



Body growth in Hawaiian monk seals

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ABSTRACT

Body length and axillary girth measurements of more than 600 free-ranging Hawaiian monk seals from 1 to 20 yr old were analyzed. Comparison of fitted von Bertalanffy growth models confirmed there is no evidence of sexual dimorphism in this species. Substantial differences in growth patterns were detected among seven subpopulations representing the species entire geographic range. The age at which seals would be expected to attain a reference length of 180 cm ranged from just over 3 yr up to almost 7 yr at the various sites. Subpopulations exhibiting slower growth have previously been found to also exhibit lower age-specific reproductive rates. Differences in growth of seals among sites likely indicate varying environmental conditions determining growth during the time periods represented in the sampled data.

Key words: Hawaiian monk seal, *Monachus schauinslandi*, body growth, length, girth, von Bertalanffy.

The Hawaiian monk seal (*Monachus schauinslandi*) is both one of the most endangered and well-studied pinniped species. Approximately 1,200 Hawaiian monk seals remain (Carretta *et al.*, in press). Among pinniped species, only its congener, the Mediterranean monk seal (*Monachus monachus*), is more rare, with fewer than 500 seals remaining (Aguilar and Lowry 2008). Long-term research on the Hawaiian monk seal has characterized population dynamics, foraging behavior, and health status throughout most of the species range (*e.g.*, Reif *et al.* 2004; Stewart *et al.* 2006; Baker and Thompson 2007; Harting *et al.* 2007; Cahoon 2011; Lopez *et al.* 2012; Carretta *et al.*, in press). Notwithstanding these and many publications on various aspects of the species' ecology and conservation, basic growth patterns of Hawaiian monk seals have yet to be well-described.

Several studies have focused on early growth in monk seals. Wirtz (1968) measured the mass of pups from birth to weaning. To avoid disruption of nursing and separation of dependent pups from their mothers, subsequent research has only involved capturing monk seals after weaning. Craig and Ragen (1999) compared length, girth, and mass of monk seals from weaning to age 2 yr at two subpopulations. Baker and Johanos (2004) extended the analysis of weaned pup measurements to the species

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entire range. Two additional studies have explored ecological factors associated with size and weaning and juvenile survival (Antonelis *et al.* 2003, Baker 2008).

McLaren's (1993) study on growth in pinnipeds included a length growth curve fitted to a sparse set ($n = 9$) of Hawaiian monk seal measurements gleaned from the available literature. Subsequently, sufficient samples of length and girth measurements have accrued to characterize growth from age 1 yr through adulthood. We assess whether there is evidence for sexual dimorphism in the species and also evaluate variability in growth at subpopulations throughout the species' range.

METHODS

Data Collection

Hawaiian monk seals were measured at all times of year when captured for a variety of research and management purposes, such as tagging, health assessment, attachment of telemetry devices, removal of entangling marine debris and fish hooks, and translocation (Henderson 2001, Baker and Johanos 2002, Baker *et al.* 2011). Seals were measured from 1984 to 2011 at seven subpopulations; six in the Northwestern Hawaiian Islands (NWHI), plus the main Hawaiian Islands (MHI, see Fig. 1). Severely compromised (emaciated or wounded) seals, as well as obviously pregnant females, were typically excluded from research handling. As a precaution, captures were also avoided during and near the time when animals were molting, a period of possible physiological stress. In general, other than exclusion of those in the worst body condition (emaciation), there was no systematic size selection.

