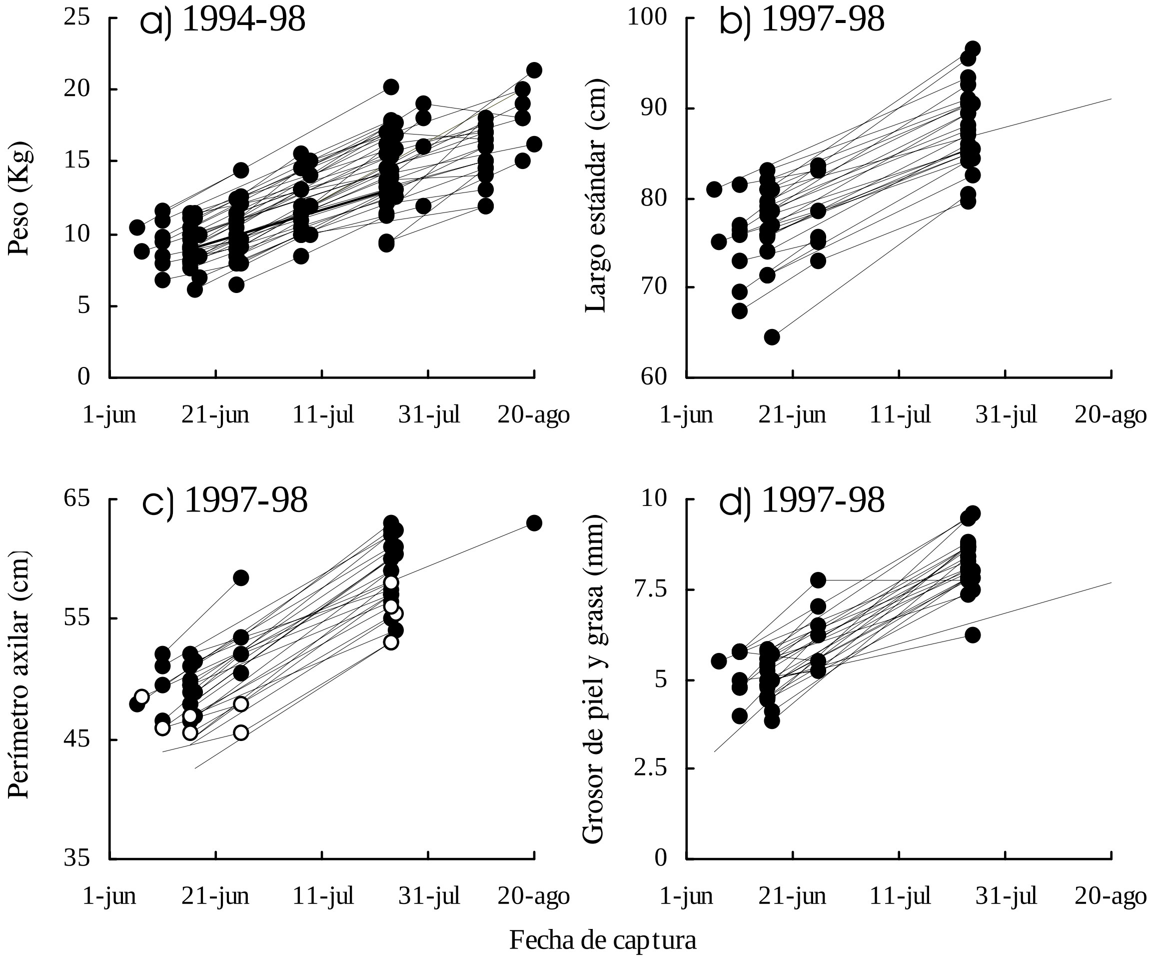


Figure 23. Changes in body mass (a), standard length (b), axillary girth (c), and sternal sculp depth (d) of serially captured pups in Los Islotes. There were no significant differences in growth rates between years, nor were there any sexual differences in these rates, except for axillary girth (c); in this case, males (filled circles) grew faster than females (empty circles).

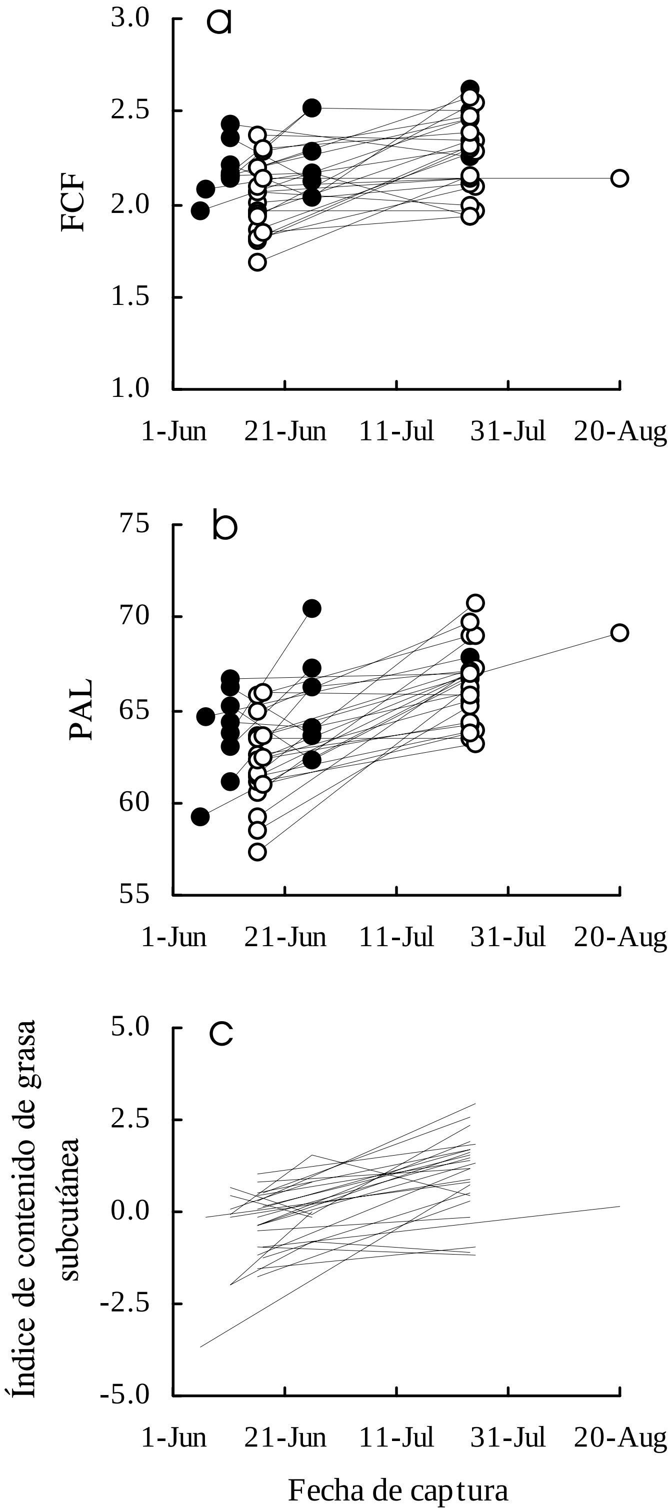


Figure 24. Changes in Fulton condition factor (FCF, a), girth to length ratio (PAL, b), and the residual from the sternal sculp depth on standard length regression (c) from serially captured sea lion pups in Los Islotes during 1997 (filled circles) and 1998 (empty circles). The lines join data points from each individual.

3.5 Relationship between indices of food abundance

Los Islotes

During the last 19 years, pup production varied considerably. Between 1980 and 1986, the number of pups counted in this rookery was relatively low and did not change much from one year to the next. Though the information is incomplete, pup production showed a large increase (>100%) from 1986 to 1993, and remained relatively high and constant for the remaining years (Figure 25a). Maximum pup production was recorded in 1999, when 125 pups were counted. The number of adult females in the rookery showed a similar pattern, although there was a small gradual reduction from 1996 to 1998.

During 1980-1986, when pup production was lowest, the FCF index also showed the lowest values (Figure 25b). From 1992 to 1995, immediately after the increase in pup production, the FCF index increased steadily, reaching a maximum in 1995, and then it decreased slightly for the next three years.

Changes in food intake rate by the colony closely followed those of pup production and body condition. Food intake rate increased by about 130% from 1980-1984 to 1994. There was an obvious gradual decrease in this variable from 1994 to 1999, concomitant with a reduction in FCF index, representing about a 68% reduction in 1999 compared to 1994 (Figure 25c).

The average SST during the summer was relatively low from 1987 to 1991, compared to the following years (Figure 25d). The relationship between SST and the previous variables was not clear.

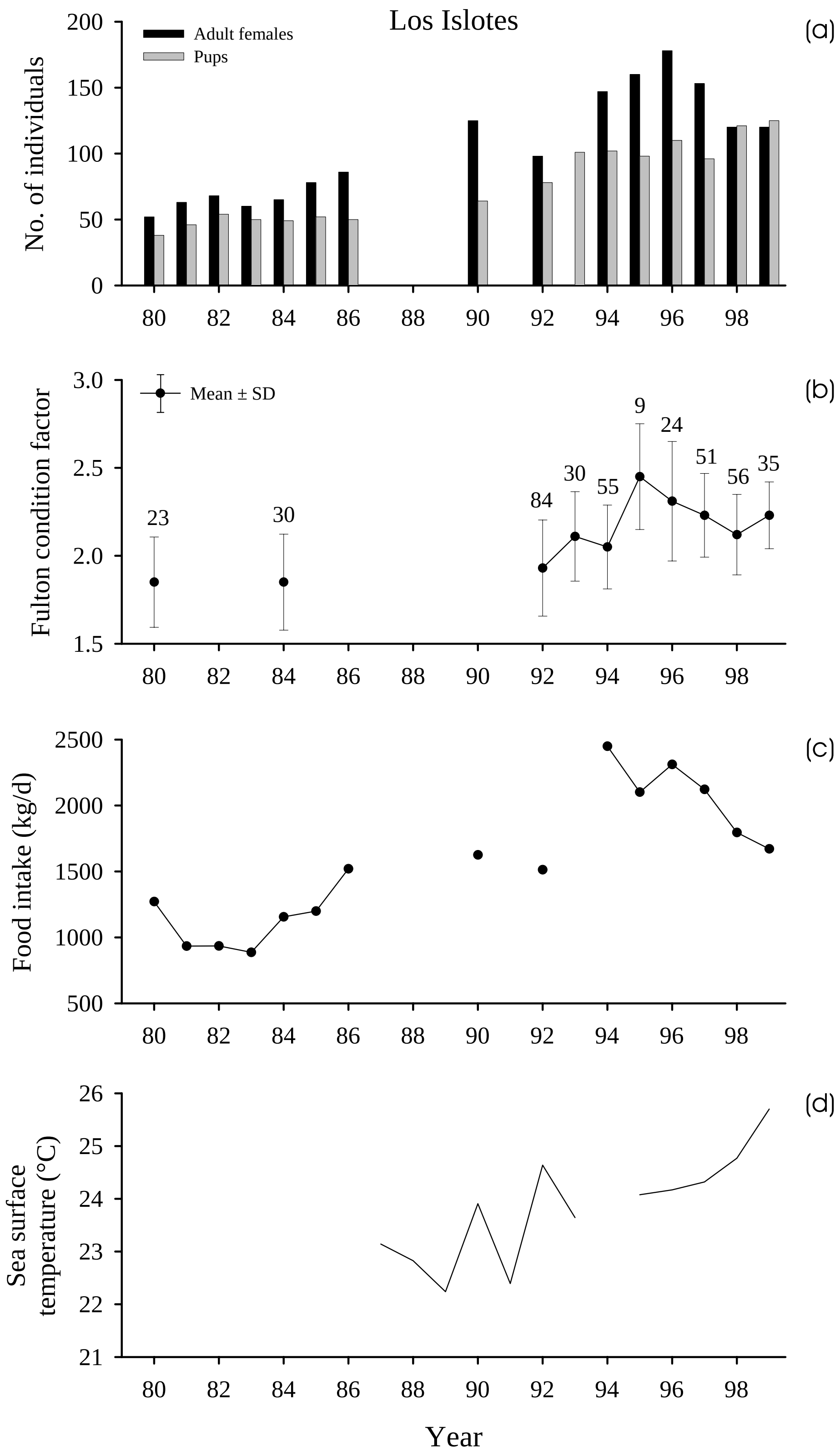


Figure 25. Interannual changes in pup production and adult females on land (a), pups' Fulton condition factor (b), food intake rate of the population (c), and sea surface temperature (d) around the rookery in Los Islotes, bay of La Paz, during the last 19 years. The numbers above the error bars represent the sample size obtained each year.

Cantiles

Though only data from one year is available for the early eighties, pup production appears to have been very low during that period. In 1981, only 270 pups were counted, but by 1987, it increased by about 83% from 1984 to 1987, when pup production was highest (Figure 26a). Pup production remained relatively constant from 1988 to 1990. Begining in 1990, pup production declined rapidly until 1995, when only 148 pups were counted; the lowest recorded. During the last three years, pup production was a little higher than in 1995, but did not change considerably. The number of adult females was more variable, but showed the same general pattern; it increased from 1984 to 1988, it decreased between 1988 and 1992. Adult female abundance did not change considerably since then.

Pup body condition was relatively low during the late eighties, particularly in 1989 (Figure 26b). However, begining in 1992, pup body condition increased gradually until 1998, concomitant with a reduction in pup production. The increase in pup production during the last three years was not associated with changes in FCF index.

Food intake rate in this rookery varied greatly between 1984 and 1990 (Figure 26c). It increased from 1984 to 1987 by about 45%, reaching the maximum values, but it declined rapidly to the initial levels by 1990. From then on, there was a clear negative trend that was maintained for the last 8 years; the lowest intake rate was observed in 1998. The variation in food intake rate was positively related to pup production and negatively related to pup body condition during all this time series.

There were two trends in SST changes during the summer in Cantiles. From 1987 to 1991, SST declined steadily about 1 degree Celsius, while in 1992, it increased back to the values observed in 1987, and remained relatively constant from then until 1998 (Figure 26d). The temporal variation in SST during 1987-1998 was not clearly related to any of the variables studied above.

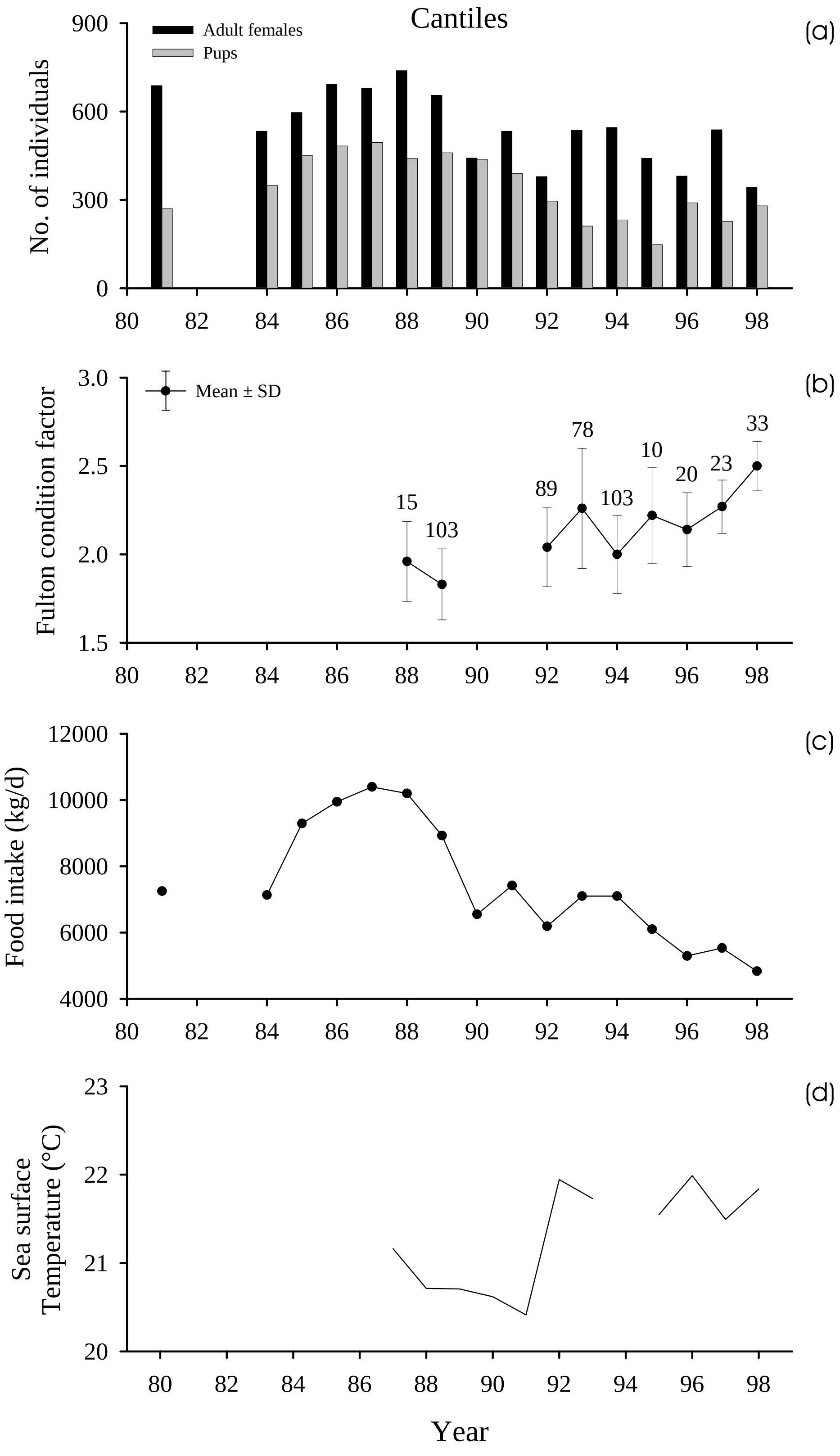


Figure 26. Interannual changes in pup production and adult females on land (a), pups' Fulton condition factor (b), food intake rate of the population (c), and sea surface temperature (d) around the rookery in Cantiles, Ángel de la Guarda island, during the last 18 years. The numbers above the error bars represent the sample size obtained each year.

4 DISCUSSION

4.1 Sources of error

The beaches where pups were captured were limited by their accesibility. Trites (1991a, 1993) found that the distribution of northern fur seal (*Callorhinus ursinus*) pups was not homogeneous with respect to body size and thus possibly age, so smaller and perhaps younger pups were more susceptible to being captured than were larger and older pups. However, a preliminary analysis of a small sample of pups from Cantiles and Granito in 1998 does not suggest there are differences in body mass between pups captured in open, sandy beaches (14 males: 12.08 ± 0.57, 19 females: 10.45 ± 0.25), compared to those captured in beaches with large boulders (10 males: 11.28 ± 0.64, 20 females: 10.33 ± 0.42). There is no evidence of this kind of bias in other studies that used the same approaches as in this one (Morales-Vela 1990; Morales-Vela and Aguayo-Lobo 1992). Using n=30, it was possible to cover all the estimated variance in pup body mass among rookeries and among years at most Gulf of California rookeries since the eighties. Therefore, pup body size or condition bias may have been small compared to the larger differences that were observed between rookeries. Even if such bias is allowed for, comparisons among rookeries were done under the same conditions, because the methodology was the same for all them and sampling was done in a short period of time (less than 15 days) each year, so the bias was probably of the same magnitude in each rookery.

Some factors that have not been considered in this study, but that have been shown to influence pup body size and possibly body condition are the body size, age, and condition of their mothers. However, the evidence for such influence in pinnipeds is equivocal. For example, Ono and Boness (1996) did not find any relationship between maternal and newborn pup body size, but concluded that pup growth rate and maternal body size were positively related in California sea lions. In the Antarctic fur seal, older, more experienced, and possibly fatter mothers gave birth to larger pups earlier in the season, compared to younger, leaner, and relatively inexperienced mothers (Boyd and McCann 1989; Lunn and Boyd 1993a; Lunn *et al.* 1994). Unfortunately, the effects of maternal physical characteristics have not been studied in the Antarctic fur seal, precluding comparisons with the results of Ono and Boness (1996). If, in fact, there is a relationship between maternal and pups characteristics in California sea lions from the Gulf of California, and adult females are distributed heterogenously and differently with respect to age and size within each rookery, then our samples may have been biased. Clearly, more studies aimed at investigating the spatial distribution of adult females with respect to age, size, and pup characteristics are needed to assess the magnitude of such bias.

4.2 Morphometry and sexual dimorphism

Interannual variation

Interannual differences in pup body size were largely a result of the variation in sampling date. This conclusion was based on the following observations: i) pup body mass, standard length, and axillary girth were larger in 1996 than in 1997, when only those rookeries studied during the three years, and ii) the interannual difference in mean sampling date was largest between 1996 and 1997 (14 days) and minimum between 1996 and 1998 (1 day). This result is consistent with the evidence of synchronized births in the gulf, corresponding to the second and third week of June (Morales-Vela 1985, 1990; Heath 1989; Aurioles-Gamboa 1988). This is also supported by the observation that the largest percentage of newborn pups (3% of pups found with umbilical cord) was found in 1997, as would be expected based on the information from those studies. Similarly, pup body mass and standard length from 1980 to 1999, as functions of capture date within the reproductive season (Figure 27), suggest that the probability of capturing newborn pups is very low after the second week af July.