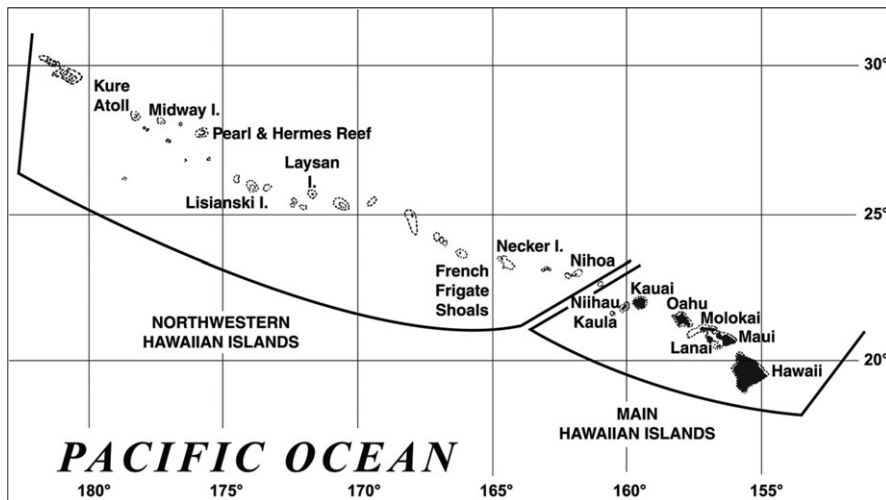


Figure 1. The Hawaiian Archipelago with primary subpopulations of Hawaiian monk seals indicated. In the Northwestern Hawaiian Island subpopulations, body growth was analyzed for six subpopulations: Kure Atoll, Midway Atoll, Pearl and Hermes Reef, Lisianski Island, Laysan Island, and French Frigate Shoals. Data from all main Hawaiian Islands sites were pooled for analysis.

Seals were typically captured in a hoop or stretcher-type net, and often sedated with intravenous diazepam depending on the primary goal of the capture and the size of the individual. Because of their manageable size, only approximately 20% of 1 and 2 yr old seals were sedated when measured, compared to over 50% of 3 yr olds, and over 90% of seals age 4 yr and older. Dorsal straight length (from tip of nose to tip of tail) and axillary girth (just posterior to the insertion of the foreflippers on inhalation) were measured.

Data Analysis

We analyzed measurements of live, free-ranging monk seals. Dead seals were excluded as were measurements of seals brought into captivity for rehabilitation or permanent care during the calendar years when held captive. When more than one measurement was available for an individual in a given year, we selected the most complete set of measurements (*i.e.*, simultaneous length and girth) and, secondarily, the measurements taken closest to 30 June (mid-year). Measurements from different dates in the same year were combined if, for example, length was taken on one date and girth on another. Repeat measurements of the same seal in different years were treated as independent. Integer ages were assigned and incremented on 1 January.

We further limited our analysis to seals whose ages were known from marking with flipper tags in the birth year. Measurements from seals aged 1 yr and older were analyzed, thereby excluding immediate postweaning measurements, to best characterize lifetime growth following the period of maternal care.

Consistent with McLaren's (1993) summary of growth in pinnipeds, we used the generalized von Bertalanffy function (Schnute 1981) for growth in length:

$$L_x = L_\infty(1 - e^{a(x-x_0)})^b$$

where L_x is length at age x , L_∞ is the asymptote, a determines the rate of approach to the asymptote and b determines the curvilinearity of that approach. The parameter x_0 is the time before birth when length equals zero. Rather than attempt to fit x_0 we instead assigned a fixed value. Johanos *et al.* (1994) estimated the mean time from mating until birth in Hawaiian monk seals to be 330 d, or 0.9 yr. However, many pinnipeds have delayed implantation and it is not known whether this occurs in Hawaiian monk seals. Any such delay would reduce x_0 below 0.9 yr. Consistent with McLaren (1993) we fixed x_0 at 0.73 (approximately 9 mo). This age-offset parameter has little effect on the lifetime growth curve when it is small relative to the life span. The same von Bertalanffy function was used to fit growth in axillary girth.

Curves were fitted using the nls (nonlinear least squares) function in R (R Development Core Team 2009). Typically, three parameters (L_∞ , a and b) were estimated. We evaluated the influence of sex and subpopulation by comparing the small sample Akaike information criterion (AIC_c) of competing models. Sample sizes were insufficient to evaluate temporal variability in growth; all years were combined in analyses. We used nlsBoot in the R package nlstools (Baty and Delignette-Muller 2011) to bootstrap (1,000 iterations) confidence intervals for fitted parameters and the predicted growth curves. For some data sets, convergence was not achieved despite multiple trials with varying starting parameters. In these cases, we fitted multiple curves changing the value of a fixed asymptote (L_∞) so that only a and b were estimated. This process continued, changing the value of L_∞ by 1 cm, until the model with the lowest residual sum of squares was obtained.

RESULTS

A total of 655 length and 632 girth measurements were recorded, approximately evenly represented by female (52%) and male (48%) seals. The sample distribution of measurements was uneven across subpopulations, years, and ages (from age 1 to 20 yr), with a high proportion of young seals and most seals measured at French Frigate Shoals and Laysan Island (Table 1, Fig. 2). Nearly all seals had been born at the same subpopulation where they were measured. For example, at all sites except Midway Atoll, only 0–4 seals measured had been born elsewhere. At Midway Atoll, in contrast, only 27 of 43 (63%) measured seals had been born there. Notably, only 1 of 10 seals older than age 7 yr measured at Midway had been born there. Eight measurements were from seals that had moved to Midway Atoll from Pearl and Hermes Reef, three were from Kure Atoll, and four were from seals that had been born at French Frigate Shoals, rehabilitated in captivity, and released at either Midway or Kure Atoll. Previously rehabilitated seals from French Frigate Shoals also accounted for one and two measurements, respectively, at Pearl and Hermes Reef and Kure Atoll.