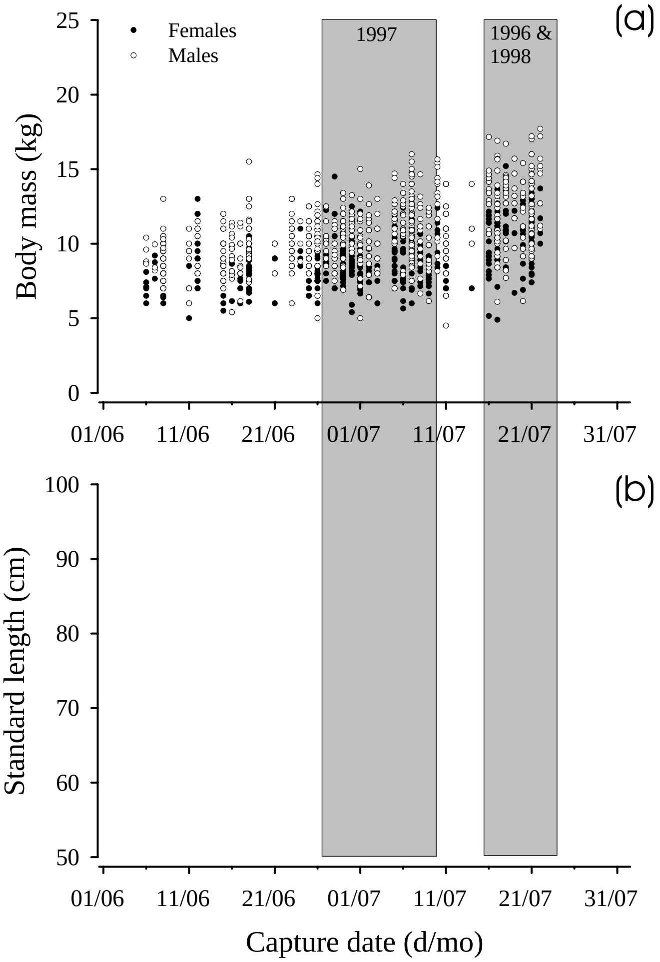


Figure 27. Pup body mass (a) and standard length (b) as a function of capture date at most rookeries of the Gulf of California during the 1980-81, 1984, 1989, 1992-98 reproductive seasons. The shaded area represents the time frame in which samples for this study were obtained.

According to Temte and Temte (1993), the latitudinal variation in birth timing in captive sea lions (Temte 1993), is mainly a response to a photoperiod of 11.48 h · d^{-1}, which occurs 242 days before parturition. Assuming that wild sea lions respond the same way, the maximum birth time difference to expect in the range of latitudes covered by rookeries in the gulf would be four days (between San Jorge and Los Islotes). This means that mean birth date would vary between 11 and 15 June from San Jorge to Los Islotes. If Los Islotes, the only rookery in the southern gulf, is excluded from this calculation, the difference would be only one day. The estimated mean pup age for the four rookeries that were visited all three years of study, using 15 June as mean birth date, would then be 34 and 33 days in 1996 and 1998, respectively, and 20 days in 1997. Therefore, morphometric measuremets of pups captured in 1997 should resemble those of newborn pups more than those of pups captured in 1996 or 1998. Another observation supporting this conclusion is that predictions of body size differences, based on growth rate estimates, between 16-day-old pups and older pups are fairly consistent with the actual data.

Newborn pup body mass and length reported here were similar to data obtained in two previous studies (Morales-Vela 1990; Morales-Vela and Aguayo-Lobo 1992) in Cantiles (Ángel de La Guarda Island), though they were a little lower than therein. The small discrepancy may be a result of the inclusion of data from many rookeries with varying pup body size in this study, as opposed to data from a single rookery, as in those studies. Other studies reporting data from pups at least 10 days old in the gulf (Lluch-Belda 1969) and in the Channel Islands, California (Oftedal *et al.* 1987; Boness *et al.* 1991) report slightly lower measurements for newborn pups than in this study, suggesting that most of the pups I studied were growing under "normal" conditions. Le Boeuf *et al.* (1983) obtained similar pup body size measurements from four colonies in 1981, which were also studied in 1996-1998, but for 1- to 3-week-old pups. Possibly, some of the pups in their analyses were newborns, because their sampling dates included the period when most births occur. However, judging from the authors' estimation of mean pup age, the proportion of newborns in their samples was probably low. This suggests that the pups from these four rookeries were smaller in 1981 than during 1996-1998. More accurate measurements of pup age are needed to adequately compare pup body size.

Although the variation in pup morphometrics was largely explained by age, pup body mass and standard length in 1998 were significantly lower than in 1996, despite their similar age. In fact, axillary girth was the only morphometric variable that had similar values in 1996 and 1998. Relatively large differences were expected between pups captured in 1996 and 1997, because their age difference was approximately 14 days, but no large differences were expected between pups captured in 1996 and 1998, because their age difference was only 1 day. These differences meant that pups captured in 1998 were similar in size to pups captured in 1997, even though they had a 13-day age difference. The reason for such a large difference cannot be determined with the available data, but possibilities to investigate are: i) error in the estimation of mean pup age, ii) pups were born smaller and/or grew at a lower rate in 1998, compared to the previous years, or a combination of these factors.

Several studies in Trillmich and Ono (1991) document delayed reproductive seasons and lower pup growth rates associated with nutritional stress in several otariid pinnipeds. Boyd (1996b) found a delay in mean parturition date associated with lower food availability during gestation in the Antarctic fur seal from South Georgia. It is interesting to note that the date of maximum pup count in Los Islotes shifted from 8 July in 1996 to 26 July in 1998 (Hernández-Camacho, personal communication). Unfortunately, no similar data are available for other rookeries of the gulf.

One of the strongest recorded El Niño (EN) events in history unfolded from May 1997 through June 1998, and it was evident in the coasts of California by July 1997 (Climate Diagnostics Center, NOAA-CIRES 1999). Aurioles and Le Boeuf (1991) have shown that California sea lion pup production and mortality in the Gulf of California were not affected by the 1982-1983 EN, which was of similar magnitude to that in 1997-1998. If food availability was in fact reduced during these events, it is possible, however, that it was harder for lactating females to give birth to pups of "normal" body size, allow them to grow normally, and wean them during these periods. It was not possible to study the interannual variability in newborn pup body size in the gulf during these events, but Boness *et al.* (1991) found that in San Nicolas Island, Pacific Ocean, this variable was not negatively affected by the 1982-1983 EN. This is in contrast to the results obtained by Trillmich (1986), who reports significantly lower pup body mass during the same event in Galápagos fur seals (*Arctocephalus galapagoensis*). In mammals, maternal investment *in utero* is small relative to the costs of lactation (Clutton-Brock *et al.* 1989), but it may represent a significant proportion of the maternal energy budget during gestation (Boyd and McCann 1989). Therefore, the discrepancy in the results obtained by Trillmich (1986) and Boness *et al.* (1991) may be explained by the fact that the effects of EN 1982-1983 were stronger and remained so for a longer proportion of gestation duration in the population of fur seals studied by the former, compared to that studied by the latter. This suggests that it is very important for pregnant females to maintain newborn pup body size in the face of sharp reductions in food availability, and that such reductions may have to be larger than a certain threshold to affect newborn body size. If newborn body size was not affected in California, where the negative effects of EN on otariids were smaller than in Galapagos, but much larger than in the Gulf of California, newborn body size in the gulf was not likely to be negatively affected by the 1997-1998 EN. Therefore, a reduction in newborn body size may not explain why pups were so small in 1998, in relation to mean capture date. On the other hand, it is not possible to eliminate the possibility of a delay in mean birth date. Such delay could have meant that mean pup age was lower in 1998 compared to 1996, even though they were captured on similar dates.

The possibility of reduced pup growth rates in 1998 is not supported by the evidence gathered in Los Islotes, where the negative effects of EN are expected to be strongest in the gulf. Pup growth rate in this rookery did not vary significantly from 1994 to 1998. This indicates that the postnatal development of pups was not adversely affected by the latest EN event, probably because starting in June 1998, oceanographic conditions in the Pacific Ocean had already returned to "normal", according to the changes of a multivariate index of the intensity of EN (Climate Diagnostics Center, NOAA-CIRES 1999). In addition, gody mass and axillary girth growth rates were similar or slightly higher than those reported for the Channel Islands, California, during "normal" non-EN years (Boness *et al.* 1991). Therefore, the first option, that of an error in the estimation of mean pup age in 1998, cannot be eliminated, and thus appears to be the most likely explanation for the relatively small pup body size during that year. The most plausible explanation for such an error is a delay in mean birth dates at most rookeries.

Sculp depth and weight

Sculp depth estimations were similar to those obtained using the same methods from Steller sea lions (*Eumetopias jubatus*) of similar age in Alaska (Castellini *et al.* 1993). Steller sea lion pups are almost twice as large as California sea lions, and they are exposed to lowere temperatures throughout the year, so their sculp depth was expected to be larger also. However, their larger size also means that the fraction of metabolic rate destined to thermoregulation would also be smaller, compared to California sea lions (Peters 1983), and this could explain why they do not need a thicker blubber layer. Sea lion pups use a relatively large proportion of their energy intake to thermoregulation and their blubber layer may not yet be fully developed (Thompson *et al.* 1987). Mattlin (1978) reported values of 4 to 6 mm for sternal blubber layer in New Zealand fur seals (*Arctocephalus forsteri*), which are close to the values reported here. Although Mattlin (1978) did not describe the methods used to measure this variable, they appear to be direct measurements on pups that had died recently. The method used in this study tends to underestimate blubber depth because some blubber remains attached to the underlying tissue and cannot be included in the skinfold measurements. Thus, the blubber layer is probably thicker in California sea lions than in fur seals, such as the New Zealand fur seal, which are about 50% smaller than the sea lions (Bonner 1981). Though there are few additional data to support it, this observation is consistent with the large difference in blubber depth between adult male Australian fur seals (*Arctocephalus pusillus doriferus*), which had a blubber layer 1.6 ± 1.3 cm (mean ± SD) deep (Pemberton *et al.* 1993), and an adult male California sea lion, found dead in San Jorge island in the Gulf of California, which had a 5.0 cm deep blubber layer.

There is no information available to compare the sculp depth distribution in sea lions with other otariids, but it was similar to that described for phocids, such as harbor seals (*Phoca vitulina*) (Rosen and Renouf 1997), harp seals (*Phoca groenlandica*) (Beck *et al.* 1993), and ringed seals (*Phoca hispida*) (Ryg *et al.* 1988). Several factors are thought to influence the distribution of blubber in mammals (see Pond 1978 for review), but in marine mammals, the most important ones are the optimization of energy storage in relation to environmental fluctuations, minimization of drag through the water, adjustment of buoyancy, and thermoregulation. Ryg *et al.* (1988) and Rosen and Renouf (1997) suggested that, in pinnipeds, thermoregulatory ability is maximum if the proportion of the radius of the body to the blubber depth is constant throughout the body. These authors added that several phocid seals tend to loose blubber from those points in the body where blubber depth is small compared to body radius. If this is true for all pinnipeds, then sternal blubber depth may be one of these points in the body of sea lion pups because it showed the highest variability of all sites measured. This has the advantage of being the site that is most commonly measured in studies of body condition in pinnipeds (American Society of Mammalogists 1967). Beck *et al.* (1993) and Ryg *et al.* (1988) found that, in harp and ringed seals, the most variable blubber depth site along the body was in the dorsal region, approximately 50% and 60% of body length, respectively. To be able to compare blubber distribution and variability among otariid and phocid seals, it is necessary to obtain more information from otariids about the seasonal variability and changes in age of this variable. The mechanics of locomotion on land and in water, characteristics of the reproductive cycle, and lactation strategies must have been important phylogenetic factors determining differences in blubber distribution and variability among phocids and otariids.

The weight of the sculp in relation to total body mass was similar to estimates obtained from Antarctic fur seals (Arnould *et al.* 1996b), though slightly larger. Arnould *et al.* 1996b reported that sculp weight comprised, on average, 21% of body mass in 4 Antarctic fur seal pups, compared to 24% in sea lion pups from this study. The values from this study may subestimate the relative weight of the sculp because 3 of the pups I measured were clearly undernourished and because an unknown amount of blubber could not be separated with the skin. Therefore, sea lion pups appear to have larger relative stores of blubber than Antarctic fur seals. This difference may be explained by the fact that, in fur seals (subfamily: Arctocephalinae), the skin is covered by two hair layers, which offer better insulating capabilities to the animals than the single layer of sea lions (subfamily: Otariinae) (Bonner 1981; King 1983) (see above).