A total of 399 seals were measured at just one age, and 115 seals were measured twice (at two ages), seven were measured three times, and one was measured four times. The majority of the repeat measurements involved young seals; 77% of the repeat measurements were at ages 2 and 3 yr. The rest were sprinkled among the older age classes. Laysan and French Frigate Shoals had the highest proportion of repeat length measurements (31% and 26%, respectively), whereas no repeat measurements occurred at Lisianski Island and Kure Atoll. To address potential influences of repeated measurements on results, we created a data set consisting of just one length measurement per individual seal (selected with a random number generator) and compared statistical results using these data to the full data set with repeated measures.

We did not find evidence that length growth patterns differed among male and female monk seals. Beyond age 3 yr, sex-specific sample sizes at individual subpopulations were insufficient (in many cases zero, see Table 1), so that all sites were pooled to evaluate sex differences in growth curves. A model with separate parameters for the sexes was less well supported (AIC_c increased by 3.7) relative to a model with one set of parameters for both sexes. Using the fully independent reduced data set (without repeat measures of individuals), the model with separate parameters for the sexes also had lower support (AIC_c increased by 2.6). A model with separate parameters for each of the seven subpopulations failed to converge, however, such a model did converge when the length data from French Frigate Shoals was excluded. This model was a much better fit than one with shared parameters for the six remaining subpopulations after French Frigate Shoals was excluded ($\Delta AIC_c = -53.624$ for the full data set, $\Delta AIC_c = -34.857$ for the reduced data set). A French Frigate Shoals length curve was fitted by iteratively fixing the asymptote at varying values as described in the Methods. Resulting curves for each subpopulation exhibit marked variability. To demonstrate differences in the growth trajectories, we chose an arbitrary reference length (180 cm) and calculated the expected age when this length would be attained at each site. This ranged from just over age 3 yr at sites with relatively rapid growth to between age 6 and 7 yr at French Frigate Shoals and Lisianski Island (Fig. 3).

As with length, we found no support for sex differences in axillary girth growth. A sex effect model of pooled data was not an improvement compared to equal parameters for males and females (AIC_c increased by 0.485). Testing for subpopulation

Table 1. Sample size of Hawaiian monk seal length measurements by subpopulation, age and sex. Subpopulations abbreviated as follows: MHI = Main Hawaiian Islands, FFS = French Frigate Shoals, LAY = Laysan Island, LIS = Lisianski Island, PHR = Pearl and Hermes Reef, MDY = Midway Atoll, KUR = Kure Atoll. Sexes denoted by F = female, M = male.

Age (yr)	Subpopulation																							
	MHI			FFS			LAY			LIS			PHR			MDY			KUR			All		
	F	M	All	F	M	All	F	M	All	F	M	All	F	M	All	F	M	All	F	M	All	F	M	All
1	0	4	4	102	66	168	62	57	119	2	7	9	2	6	8	8	7	15	1	3	4	177	150	327
2	0	1	1	28	31	59	31	32	63	5	4	9	7	11	18	2	4	6	3	2	5	76	85	161
3	1	3	4	9	7	16	8	4	12	4	2	6	1	2	3	3	2	5	5	4	9	31	24	55
4	2	0	2	2	3	5	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	4	5	9
5	0	1	1	1	1	0	1	0	0	1	0	1	1	2	3	1	0	1	0	0	0	4	3	7
6	0	1	1	1	1	2	0	1	1	0	0	0	2	0	2	2	0	2	0	0	0	5	3	8
7	0	2	2	4	1	5	0	1	1	0	0	0	1	1	2	2	1	3	0	0	0	7	6	13
8	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	4	0	4
9	0	0	0	1	0	1	0	0	0	0	1	1	0	2	2	1	0	1	0	0	0	2	3	5
10	0	0	0	2	5	7	0	2	2	0	0	0	0	3	3	2	0	2	0	1	1	4	11	15
11	0	1	1	1	5	6	0	0	0	0	0	0	1	1	2	1	0	1	0	0	0	3	7	10
12	0	0	0	5	3	8	0	0	0	1	0	1	2	0	2	1	0	1	0	0	0	9	3	12
13	0	0	0	1	1	2	1	1	2	0	0	0	1	0	1	1	0	1	0	0	0	4	2	6
14	0	0	0	1	2	3	0	1	1	0	1	1	0	2	2	1	1	2	0	0	0	2	7	9
15	0	1	1	1	1	2	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	2	3	5
16	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	1	0	1	0	1	1	1	3	4
17	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	1	3	0	3
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2
20	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
All	3	15	18	161	126	287	103	102	205	14	15	29	18	31	49	27	16	43	13	11	24	339	316	655