Sexual dimorphism

The sex differences in body size observed in this study add to the evidence of sexual dimorphism from birth in this species (Lluch-Belda 1969; Oftedal *et al.* 1987; Ono and Boness 1996). The degree of dimorphism in body mass (on average, 18%) and in linear dimensions (on average, 6%) was similar to that reported in those studies and for other otariids (Costa and Gentry 1986; Trillmich 1986; Croxall and Gentry 1987; Cappozzo *et al.* 1991; Boyd 1996b). Such degree of sexual dimorphism was also similar to the values of 22% and 6% obtained from newborn pups, consistent with the evidence of similarity in growth rates among males and females. Trites (1991b) observed that male northern fur seal (*Callorhinus ursinus*) fetuses grew faster in body mass and length than female pups and that this difference increased throughout gestation. This would pose greater energetic demands on pregnant females carrying male fetuses than other females. In fact, the growth of male Antarctic fur seal fetuses is limited by maternal reserves to a larger extent than that of female fetuses (Boyd and McCann 1989). Assuming that this can be extrapolated to other otariids, such as the California sea lion, we would expect larger body size differences between male and female newborn pups when food availability is high during gestation, while the opposite would be true when food availability is low during that period. Based on this logic, adult females that got pregnant during the summer of 1997 may have experienced some food stress, because pups born in 1998 showed the smallest degree of sexual dimorphism. Sexual dimorphism in body mass was 17% in 1996 and 1998, and 24% in 1997, while sexual dimorphism in linear dimensions were 6%, 8%, and 4%, in 1996, 1997, and 1998, respectively.

The absence of sex differences in sculp depth in 1996 was probably a result of the low accuracy of the measuring instrument, as well as the small magnitude of such differences when such differences were found (1997).

Though males were heavier and larger in their linear dimensions than females, differences in sculp depth were few and small. Four out five dorsal measurement sites (*i.e.* all of them, except over the head) and two lateral ones (at approximately one half the body length) were larger in males than in females in 1997, while none of the ventral sites showed sex differences in any year. This suggests that there is a difference in both the distribution of blubber and its relative amount in the body among the sexes. Pond (1978) put forth 4 hypotheses to explain the distribution of blubber in verebrates on a functional basis, and concluded that the most probable were its function in regulating buoyancy, in locomotion, and as social and sexual cues. The latter function would make little sense in sea lion pups, at least during the range of ages found during the reproductive season, but it could be under natural selection during and after the subadult stage. In otariids, the neck of adult males is proportionally thicker and longer than that of females of similar age (Ridgway and Harrison 1981; King 1983) and is the part of the body which is most badly hurt during territorial disputes among males (Peterson and Bartholomew 1967). Although the slightly thicker and longer hair in the neck would result in such a profile in otariid males, blubber thickness is also a contributing factor. The development of these characteristics in male pups could thus provide them with an advantage if this is related to reproductive success during adulthood.

Because there were no sex differences in ventral sculp depth measurements, and at least in one lateral site, males are leaner in these parts of the body because males are larger than females. The implications of this finding will be discussed later in the section of sex differences in body condition indices.

4.3 Body condition indices

Relationships between morphometric variables

In marine mammals, body condition refers to the relative amount of lipids available in the body of an individual (Lockyer *et al.* 1985; Beck *et al.* 1993; Arnould, 1995). Lipids are the main form of energy storage in most mammals; in cetaceans and pinnipeds in particular, most of the total body lipids are concentrated (>80%) in a subcutaneous layer (Lockyer, 1987; Beck *et al.* 1993; Arnould *et al.* 1996b). Therefore, the amount of blubber has been used as a reliable indicator of energy reserves in pinnipeds. However, the amount of blubber is difficult to estimate and obtaining large samples, without killing the animales, is very costly. McLaren and Smith (1985) recognized the need to develop practical and efficient means to estimate the nutritional status of pinnipeds. The search has thus been to find a variable that is easy to measure in the field, which is directly related to the amount of total body lipids. The weight or depth of the sculp have shown such a relationship in some phocids (Beck *et al.* 1993; Ryg *et al.* 1990; Gales *et al.* 1994) and in one otariid species, the Antarctic fur seal (Boyd and Duck 1991; Arnould 1995). However, Arnould (1995) found that body mass was directly related to total body water, which in turn could be used to estimate the relative amount of total body lipids in adult female and juvenile Antarctic fur seals. Although it has not yet been shown that these relationships hold for other otariids, body mass and blubber depth could provide a rough estimation of the energy reserves in individual otariids. For example, Costa *et al.* (1991) found that body mass is related to total body water in adult female California sea lions.

The slope of the body mass-standard length relationship was similar among years and sexes, indicating that it can be generalized to all the pups within the age and size ranges included in this study. The estimated value of the slope for all data combined (b=2.81), suggests that this relationship shows a slight negative allometry, i.e., growth in body mass is smaller than that in standard length. The estimated regression equation ($BM=0.0000525 \cdot SL^{2.81}$) is similar to that obtained by Trites (1991b) ($BM=10^{-4.20} \cdot SL^{2.75}$) for northern fur seal fetuses. The relationship is also remarkably similar to those estimated by Chabot (1994) ($BM=0.0000547 \cdot SL^{2.86}$) for adult male Australian fur seals (*Arctocephalus pusillus doriferus*); by Markussen *et al.* (1989, op. cit. in Chabot 1994) ($BM=0.0000404 \cdot SL^{2.89}$) for the harbor seal; and by Innes *et al.* (1981, op. cit. in Chabot 1994) ($BM=0.0000645 \cdot SL^{2.81}$) for the harp seal, which suggests that the relationship between these variables may be common to all pinnipeds. Chabot (1994) reasons that because body volume has been found to be related to standard length elevated to the third power in harp and hooded seals (*Cystophora cristata*), and because body mass should be linearly related to body volume, body mass should scale to standard length elevated to approximately the third power. However, all the available evidence, including that from this study, indicates that body mass scales to standard length elevated to a power smaller than 3.00 in pinnipeds. It should be noted that Australian fur seals and California sea lions are highly dimorphic species, as most otariids, so sex differences in this relationship would be expected during the juvenile stage when sexual dimorphism becomes more pronounced.

Male sea lion pups were about 20% heavier than female pups, but this difference may be as large as 300% during adulthood (Lluch-Belda 1969). Although there are few data, the body mass-standard length relationship in pups from 1996-1998 predicts the body mass of adult female and juvenile male and female sea lions reasonably well (Figure 28). Figure 28 also shows that this relationship is very similar to that of Antarctic fur seals, adult male and female South American sea lions, but not that of adult female Guadalupe fur seals. With a larger sample, Lluch-Belda (1970) concluded that the slope of the relationship in female California sea lions (b=2.20) is almost one half that of males (b=4.12). His values are very different from those obtained from this study (b=2.72-2.93 and b=2.73-3.085, female and male pups, respectively), probably because Lluch-Belda (1970) grouped the data into 1-year age groups and used the means of each variable in those groups to define the relationship. This could have resulted in unknown biases, since each observation would not reflect the true relationship between the variables for any individual in particular. To adequately compare this

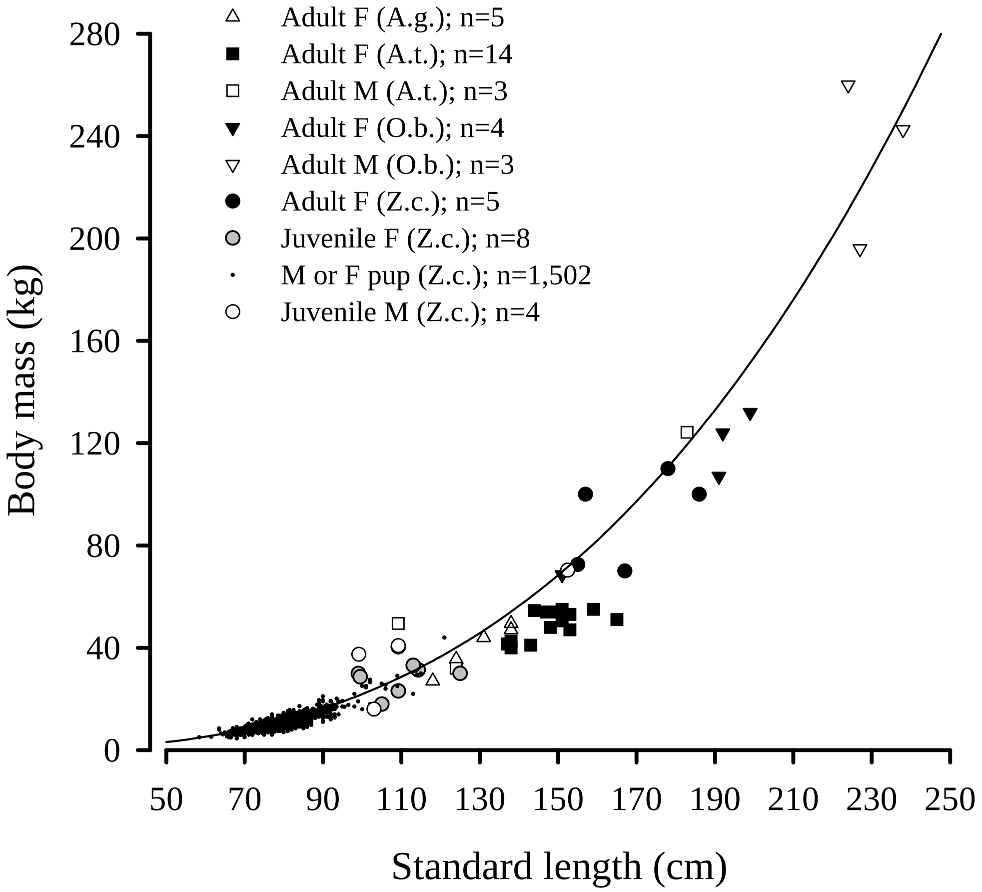


Figure 28. Relationship between body mass and standard length in California sea lion (*Zalophus californianus*, Z.c.) pups, juveniles, and adults (Marine Mammal Laboratory, CICIMAR-IPN), Antarctic fur seal (*Arctocephalus gazella*, A.g.) juveniles and adults (Arnould *et al.* 1996b), adult Guadalupe fur seals (*Arctocephalus townsendi*, A.t.) (Gallo-Reynoso y Figueroa-Carranza 1996), and South American fur seals (*Otaria byronia*, O.b.) (Vaz-Ferreira 1981). The line represents the function that describes the relationship between body mass and standard length in California sea lion pups from the Gulf of California. M=male and F=female.

relationship among different sexes, ages, and species, it is necessary to obtain larger samples, covering all ages, and be able to associate both variables in the same individuals.

The value of the slope of this relationship was smaller than 3.00 only when all the data were combined. This resulted from the particularly low values obtained for both sexes in 1996 and 1998, which was associated with the older age of these pups, with respect to those in 1997. In the latter case, the slope of the relationship was very close to the isometry value 3.00 for both sexes (b=2.93 and b=2.94, males and females, respectively), suggesting that young pups (0-20 days old) grow isometrically, while older (>30 days old) pups grow allometrically with respect to these variables.

Because of the changing nature of the relationship between body mass and standard length, it is important to verify whether its slope is equal to 3.00 or not, before using an index based on these variables and making comparisons among different categories. The Fulton condition factor ($FCF = body\ mass/standard\ length^3$) proved to be a useful index for comparing the body mass in relation to the standard length of young pups during a reproductive season. The limitation of this index, however, is that samples must be obtained within a short period of time (~15 days) in one reproductive season and when pups are younger than 2 months old. If researchers intend to compare the body condition of pups among different years and older ages, it is more appropriate to use the exponent of the relationship obtained empirically. In addition, the FCF index is not appropriate in older pups because of the difference in the elevation of the regression equation between males and females that was found in 1996 and 1998. In these years, males were 3 and 4% heavier than females of similar length, respectively.

The relatively smaller r^2 values obtained for the axillary girth-standard length relationship were possibly related to the larger error when measuring axillary girth. Body mass and length measurements have higher precision than girth because the latter vary with the respiratory cycle of the pups. The proportion of the variance in girth measurements that can be attributed to this factor is unknown at this point, since alveolar pressure changes with inhalation and exhalation vary considerably both intra- and interindividually (Lin *et al.* 1972).

The slope of this relationship was similar among the 3 years of study and significantly different from 1.00 in all of them. The small values that were obtained (b=0.64-0.72) indicate that longer pups had proportionately smaller axillary girth measurements than shorter pups. Assuming that girth was related in the same manner along the length of the pups' body, this suggests that longer pups also had a smaller surface-area-to-volume ratio than shorter pups. Keeping everything else constant, a reduction in this ratio would result in lower heat exchange rates with the environment (Eckert *et al.* 1988). Because standard length is closely related to age, older pups are expected to be better thermically insulated than younger pups.

The use of the residuals of the axillary girth-standard length regression was not more useful than the GL ratio in adjusting girth for length. Although the GL ratio is a frequently used index of body condition in pinnipeds (*e.g.* Pitcher 1986, Andersen *et al.* 1999), the relationship between the variables involved has never been studied to assess whether it could be used validly. The close relationship between the GL ratio and the residuals of the corresponding regression (r^2=0.98-0.99) suggests this index can be used validly to adjust axillary girth for length.

Of all the relationships that were studied, the one between sculp depth and standard length was the weakest. The regression coefficients were lower than 0.25 in 1997 and 1998, and lower than 0.11 in 1996. As was the case with axillary girth measurements, sculp depth is subject to considerable measurement errors. The mean range of repeated measurements on the same individual (3 per pup) on the same sites was 1.52 mm, or approximately 28% of the mean of the 3 measurements. Another source of error in the measurement of this variable was that, in large pups, the deepest part of the blubber could not be included in the skinfold measurement (personal observation). This error was not detected in smaller pups. The fact that large pups generally have a thicker and more rigid sculp than smaller ones may have contributed to this error.

Although body volume estimated from the geometric models underestimated the true volume of pups, they provided reliable relative indices of body volume. The values obtained from the models were closely related to the values obtained by water displacement. However, the slope of the regression of body volume, as calculated with the models, on standard length showed positive allometry, while it was isometric when the water displacement value was used. The reason for this discrepancy is not clear, but the allometric relationship between these variables is consistent with the analysis of the axillary girth-standard length relationship. If the surface-area-to-volume ratio decreases as length increases, as was concluded above, then the ratio of volume to any other linear variable should increase as well.

Sculp volume was more closely related to standard length than sculp depth, probably because it used the average of 3 measurements throughout the perimeter of the pup, as opposed to only one. The slope of this relationship suggests that an increase in length, and possibly body volume, results in a proportionally larger increase in sculp volume. This result is consistent with the previous suggestion that pups increase their thermal insulation as they grow. Pups not only reduce their surface-area-to-volume ratio, but also their surface becomes more insulated during this early growth phase.

The interannual differences in the slope of the body mass-body volume relationship may reflect methodological differences, rather than differences in the nature of the relationship *per se*. In 1996, the distance between girth measurements were interpolated from measurements taken in 1997. This resulted in lower accuracy of volume estimates in 1996. In addition, no interannual differences in the slope of this relationship were expected based on the analyses of other morphometric relationships.

Other researchers have used a body volume index to estimate body mass in phocids (Castellini and Kooyman 1990) and otariids (Castellini and Calkins 1993). Hammill *et al.* (1995) investigated the relationship between these variables to infer changes in body condition of harp seals. However, Castellini and Calkins (1993) pointed out that the body volume index they used (standard length × axillary girth^2, which was also used by Hammill *et al.* 1995) is not adequate because it overestimated the true density of the animals. Castellini and Calkins (1993) forced the regression between these variables through the origin, under the premise that animals with zero volume should have zero body mass. Although this is a valid premise, the relationship between these variables may not be the same throughout the size range of any particular species.

Very little variation in body condition indices were associated to differences in relative sculp volume. This result suggests that they measure different physical characteristics of pups, which may not necessarily be related to body condition. The FCF index and the residuals from the regression of body mass on body volume provide information about the relative weight of individuals. The first index is a measure of the overall growth and development of internal organs, muscles and blubber with respect to the size of the pup, while the second index is a measure of the pup’s density. The residuals from the regression of body volume on standard length provide a measure of the “sphericity” of the pups, which may be related to their fatness.

Studies aimed at investigating the relationship between these indices and blubber depth measured directly on carcasses are needed to assess the value of these body condition indices.

The residuals from the regression of body mass on body volume had the lowest correlation with those from the sculp volume on standard length regression. However, the negative, though non-significant, relationship between these indices was expected, as denser pups should have lower relative blubber content. Keeping everything else constant, an increase in blubber content reduces the density of the body because fat is less dense than other components of the body.

Pitcher (1986) and Ryg *et al.* (1990) also found a weak relationship between the GL ratio and relative sculp depth or volume in harbour and ringed, harp, and grey seals, respectively. Beck *et al.* (1993) found that blubber depth divided by standard length predicted the percentage of body mass composed of blubber better than the GL ratio in harp seals. These relationships suggest that to adequately assess body condition in pinniped populations, it may be necessary to use an index of the relative content of blubber, and another of the relative muscular and skeletal mass of the body. The residuals of the regression of scup depth or volume on standard length could be used as a measure of relative blubber content. Likewise, the FCF index could be used as a measure of muscular and skeletal mass, in the absence of direct measurements.

The FCF index, the GL ratio, and the residuals from the regression of sculp depth on standard length were positively related to the age of pups in all years, except 1996. This suggests that pups were able to accumulate energy reserves, in addition to covering the needs of normal growth. The relationship between these indices and age was weak, but detectable in a period of approximately 40 days. Thus, when comparing such indices among pups, it is important that their ages are similar.

Annual and sexual variation in body condition

Some sex differences in morphometric relationships were expected based on the differences that were found in the univariate analyses. For instance, the similarity of sculp depth measurements at most sites among the sexes, although males were larger than females in all the other variables, suggested that females had a proportionately deeper or more voluminous sculp than males. The relationship between sculp depth and standard length in 1997 showed evidence of this suggestion. However, support for this view was most strongly provided by the sex differences in the relationships between body mass and standard length and body volume. Males were approximately 3.5% heavier than females of the same length in 1996 and 1998. This result is consistent with those obtained by Crawley and Wilson (1976), who found that male New Zealand fur seal pups were heavier, but not longer, than females of the same age. Trites (1991b) reached the same conclusion for northern fur seal fetuses. Male

California sea lion pups from the Gulf of California were also ~3% denser than females of the same age in 1996 and 1997. All this evidence supports the view that female otariid pups may have proportionately larger fat stores than male pups.

Direct analyses of body composition in Antarctic fur seal pups from South Georgia showed that females had larger lipid stores than males of the same size (Arnould *et al.* 1996a, pero lea respecto al lobo marino de Steller). However, Steller sea lion pups do not show such differences (Davis *et al.* 1996). If most of the total body lipids are stored as blubber (Arnould *et al.* 1996b), then females should have a proportionately deeper blubber layer than males. These arguments are consistent with the sex differences that were found in this study, but the mechanism whereby they may arise are not yet clear and appear to depend on the species. In Antarctic fur seals, male and female pups consume the same amount of milk, but whereas the former allocate more of this energy to muscular and skeletal growth, the latter allocate a greater proportion of milk energy to fat stores (Arnould *et al.* 1996a). In California sea lion pups from the Channel Islands, California, male pups consume more milk than females, although these differences disappeared when size was controlled for (Ono and Boness 1996). In addition, they showed that males have lower metabolic rates than females, even after controlling for size effects. Unfortunately, pup body composition was not determined.

The sex differences in body condition were no associated to differences in growth rates. Male pups grew faster than female pups in the Channel Islands of California (Ono and Boness 1996). Lunn *et al.* (1993) did not find any sex differences in growth rates among Antarctic fur seal pups in South Georgia. These studies highlight the importance of local environmental conditions, as well as interspecific factors, in determining intersexual differences in growth rates.

The study of differential maternal investment among the sexes has received considerable attention in pinnipeds (*eg.* Boyd and McCann 1989; Boness *et al.* 1991; Arnbom *et al.* 1993; Kretzmann *et al.* 1993), particularly in species with pronounced sexual dimorphism, such as otariids, where such differential investment is expected (Trivers and Willard 1973). Because reproductive success varies greatly among the sexes in pinnipeds (Stirling 1983; Boness 1991), the sex of the offspring should have an important effect on maternal fitness. Mothers should invest more in the sex whose reproductive succes is most variable, or, in the case of otariids and some phocids, in male offspring. However, this deduction is based on the assumption that maternal investment and future reproductive success of the offspring are closely related (for review of theory, read Frank 1990). The evidence for such relationship is scant (Baker and Fowler 1992; Baker *et al.* 1994), but the male reproductive success and body size appear appear to be related (McCann 1987; Boyd and Duck 1991). Recent evidence suggests that reproductive succes depends more on environmental conditions after weaning, than on maternal investment (Lunn and Arnould 1997; Ono and Boness 1996). In the Gulf of California, pups begin ingesting solid food (crustaceans) when they are about 8 months old (Aurioles-Gamboa 1988) and the body condition of pups during that stage is probably more indicative of their future reproductive success than when they are younger.

Pup body mass and axillary girth were larger in 1998 than in other years, even after adjusting for standard length. Body volume and sculp volume, on the other hand, did not vary between 1996 and 1997. No differences were found between 1997 and 1998 in the sculp depth-standard length relationship. Pups were heavier in 1997 than in 1996, even after controlling for standard length, which was not associated to a similar difference in axillary girth. These observations suggest that pups were in better nutritional condition in 1998 than in other years, which strengthens the evidence of no negative effects of El Niño on food availability for lactating females in the Gulf of California.