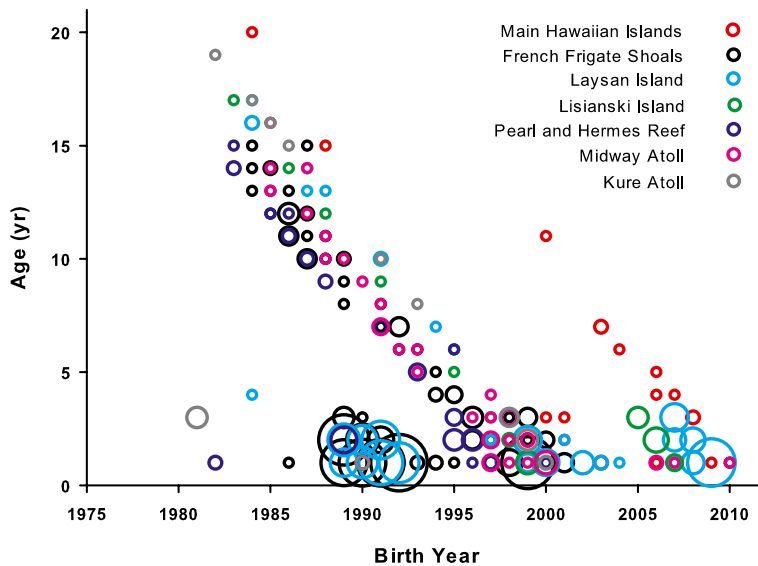


Figure 2. Distribution of Hawaiian monk seal length measurements according to age and birth year. Area of circles is proportionate to sample size. Girth measurements were nearly identically distributed.

differences in girth growth patterns within a model comparison framework was hampered by difficulties in achieving convergence. Efforts to fit the three-parameter model to data from three (French Frigate Shoals, Laysan Island, and Pearl and Hermes Reef) of the seven subpopulations failed. Therefore, two-parameter (with the asymptote estimated iteratively) models were fitted to these sites. Site-specific girth growth curves varied similarly to growth in length. The age when seals were expected to reach an arbitrary reference (120 cm) girth varied from just over 3 yr in the main Hawaiian Islands to 9 and 12 yr at French Frigate Shoals and Lisianski Island, respectively (Fig. 4). Table 2 presents estimated parameters for length and girth models.

DISCUSSION

Kenyon and Rice (1959) reported that adult female Hawaiian monk seals appeared to be larger than males. This was apparently based only on visual assessment, and in the context of the authors' landmark comprehensive description of the species' natural history, was likely offered as a tentative observation. Yet, adult female monk seals exceeding males in size has been oft-repeated in publications and has seemingly taken on a certainty that the original authors likely did not intend. Here we find no evidence of sexual dimorphism in growth or body size. Antonelis *et al.* (2003) likewise found no sex differences in the size of pups at weaning.

There were striking differences in growth curves among the various monk seal subpopulations. The fitted parameters (Table 2) for each site are provided for reference, though when considered individually, they provide limited insight into growth patterns. For example, asymptotic length (L_{∞}) estimates varied substantially among

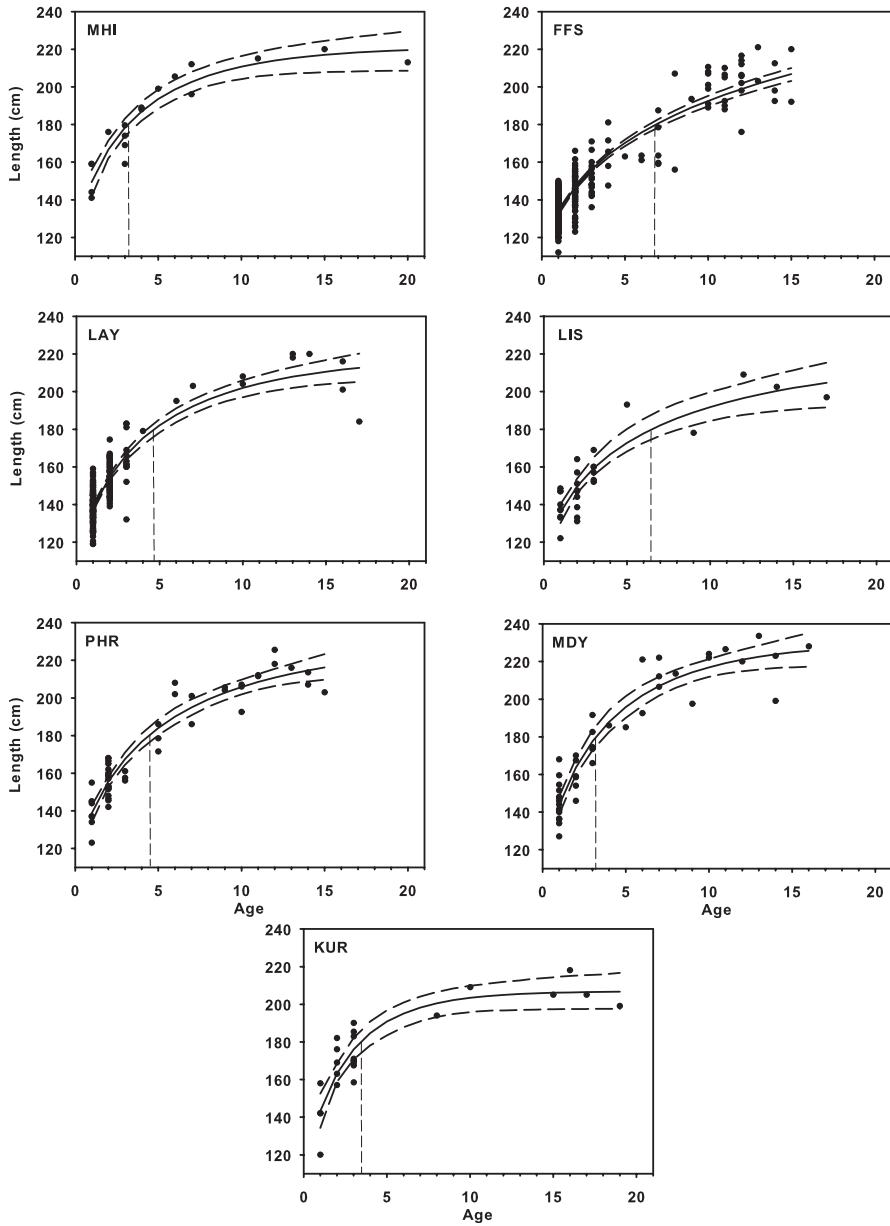


Figure 3. Fitted length-at-age curves with bootstrapped 95% confidence intervals for Hawaiian monk seals from seven subpopulations (MHI = Main Hawaiian Islands, FFS = French Frigate Shoals, LAY = Laysan Island, LIS = Lisianski Island, PHR = Pearl and Hermes Reef, MDY = Midway Atoll, and KUR = Kure Atoll). Dots mark individual measurements. The age range plotted corresponds to the maximum aged seals measured at each site. Drop lines indicate the age when 180 cm length is attained in order to facilitate comparison among subpopulations.