4.4 Pup body size and body condition differences among rookeries

Compared to the 4 pups that most probably died of starvation, pup morpometrics and the body condition of sea lion pups in the samples from the Gulf of California indicate that these pups were not suffering from any lack of nutrition during the study period. These observations suggest that the Gulf of California is, in general, a favorable environment for the growth and development of sea lion pups. Two of the strongest recorded EN events developed in 1982-83 and 1997-98, but they did not result in any negative effect on pup production and growth or body condition (Aurioles and Le Boeuf 1991; this study). The strong tidal mixing in the northern gulf buffered the negative effects of the 1982-83 EN (Santamaría-del-Ángel *et al.* 1994). In contrast, marine productivity at similar latitudes outside the gulf depends on the coastal upwelling created by the trade winds and the California current. The weakening of such upwelling system in the Pacific Ocean lead to a reduction in primary productivity and a shift in the distribution of many consumers in the 1982-83 EN (Arntz *et al.* 1991).

Differences in body size and condition among Gulf of California rookeries were small and gradual. Relatively large interannual variations were evident; for instance, whereas pups from San Pedro Mártir were among the largest and in best body condition in 1996, they were of average size in 1997. However, differences in body condition among some rookeries remained constant throughout the study period. Most notably, pups from Machos were among the largest and in best body condition every year, although this was not evident in the principal components analysis in 1998. In the latter case, the analysis may have been affected by the small number of rookeries that were studied that year, causing differences among rookeries to be more easily detected (*i.e.* greater power). These consistent differences suggest that the quality of the habitat of sea lions varies geographically in the Gulf of California. Although the two body condition indices that were used were correlated, they were not adequate for predicting one another. This indicates that both indices are helpful in determining the body the relative growth and extent of energy reserves in pups.

Although there is a clear geographic pattern in sea lion pup body condition in the Gulf of California, such pattern can only be explained by a study addressing, simultaneously, all the factors that influence the energy budget of lactating females and pups. However, some insight may be gained by taking a subsample of the data on the relative importance of prey items obtained from 8 colonies located in the midriff island region by García-Rodríguez (1999), and comparing them with the fat percent content in them. The data from June and September 1995 from that study represent such a subsample, as they include the breeding season. Of course, estimations of fat content are only available for some species and for other locations.

In spite of this limitation, these data could be used to compare Machos and Rasito, which were the rookeries that showed the most pronounced and consistent differences in pup body size and condition throughout the study. Animals from both rookeries share the Pacific sardine (*Sardinops caeruleus*) and the chub mackerel (*Scomber japonicus*), as important prey items in their diet (Table 14). The importance of these species in the diet of sea lions appear to be slightly larger in Machos than in Rasito, and this difference is more pronounced when data from other months are included in the analysis (García-Rodríguez 1999). Both species are rich in fat, so, if everything else remains constant, pups from Machos are expected to be fatter than those from Rasito. However, hake (*Merluccius sp.*) and largehead hairtail (*Trichiurus lepturus*), which are also important prey items in Machos but not in Rasito, are poor in fat content. In addition, Pacific jack mackerel (*Trachurus symmetricus*), which is an important prey item in Rasito but not in Machos, is rich in fat content. Thus, there is no obvious relationship between pup body condition and the relative fat content of important prey species consumed by their mothers. This suggests that other factors affecting the energy budget of animals, such as the size and behaviour of prey, do not remain constant. Furthermore, the high diversity of the diet of animals from Rasito may indicate that their foraging efficiency is lower, compared to places where diet is less diverse, because they have to spend more energy in search and pursuit of small schools of fish. In contrast, females from Machos, which feed almost exclusively on sardine, rely heavily on the availability of few, though highly abundant and densely aggregated, prey items (Aurioles-Gamboa 1999). Data on dive pattern and effort, as well as on foraging locations and diet, are needed to clarify this issue (Boyd 1996a; Gentry 1998).

Table 14. Relative importance (%) of the most common sea lion prey found at seven rookeries of the midriff region of the Gulf of California during June and September 1995 (from García-Rodríguez 1999), and each of these prey species' fat content (%) (based on data from different areas of the Pacific Ocean). Fat content data are from Bykov (1983), except where noted.

Species	Group (Family)	% Fat	Rookery[*]						
		content	MAR	EST	RAS	MAC	CAN	GRA	LOB
Cetengraulis mysticetus	Fish (*Engraulidae*)	2.4							32.7
CRANC1 (no ident.)	Cephalopoda (*Enoploteuthidae*)	n.d.	27.3	16.9					
Engraulis mordax	Fish (*Engraulidae*)	6.8	29.7					49.3	
Merluccius sp.	Fish (*Merluccidae*)	1.7				15.4			
MYCTG (no ident.)	Fish (*Myctophidae*)	n.d.			16.4				
Octopus sp.	Cephalopoda (*Octopodidae*)	0.8[1]			11.5				
Peprilus snyderi	Fish (*Stromateidae*)	7.2							23.5
Pontinus sp.	Fish (*Scorpaenidae*)	n.d.			11.5				
Porichthys sp.	Fish (*Batrachoididae*)	n.d.	11.2		26.2		41.1	18.2	10.3
Sardinops caeruleus	Fish (*Clupeidae*)	8.02		22.1	40.1	42.6			
Scomber japonicus	Fish (*Scombridae*)	5.3[2]			13.8	19.0			
Sebastes macdonaldi	Fish (*Scorpaenidae*)	1.2[†]	10.4						
SPM0695-1 (no ident.)	Fish (*Myctophidae*)	n.d.	19.8	11.8			17.6		
Trachurus symmetricus	Fish (*Carangidae*)	6.3[3]			22.0				
Trichiurus lepturus	Fish (*Trichiudidae*)	1.0[‡]		24.9		11.7	30.2	46.1	26.5

Note: Only those species with a relative importance index higher than 10% in the diet of sea lion were included (García-Rodríguez 1999). If a prey item had a relative importance index higher than 10% in both months, the values were averaged, otherwise only the higher value is presented. Blank cells indicate that the prey item had a relative importance indes lower than 10% in both months; n.d.=no data. [*] The abbreviations for the rookeries correspond to those shown in Table 1. [1] Watt and Merril (1963), [2] Sidwell *et al.* (1974), [3] Frimodt (1995), [†] *Sebastes sp.*, Sidwell *et al.* (1974) [‡] *Trichiurus nitens*, Bykov (1983).

Other factors that may be responsible for the differences in pup body size and condition among Machos and Rasito are the characteristics of the terrestrial habitat and the density of animals in the foraging areas. Rasito is a small islet (<200 m long), which probably cannot sustain more than the ~215 that currently occupy it. This place lacks any shady areas, such as small caves or large boulders, where pups are frequently found resting elsewhere and that may help pups to thermoregulate during the summer. Furthermore, there are no beaches with gentle slopes in Rasito, so it is not common to observe pups playing in shallow water. In contrast, Machos is a rookery backed by tall cliffs, where there are numerous coves and boulders that provide plenty of shade. Most beaches there have gentle slopes and tide pools, where pups are frequently found playing.

Lactating females from Rasito and Machos may feed in different areas and animal densities in those areas may differ. Rasito, San Esteban, and Roca Blanca had pups that were among the smallest and in worst body condition of all pups studied. These rookeries are close to each other (<40 km) and represent about 5,000 animals feeding within a 60 km^2 radius. The proximity of these rookeries to each other and the similarity in the diet of sea lions among them (García-Rodríguez 1999) indicates there is some potential for competitions among these animals. Offspring body size and condition have been shown to vary with animal density in several populations of mammals, including pinnipeds (Fowler 1987). Steller sea lion pups born in an area of low density were heavier than those born elsewhere (Merrick *et al.* 1995). The GL ratio of the pups born in these areas was also higher than that of pups born in areas or higher density (Brandon *et al.* 1996). Consistent with these changes, foraging trips of lactating females were shorter in duration in those populations with lower density (Davis *et al.* 1996). Foraging trips of lactating females in the Gulf of California do not appear to vary greatly; in 1985, Heath (1989) estimated they were, on average, 1.9 days long in Cantiles (Ángel de la Guarda Island), while García-Aguilar and Aurioles-Gamboa (1997) found they were 1.6 days long in Los Islotes (bay of La Paz). However, pup body size and condition of pups from these colonies did not differ greatly, compared with differences found among pups from Rasito and Machos. Thus, the greatest differences in foraging trip duration are expected among females from the latter pair of rookeries (but read Boyd *et al.* 1991). Unfortunately, this kind of data are not yet available, but they could be easily obtained in the future.

4.5 Relationship between indices of food abundance

The time series on indices of food abundance at two different rookeries of the Gulf of California offered the opportunity to how this variable may affect a colony or population of sea lions. The analysis of these time series indicated that population condition was not the same at these rookeries. This could not be determined by analyzing one year in particular, and is consistent with the arguments set forth in Hanks (1981), who suggested that, by simultaneously monitoring population dynamics and indices of physiological indices at the individual level, one can adequately assess the condition of a population.

Cantiles showed signs of density-dependence in pup body condition and the food intake rate of the colony. Pup body condition was negatively related to pup production, suggesting the amount of energy available per lactating female was higher during times when natality was lower. This type of relationship has been described for several species of mammals (Robinson and Redford 1986; Leberg and Smith 1993; Gaillard *et al.* 1997), including the northern fur seal (Fowler 1990), and is thought to reflect the intensity of intraspecific competition for available resources, usually food. I expected pup production changes to lag behind food intake rate by the colony, as has been shown for Antarctic fur seals (Lunn *et al.* 1994), based on the idea that, during years of “normal” food availability, most adult females would be in good condition, a higher proportion of females would implant their embryos, and a fewer percentage of pups would be aborted, resulting in a large pup production the following year (Boyd 1984). The absence of such an effect may have been a bias in the food intake rates caused by the number of subadult males counted in any given year, because they exhibit large intra-annual movements (García-Rodríguez 1999), leading to errors in the estimation of animal abundance in a rookery. Because subadult males are most consistently found in the rookeries during the winter, monitoring changes in their numbers throughout several years in association with changes in pup production during the summer should provide a better sampling protocol to study the relationship between food abundance and population condition in the future.

In most large mammals, populations tend to show density-dependent effects when they are at or close to the carrying capacity of their environment (Fowler 1981). Thus, this may be the case with Cantiles, and consistent with this view, Aurioles-Gamboa (1999) found that changes in the commercial catch of Pacific sardine, an important prey species for sea lions from Cantiles, closely followed those of pup production in this rookery during the same period, which included the data analyzed in this study. Changes in SST may have indirectly affected the availability of sardine, as suggested by the relationship between SST and pup production. Supporting this suggestion, Pacific anchoveta, an important prey species for sea lions from Cantiles during the winter, prefer to spawn in waters 15-17°C of temperature in the Gulf of California (Green-Ruiz and Hinojosa-Corona 1997).

Los Islotes, on the other hand, did not show any signs of density-dependence in any of the variables analyzed. However, these variables, as a whole, indicated an improvement in habitat quality from the early 80s to the late 90s, associated with an increase in SST. The growth of the population during this period has been remarkable; pup production increased by 100% and the breeding sites now occupy most of the rookery (Aurioles-Gamboa *et al.* 1995). The negative trend in pup body condition and food intake rate between 1996 and 1998 is intriguing, and it was not associated to any significant change in pup production.