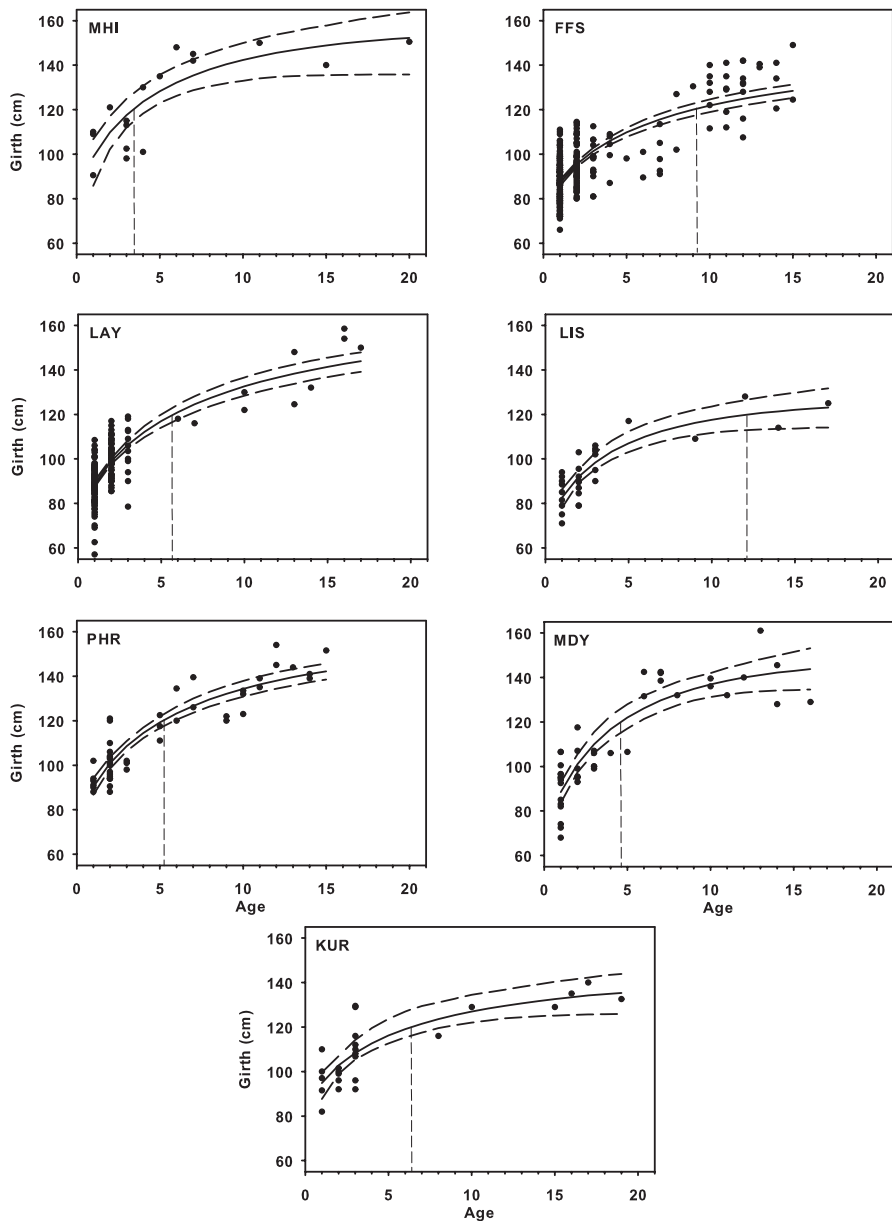


Figure 4. Fitted girth-at-age curves with bootstrapped 95% confidence intervals for Hawaiian monk seals from seven subpopulations (MHI = Main Hawaiian Islands, FFS = French Frigate Shoals, LAY = Laysan Island, LIS = Lisianski Island, PHR = Pearl and Hermes Reef, MDY = Midway Atoll, and KUR = Kure Atoll). Dots mark individual measurements. The age range plotted corresponds to the maximum-aged seals measured at each site. Drop lines indicate the age when 120 cm girth is attained to facilitate comparison among subpopulations.

Table 2. Estimated generalized von Bertalanffy growth function parameters fitted to Hawaiian monk seal length- and girth-at-age data.

Subpopulation	Length			Girth		
	L_{∞}	a	b	G_{∞}	a	b
All	225.3	-0.102	0.276	180.1	-0.023	0.220
Main Hawaiian Islands	221.3	-0.174	0.292	156.7	-0.111	0.265
French Frigate Shoals	277.0 ^a	-0.018	0.210	142.0 ^a	-0.063	0.215
Laysan Island	219.1	-0.130	0.288	160.0 ^a	-0.061	0.256
Lisianski Island	219.5	-0.075	0.227	126.1	-0.140	0.275
Pearl and Hermes Reef	228.8	-0.109	0.283	155.0 ^a	-0.082	0.267
Midway Atoll	230.4	-0.171	0.347	148.3	-0.146	0.345
Kure Atoll	206.9	-0.296	0.402	142.4	-0.075	0.193

^aAsymptotes (L_{∞} and G_{∞}) fitted manually by iteratively fixing different values until residual sum of squares was minimized.

sites, but Kure Atoll, with the lowest estimated asymptote also had the fastest growth rate (a). Estimates of L_{∞} and G_{∞} (for girth), were probably influenced by the maximum age of seals measured. At most sites, seals were apparently still growing at the oldest ages sampled, so that estimation of the asymptotes was not well informed by the available data. More sampling of older animals would be required to adequately characterize growth throughout the life span.