The diet of sea lions differ markedly between both of these rookeries; whereas, midshipman species (*Porichthys spp.*), largehead hairtail (*Trichiurus lepturus*) and Pacific sardine (*Sardinops caeruleus*) are the most important prey in Cantiles (García-Rodríguez 1999), Eastern Pacific flagfin (*Aulopus bajacali*), bigeye bass (*Pronotogrammus eos*) and a midshipman species (*Porichthys notatus*) are most commonly preyed upon by sea lions in Los Islotes (Aurioles *et al.* 1984; García-Rodríguez 1995). The way in which SST affects populations of these fishes may be very different because they have different habits. Fish species consumed by sea lions in Cantiles are pelagic, while those consumed in Los Islotes are benthic. Understanding how the physical characteristics of the environment affect the reproduction, distribution, and trophic relationships in these species should prove useful in explaining the different trajectories of Los Islotes *vs.* Cantiles. As shown here, SST cannot be used to infer changes in food availability for sea lions very easily, since it is only one of the many physical characteristics of the environment that affect it. Akçakaya (1992) showed that cyclic fluctuations in several populations of mammals may be explained by predator-prey or herbivore-plant interactions. Thus, studying such relationships is important to understanding how these interactions affect the energy balance in top predators such as sea lions.

5 CONCLUSIONS

1. The interannual variation in pup body size was a function of pup age. There was evidence that the yearly period of maximum birth frequency was delayed in 1998 compared to the previous 2 years. Pup body size was similar to that reported for pups of similar age from rookeries in the Pacific Ocean.
2. Sculp depth was larger than that reported for northern fur seal pups of similar age. Sculp represented approximately 25% of total body mass. The distribution of blubber followed the external profile of pups; the blubber layer was thickest around one half the length of the pup. The site of maximum sculp depth variability was over the sternum, where blubber depth is traditionally measured. Therefore, this site is the most appropriate one for measuring changes in blubber depth.
3. Male pups were 20% heavier and 7% larger in their linear dimensions than female pups. There were no sex differences in growth rates during 4 years in Los Islotes, bay of La Paz; pups grew at 0.150 $kg \cdot d^{-1}$ and 0.20-0.30 $cm \cdot d^{-1}$. Additionally, males were on average 3% denser than females, particularly during older ages. Part of this difference was a result of the larger relative blubber stores in females.
4. The body mass-standard length relationship was similar to that reported for other pinnipeds, but varies with pup age. There was isometry in this relationship in young (<30 d old) pups and allometry in older pups.
5. The Fulton condition factor was adequate for comparing the body mass of pups of different length only in pups younger than 2 months. Otherwise, the empirically estimated exponent of the relationship (b=2.81) was more appropriate.
6. The Fulton condition factor, girth-to-lenth ratio and the residuals from morphometric relationships did not adequately predict relative sculp depth or volume. Therefore, it is necessary to use two indices of body condition: one to estimate the relative growth and development of muscles and bone, and another one to estimate the relative amount of blubber. The Fulton condition factor was useful for the first purpose, while the residuals from the sculp depth or volume on standard length regression was useful for the second purpose. However, the latter index should be used with a more reliable measure of blubber depth or volume than skinfold measurements, particularly in old (>2 months) pups.
7. The relative blubber content and the axillary-to-length ratio increased with the pups' age, which suggests that they increased their thermal insulation. The Fulton condition factor, in contrast, varied considerably with the pups' age, concomitant with changes in the body

mass-standard length relationship.

8. Both pup body size and body condition varied considerably among years and rookeries in the Gulf of California. In spite of this, there were major consistencies during the two years of study on a spatial scale. Pups from Machos were consistently among the largest and in best body condition during the study period, while those from Rasito, San Esteban, and Roca Blanca were among the smallest and in worst body condition during the same period. Body size and body condition differences were determined mainly by pup body mass and Fulton condition factor and relative sculp depth or volume, respectively. Factors such as prey abundance, behaviour, and energy content in the vicinity of the rookeries, the physiography of the terrestrial habitat, and the density of animals in the foraging grounds were identified as the main variables responsible for the spatial pattern in pup body size and body condition.

9. The study of changes in animal density, pup production and body condition, and estimated food intake rates at two colonies provided a broad overview of population condition. The monitoring of these indices during the last 19 years in Cantiles, a rookery located in the northern Gulf of California, suggested that the colony fluctuated close to its carrying capacity because pup body condition and food intake rate were density-dependent. In Los Islotes, bay of La Paz (southern gulf), the carrying capacity appeared to have increased during the late 90s compared to the early 80s. Unlike Cantiles, this colony did not show density-dependence in any of the variables that were studied. Although sea surface temperature was not a good indicator of food abundance for sea lions, an understanding of the effects of physical characteristics of the environment on the ecology of prey species should provide useful insights into the changes in population condition in both of these rookeries.

RECOMMENDATIONS

1. Most of this study dealt with methods of estimation of pup body condition in sea lions through morphometric analyses. Unlike phocid pups, otariid pinniped pups develop their musculature, bones and blubber stores during their growth. The analyses presented here showed the importance of measuring body condition based on all these aspects of growth. Ideally, the measurement of body composition and its changes with growth would provide the most accurate and detailed assessment of body condition. In spite of the evidence of the usefulness of body mass as a predictor of body composition, I recommend performing experiments aimed at quantifying the relationship between these variables in California sea lions. Such experiments should involve obtaining indirect estimates of body composition and direct analyses of on carcasses.

2. Meanwhile, the Fulton condition factor may be used an overall indicator of relative pup body mass. This index has the advantage of being easily obtained while in the field, although this comes with a cost. The age differences in the slope of the body mass-standard length relationship, on which the index is based, suggest that the index should be used with caution. Further studies should be done to more accurately determine the nature of such differences. These studies should be carried out with marked pups of known age. Without this additional information, it is appropriate to use the Fulton condition factor only with pups older than 1 week and younger than 50 days of age. Otherwise, the empirically-determined slope of the body mass-standard length relationship should be used instead of the exponent 3 in that index. If this is not possible, then the value 2.81 obtained from the combined data in this study could be used as an approximation.

3. I recommend obtaining additional data on sculp depth and weight measured directly on pup caracasses to develop a reliable index of relative blubber stores. Skinfold measurements are subject to considerable errors, so whenever this method is employed, the average of multiple measurements at the same site should be used. Skinfold measurements are not useful indicators of blubber depth in pups older than 3 months of age. Therefore, it is necessary to search for more accurate methods to estimate blubber depth.

NOTES

1. The effects of rookery of birth on pup standard length (cm), body mass (kg), and axillary girth (cm) in Cantiles, Granito, Machos, and Rasito from 1996 through 1998, were as follows:

Effect	Variable	Effect mean square	Error mean square	$F_{3,206}$	*P*
rookery	standard length	202.55	18.81	10.77	<0.001*
	body mass	78.62	4.12	19.083	<0.001*
	axillary girth	290.48	16.41	17.70	<0.001*
rookery x year	standard length	89.27	18.81	4.75	<0.001*
	body mass	11.63	4.12	2.82	0.012*
	axillary girth	47.89	16.41	2.92	0.009*

* Significant effect ($P<0.05$).

2. Mann-Whitney *U* tests for compararing morphometric measurements between pups with umbilical cord, $n=28$, and without it, $n=456$: $U=3\ 198.5$, $P<0.001$ (body mass); $U=3\ 509.5$, $P<0.001$ (standard length); $U=3\ 962.5$, $P=0.002$ (sternal sculp depth). All these differences were significant.

3. The separation among rookeries in 1996 was significant when all discriminant functions in the analysis were kept: Wilks' Lambda=0.237, $P<0.001$, $n=128$. Two of these functions, however, contributed significantly to the discrimination among rookeries ($\chi^2=172.85$, and $\chi^2=60.34$, $P<0.001$, first and second functions, respectively). Taken together, both functions explained 91% of all the variance in the sample.

4. The standard coefficients for each variable and discriminant function in 1996 were as follows:

Variable	Function 1	Function 2
Standard length	-0.87	0.38
Body mass	2.53	-0.63
Girth 2	-1.12	0.046
Girth 3	-0.68	0.16
Girth 4	-0.40	0.81
Sum of sculp depth measurements	0.44	0.43

5. The separation among the subsample of rookeries in 1997 was significant when all discriminant functions in the analysis were kept: Wilks' Lambda=0.267, $P<0.001$, $n=164$. Three of these functions contributed significantly to the discrimination among rookeries ($\chi^2=205.07$, 106.48, and 50.75, $P<0.001$, first, second, and third functions, respectively) and together explained 92% of all the variance in the sample.

6. The standard coefficients for each variable and discriminant function in 1997 (8 of the 11 rookeries studied) were as follows:

Variable	Function 1	Function 2	Function 3
Standard length	-0.32	-1.87	-0.13
Body mass	2.61	2.78	0.91
Girth 2	-0.6	-0.94	-0.07
Girth 3	-1.33	-0.32	1.13
Girth 4	-0.68	0.13	-0.44
Sum of sculp depth measurements	-0.58	0.28	-1.17

7. The separation among rookeries in 1997 was significant when all discriminant functions in the analysis were kept: Wilks' Lambda=0.193, $P<0.001$, $n=236$. In this case, there were 5 significant discriminant functions, but only 3 were kept ($\chi^2=371.09$, 237.79, and 154.80, $P<0.001$, first, second, and third functions, respectively). The other 2 functions were not kept because they did not change the relative position of the rookeries or the interpretations of the differences. The 3 functions together explained 82% of all the variance in the sample.

8. The standard coefficients for each variable and discriminant function in 1997 (all 11 rookeries studied) were as follows:

Variable	Function 1	Function 2	Function 3
Standard length	-0.48	-0.50	1.08
Body mass	2.79	1.96	-1.77
Girth 1	-0.56	0.61	0.86
Girth 2	-0.30	-0.76	0.95
Girth 3	-0.87	-0.98	-0.11
Girth 4	-0.44	-0.70	-0.22
Girth 5	0.10	-0.86	-0.57
Sum of sculp depth measurements	-1.17	0.84	-0.30

9. The effects of sex (male and female) on the log body mass (kg) - log standard length (cm) relationship during the 3 years of study were:

Year	Source	*df*	Mean square	*F*	*P*
			Slope		
1996	Effect	1	0.003	1.81	0.18
	Error	173	0.002		
1997	Effect	1	<0.001	0.12	0.73
	Error	268	0.001		
1998	Effect	1	<0.001	0.019	0.89
	Error	156	0.001		

Year	Source	*df*	Mean square	*F*	*P*
			Elevation		
1996	Effect	1	0.011	6.19	0.014*
	Error	174	0.002		
1997	Effect	1	<0.001	0.10	0.75
	Error	269	0.001		
1998	Effect	1	0.006	4.46	0.036*
	Error	157	0.001		

* Significant effect ($P<0.05$).

10. The effects of year (1996-1998) and sex (male and female) on the log body mass (kg) - log standard length (cm) relationship were:

Effect	Source	*df*	Mean square	*F*	*P*
			Slope		
Year	Effect	2	0.001	0.86	0.42
	Error	600	0.001		
Sex	Effect	1	0.001	0.53	0.45
	Error	601	0.001		
Year x sex	Effect	5	0.001	0.80	0.55
	Error	597	0.001		
			Elevation		
Year	Effect	2	0.03	20.26	<0.001*
	Error	602	0.001		
Sex	Effect	1	0.014	9.35	0.002*
	Error	602	0.001		
Year x sex	Effect	2	0.002	1.50	0.23
	Error	602	0.001		

* Significant effect ($P<0.05$).