Subpopulation differences are clearer when comparing the fitted growth curves (Fig. 5), rather than individual parameters, and by comparing the age at which specified sizes (180 cm length and 120 cm girth; Fig. 3, 4) are expected to be attained. Differences in growth among subpopulations were evident whether using the full data set or the reduced set with repeat measures of individuals removed. The statistical conclusions were not affected by the inclusion of repeated measures, and the fitted length-at-age curves for each subpopulation were almost indistinguishable when fitted to the full and reduced data sets. Body growth at French Frigate Shoals and Lisianski Island were apparently retarded compared to the other sites. This is entirely consistent with patterns in female fecundity, whereby first reproduction is delayed and maximum birth rate is lower at these same two sites compared to Laysan Island and the MHI, where growth rates are substantially greater (Harting *et al.* 2007, Baker *et al.* 2011).

Hawaiian monk seals exhibit natal site fidelity but do move amongst subpopulations to varying degrees (Schultz *et al.* 2010). The fact that nearly all seals were born and measured at the same location suggests that the growth curves largely reflect local conditions. The notable exception is Midway Atoll, where a large portion of the measurements was from seals born elsewhere. This reflects that Midway Atoll was recovering from very low abundance during much of the study period, primarily through immigration, and few pups were born there prior to the mid-1990s.

Interpreting the variable patterns among subpopulations is complicated by the fact that the data were mostly sampled in a cross-sectional manner, as is common in pinniped growth studies. Winship *et al.* (2001) articulated eight potential biases associated with growth curves derived from cross-sectional data and we consider these here. Two bias sources having to do with age determination are not relevant to the seals in this study, which were all known-aged. Variability in birth date could have some influence as births may occur at all times of year, although with a broad, pronounced

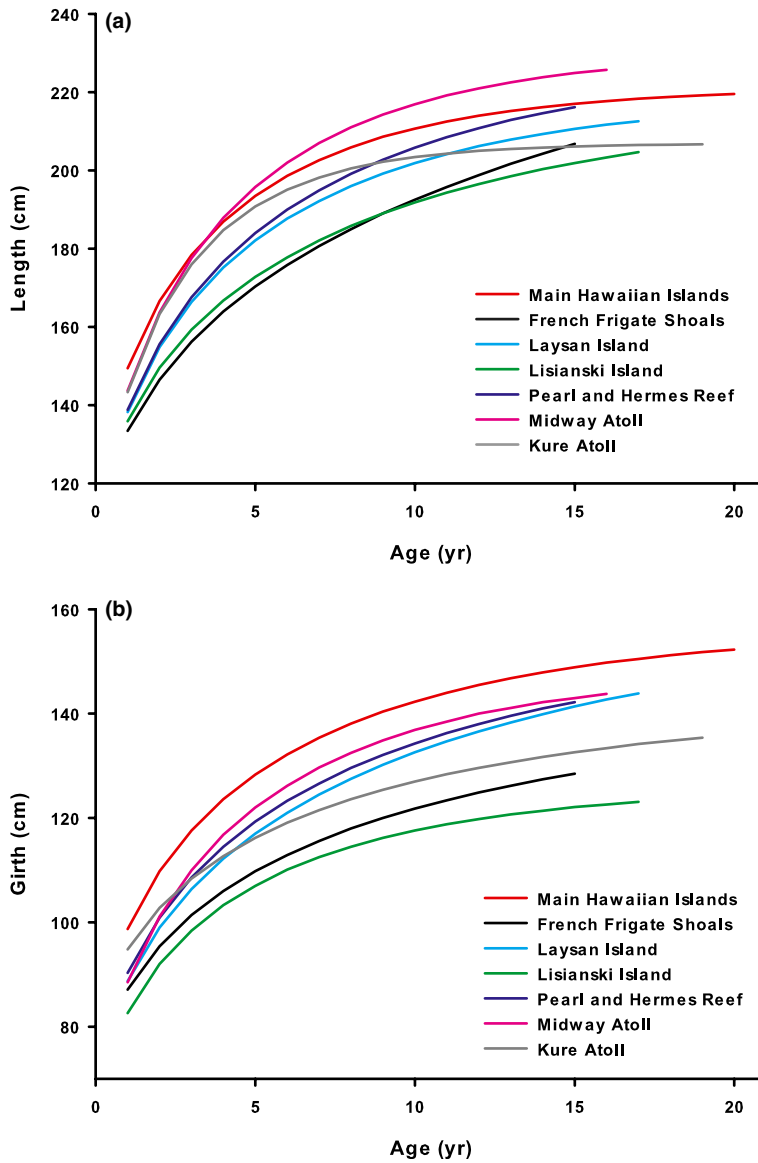


Figure 5. Fitted length and girth growth curves for seven Hawaiian monk seal subpopulations.

peak from March to August (Johanos *et al.* 1994). By convention, we incremented the age of all animals by one year on 1 January and the birth dates of most seals were not known exactly. Thus, putative yearlings could vary in actual age by several months. This source of bias is unlikely to have greatly affected the results except to increase the variance in the fitted relationship.

Nonuniform sampling with respect to size within age is another potential source of bias. This is especially an issue if, for example, large territorial males or perhaps

pregnant females are more likely to be available for capture. Monk seals do not maintain territories and obviously pregnant females were not captured. Emaciated animals were also typically not captured, which might have resulted in some positive bias in our sample. Variability in the measurement date could influence results if there are pronounced seasonal patterns in body condition as is the case with many pinnipeds (Schusterman and Gentry 1971, Ryg *et al.* 1990, Boyd and Duck 1991, Renouf *et al.* 1993, Trites and Bigg 1996, Winship *et al.* 2001). The measurement data in this study were collected throughout the year, with 26%, 40%, 24%, and 10% of sampling in the first through fourth quarters, respectively. Although there was greater sampling in the second quarter and less in the fourth, Hawaiian monk seals are not known to undergo marked variation in body condition seasonally, with the exception of pregnant, currently or recently lactating females, and possibly around the time of molting. Pregnant females were avoided, whereas lactating and molting seals were not captured. We thus conclude that date of sampling likely had little influence on the results.

Size-biased mortality likely affected the shape of fitted growth curves. Weaning size (girth) strongly influences Hawaiian monk seal first year survival (Craig and Ragen 1999, Baker 2008). It seems likely that this holds true for immature animals as well. Baker and Thompson (2007) found that Hawaiian monk seals achieve adult survival rates at least by age 5 yr and, thereafter, survival remained high (typically >0.90) and relatively invariant until senescence was apparent after approximately age 18 yr. Size-selective survival, then, would have the greatest potential effect on our fitted growth curves up to age 5 yr. If smaller immature animals died at a higher rate, then the subsequent ages would be represented by relatively larger seals, resulting in positively biased growth rates. The fitted curves (Fig. 3, 4) may consequently be steeper for the first few age classes than if sufficient longitudinal data had been available.

Winship *et al.*'s (2001) final factor influencing growth curves derived from cross-section data is that environmental conditions vary over time. In the present study, measured seals had different histories of exposure to environments that were relatively more or less conducive to growth. A likely effect of this is apparent in the length and girth data from French Frigate Shoals (Fig. 3, 4). Note that most of the measurements of 5 to 8 yr old seals are below the fitted line. Notably, all but one of the measured seals in this age range were born in 1991–1994, a period when juvenile survival was relatively low and starvation was thought to be the primary cause (Craig and Ragen 1999, Baker and Thompson 2007). In contrast, the seals measured at age 8 yr and older were all born during 1984–1989, a period of very high juvenile survival. It is likely that the 5 to 8 yr old seals born into poor foraging conditions grew more slowly, whereas the older seals enjoyed conditions more favorable to growth. The result was a lack of fit in the young adult age range, which may well explain why the 3-parameter von Bertalanffy function would not converge for the French Frigate Shoals data sets. Such effects likely occurred at other sites, because, for example, nearly all the adults measured were born prior to 1995 and their sizes may not reflect more recent conditions (Fig. 2). French Frigate Shoals has demonstrated the most pronounced variability in survival over time, so that such effects at other subpopulations may be more subtle (Baker and Thompson 2007).

Given these sampling influences, our size-at-age results represent a composite of growth patterns (likely influenced by size-selective survival in the younger ages) representing conditions sampled over several decades. Yet, sampling by year and age was similar among sites, with a few exceptions. In the early 1990s at French Frigate Shoals and at Laysan Island both in the early 1990s and again in the late 2000s,

pulses of 1 to 3 yr olds were measured, whereas years when young animals were measured at other sites were less concentrated in time. Also, because seals only became somewhat common in the main Hawaiian Islands since the latter 1990s, most seals measured from this area were born in the 2000s. Despite these distinctions, there was broad overlap in the timing of sampling and ages of sampled seals among subpopulations. Thus, observed differences among subpopulations most likely reflect real differences in environmental conditions determining growth during the span of years sampled.

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