11. Comparison of the slopes of various morphometric relationships: body mass (kg) (*BM*), standard length (cm) (*SL*), axillary girth (cm) (*AG*), sternal sculp depth (mm) (*SD3*), body volume (l) (*BV*), and sculp volume (l) (*SV*). The slopes correspond to the regressions with both sexes combined, except were noted:

Regression	Year		Slope	Theoretical isometry value	Two tailed *t-Student*	*df*	*P*
log *BM* on log *SL*	1996		2.95	3.00	-0.45	176	0.65
	1997		2.96	3.00	-0.50	271	0.62
	1998		2.83	3.00	-1.70	159	0.091
	1996-98		2.84	3.00	-3.20	608	0.001*
AG on *SL*	1996		0.72	1.00	-7.00	149	<0.001*
	1997		0.72	1.00	-9.33	270	<0.001*
	1998		0.64	1.00	-9.00	159	<0.001*
SD3 on *SL*	1996		0.08	1.00	-46.00	153	<0.001*
	1997	Males	0.18	1.00	-41.00	134	<0.001*
		Females	0.24	1.00	-38.00	142	<0.001*
	1998		0.16	1.00	-42.00	160	<0.001*
log *BV*[1] on log *SL*	1996-97		3.22	3.00	3.14	428	0.002*
log *BV*[2] on log *SL*	1996-97		3.20	3.00	2.22	275	0.027*
log *SV*[1] on log *SL*	1996-97		3.69	3.00	6.27	428	<0.001*
log *SV*[2] on log *SL*	1996-97		3.74	3.00	4.93	274	<0.001*
BM on *BV*[1]	1996		1.01	1.00	0.25	154	0.80
BM on *BV*[1]	1997		1.12	1.00	6.00	273	<0.001
BM on *BV*[2]	1997		1.03	1.00	1.50	273	0.13

* Significant difference ($P<0.05$). [1 and 2] Four and six component geometric models, respectively.

12. The effects of sex (male and female) on the axillary girth (cm) - standard length (cm) relationship during the 3 years of study were:

Year	Source	*df*	Mean square	*F*	*P*
			Slope		
1996	Effect	1	0.468	0.07	0.79
	Error	146	6.66		
1997	Effect	1	1.60	0.31	0.58
	Error	267	5.12		
1998	Effect	1	10.21	1.84	0.18
	Error	156	5.57		
			Elevation		
1996	Effect	1	5.60	0.85	0.36
	Error	147	6.61		
1997	Effect	1	0.60	0.12	0.73
	Error	268	5.11		

Year	Source	*df*	Mean square	*F*	*P*
1998	Effect	1	1.46	0.26	0.61
	Error	157	5.60		

13. The effects of year (1996-1998) and sex (male and female) on the axillary girth (cm) - standard length (cm) relationship were:

Effect	Source	*df*	Mean square	*F*	*P*
			Slope		
Year	Effect	2	8.32	1.48	0.23
	Error	572	5.63		
Sex	Effect	1	8.60	1.53	0.22
	Error	573	5.63		
Year x sex	Effect	5	5.79	1.027	0.4
	Error	569	5.64		
			Elevation		
Year	Effect	2	486.56	86.32	<0.001*
	Error	574	5.64		
Sex	Effect	1	3.24	0.58	0.45
	Error	574	5.64		
Year x sex	Effect	2	2.47	0.44	0.65
	Error	574	5.64		

* Significant effect (*P*<0.05).

14. The effects of sex (male and female) on the sternal sculp depth (mm) - standard length (cm) relationship during the 3 years of study were:

Year	Source	*df*	Mean square	*F*	*P*
			Slope		
1996	Effect	1	0.83	0.69	0.41
	Error	150	1.20		
1997	Effect	1	5.11	4.13	0.043*
	Error	272	1.24		
1998	Effect	1	3.066	2.63	0.11
	Error	157	1.17		
			Elevation		
1996	Effect	1	0.028	0.023	0.88
	Error	151	1.20		

Year	Source	*df*	Mean square	*F*	*P*
1997	Effect	1	24.31	19.39	<0.001*
	Error	273	1.25		
1998	Effect	1	0.75	0.64	0.43
	Error	158	1.18		

* Significant effect (*P*<0.05).

15. The effects of year (1996-1998) and sex (male and female) on the sternal sculp depth (mm) - standard length (cm) relationship were:

Effect	Source	*df*	Mean square	*F*	*P*
			Slope		
Year	Effect	1	2.76	2.25	0.13
	Error	431	1.23		
Sex	Effect	1	0.20	0.16	0.69
	Error	431	1.23		
Year x sex	Effect	3	3.65	3.007	0.030*
	Error	429	1.21		
			Elevation		
Year	Effect	1	2.12	1.72	0.19
	Error	432	1.23		
Sex	Effect	1	14.42	11.73	0.001*
	Error	432	1.23		
Year x sex	Efecto	1	3.790	3.082	0.08
	Error	432	1.23		

* Significant effect (*P*<0.05).

16. The effects of sex (male and female) on the log body volume (4-component model) (l) - log standard length (cm) relationship during the study period were:

Year	Source	*df*	Mean square	*F*	*P*
			Slope		
1996	Effect	1	<0.001	0.016	0.90
	Error	150	0.003		
1997	Effect	1	<0.001	0.027	0.87
	Error	271	0.002		

Year	Source	*df*	Mean square	*F*	*P*
			Elevation		
1996	Effect	1	0.002	0.78	0.38
	Error	151	0.003		
1997	Effect	1	<0.001	0.04	0.84
	Error	272	0.002		

17. The effects of year (1996-1997) and sex (male and female) on the log body volume (4-component model) (l) - log standard length (cm) relationship were:

Efecto	Source	*df*	Mean square	*F*	*P*
			Slope		
Year	Effect	1	<0.001	0.044	0.83
	Error	423	0.002		
Sex	Effect	1	<0.001	0.036	0.85
	Error	423	0.002		
Year x sex	Effect	3	<0.001	0.029	0.99
	Error	421	0.002		
			Elevation		
Year	Effect	1	0.001	0.48	0.49
	Error	424	0.002		
Sex	Effect	1	0.002	0.70	0.40
	Error	424	0.002		
Year x sex	Effect	1	0.001	0.30	0.58
	Error	424	0.002		

18. The effect of sex (male and female) on the log body volume (water displacement method) (l) - log standard length (cm) relationship in 1997 was: $F_{1,270}$=0.069, P>0.1 (slope), and $F_{1,271}$=0.42, P>0.1 (elevation).

19. The effect of sex (male and female) on the log body volume (6-component model) (l) - log standard length (cm) relationship in 1997 was: $F_{1,272}$=0.046, P>0.1 (slope), and $F_{1,273}$=0.30 (elevation).

20. The effects of sex (male and female) on the log sculp volume (4-component model) (l) - log standard length (cm) relationship during the study period was:

Year	Source	*df*	Mean square	*F*	*P*
			Slope		
1996	Effect	1	0.003	0.55	0.46
	Error	151	0.005		
1997	Effect	1	<0.001	0.001	0.98
	Error	270	0.006		
			Elevation		
1996	Effect	1	<0.001	0.049	0.82
	Error	152	0.005		
1997	Effect	1	0.009	1.54	0.22
	Error	271	0.006		

21. The effects of year (1996-1997) and sex (male and female) on the log sculp volume (4-component model) (l) - log standard length (cm) relationship were:

Effect	Source	*df*	Mean square	*F*	*P*
			Slope		
Year	Effect	1	0.003	0.51	0.48
	Error	423	0.006		
Sex	Effect	1	0.002	0.28	0.60
	Error	423	0.006		
Year x sex	Effect	3	0.002	0.35	0.79
	Error	421	0.006		
			Elevation		
Year	Effect	1	0.000	0.077	0.78
	Error	424	0.006		
Sex	Effect	1	0.005	0.92	0.34
	Error	424	0.006		
Year x sex	Effect	1	0.001	0.14	0.71
	Error	424	0.006		

22. The effect of sex (male and female) on the log sculp volume (6-component model) (l) - log standard length (cm) relationship in 1997 was: $F_{1,271}$=0.32, P>0.1 (slope), and $F_{1,272}$=2.14, P=0.15 (elevation).

23. The effect of sex (male and female) on the body mass (kg) - body volume (4-component model) (l) relationship during the study period was:

Year	Source	*df*	Mean square	*F*	*P*
			Slope		
1996	Effect	1	1.80	1.48	0.23
	Error	151	1.21		
1997	Effect	1	<0.001	0.001	0.98
	Error	270	0.26		
			Elevation		
1996	Effect	1	7.40	6.091	0.015*
	Error	152	1.22		
1997	Effect	1	3.41	13.23	<0.001*
	Error	271	0.258		

* Significant effect ($P<0.05$).

24. The effect of sex (male and female) on the body mass (kg) - body volume (6-component model) (l) relationship in 1997, fue: $F_{1,270}$=0.20, $P>0.1$ (slope), and $F_{1,271}$=10.21, $P=0.002$ (elevation).

25. The effects of year (1996-1997) and sex (male and female) on the body mass (kg) - body volume (4-component model) (l) were: $F_{1,423}$=6.99, $P=0.009$ (year); $F_{1,423}$=2.30, $P=0.13$ (sex), and $F_{1,421}$=3.33, $P=0.02$ (year x sex).

26. The effect of sex (male and female) on the body mass (kg) - body volume (water displacement method) (l) relationship in 1997 was: $F_{1,267}$=3.77, $P=0.05$ (slope), and $F_{1,268}$=8.32, $P=0.004$ (elevation).

27. The effect of rookery of birth on the Fulton condition factor (FCF) and the residuals from the regressions of sculp volume (l) (SVR) or sternal sculp depth (mm) (SDR) on standard length during the period of study was:

Year	Effect *df*	Effect mean square	Error *df*	Error mean square	*F*	*P*
			FCF			
1996	8	0.224	170	0.0443	5.047	<0.001*
1997	10	0.138	265	0.0353	3.91	<0.001*
1998	5	0.406	155	0.0344	11.81	<0.001*
			SVR			
1996^1	7	0.093	147	0.0393	2.36	0.026*
1997^1	10	0.152	264	0.0174	8.74	<0.0001
1997^2	10	0.246	263	0.02	12.51	<0.0001

Year	Effect *df*	Effect mean square	Error *df*	Error mean square	*F*	*P*
			SDR			
1996	7	2.210	147	1.246	1.77	0.097
1997	10	9.793	225	0.938	10.44	<0.0001
1998	5	3.672	155	1.09	3.37	0.0064*

[1, 2] 4- and 6-component geometric models, respectively.

28. The effects of year (*n*=9, and *n*=19; in 1997 and 1998, respectively) and sex (*n*=23, and *n*=5; males and females, respectively) on standard length (cm), axillary girth (cm), and sternal sculp depth (mm) growth were:

Variable	*Mann-Whitney U*	*P*
Sex effect (males, females)		
Standard length	43	>0.1
Axillary girth	20.5	0.026*
Sculp depth	51	>0.1
Year effect		
Standard length	81	>0.1
Axillary girth	78	>0.1
Sculp depth	72	>0.1

* Significant effect (*P*<0.05).

The effects of year (*n*=26, *n*=7, n=9, *n*=19; 1994, and 1996-98, respectively) and sex (*n*=44, *n*=17; males and females, respectively) on body mass (kg) growth were: *H* de Kruskal-Wallis=0.25, *P*>0.1 (year); Mann-Whitney *U*=284.5, *P*>0.1 (sex).

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