

Stable carbon and nitrogen isotope values in teeth of Steller sea lions: age of weaning and the impact of the 1975–1976 regime shift in the North Pacific Ocean

A.E. York, J.R. Thomason, E.H. Sinclair, and K.A. Hobson

Abstract: We measured $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and tooth width from the first 4 years' dentinal growth layer groups (GLGs) in the teeth of 113 female Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)) born between 1960 and 1983, a period that included a large population decrease and a climate regime shift. A linear discriminant analysis on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values estimated 60% of Steller sea lions were weaned in their 1st year, 30% in their 2nd year, and 8% in their 3rd year. GLG-1 was wider in "weaned" animals than those still "nursing" in their 2nd year, suggesting that faster growing pups weaned earlier. Except during the regime shift, the average age at weaning increased and the size of GLG-1 in weaned animals decreased. We suggest that during the regime shift a greater proportion of pups which survived (to have their teeth sampled for this study) grew faster and were weaned by the end of their 1st year. We hypothesize that the long-term weaning age increase and growth rate decrease are consistent with a change in relative mortality of weaned pups and those that continued to nurse, possibly caused by a reduction in available resources, characterized as a switch from a "live-fast" to a "live-slow" life history.

Résumé : Nous avons mesuré les valeurs de $\delta^{15}\text{N}$ et de $\delta^{13}\text{C}$ ainsi que la largeur de la dent dans les groupes de couches de croissance (GLG) de dentine des 4 premières années des dents de 113 lions de mer de Steller (*Eumetopias jubatus* (Schreber, 1776)) femelles nées entre 1960 et 1983, une période qui comprend une forte décroissance de la population et un changement de régime climatique. Une analyse discriminante linéaire des valeurs de $\delta^{13}\text{C}$ et de $\delta^{15}\text{N}$ estime que 60 % des lions de mer de Steller ont été sevrés durant leur première année, 30 % dans leur seconde année et 8 % dans leur troisième année. Le GLG-1 est plus large chez les animaux « sevrés » que chez ceux qui sont encore « allaités » durant leur seconde année, ce qui laisse croire que les petits à croissance plus rapide sont sevrés plus tôt. Excepté pendant le changement de régime, l'âge moyen au sevrage a augmenté et la taille du GLG-1 chez les animaux sevrés a diminué. Nous croyons que durant le changement de régime, une proportion plus grande des petits qui ont survécu (et ainsi ont eu leurs dents retenues dans notre étude) ont crû plus rapidement et ont été sevrés à la fin de leur première année. Nous posons comme hypothèse que l'augmentation à long terme de l'âge au sevrage et la diminution du taux de croissance sont en accord avec un changement dans la mortalité relative des petits sevrés et de ceux qui continuent à être allaités, ce qui pourrait avoir été causé par une réduction des ressources disponibles; le phénomène pourrait être caractérisé comme un remplacement du cycle biologique à « vie rapide » par un à « vie lente ».

[Traduit par la Rédaction]

Introduction

Isotopic signatures of prey and foraging location are retained in the hard tissues of apex predators in the form of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ levels, and they provide biologists a means of investigating historical diets (Hobson and Sease 1998). Diet is a limiting factor in the success of any predator popu-

lation, and shifting diet patterns among apex predators may indicate broad ecosystem change. Stable isotope analyses are particularly useful in providing a means for comparing historical with current diet patterns against the backdrop of physical and biological changes within the foraging environment (Hunt et al. 2002).

Measurement of naturally occurring stable isotope abundances of several elements have assisted researchers in defining trophic relationships and the source of feeding in several marine mammals (Hobson and Welch 1992; Kurle 2002; Kurle and Worthy 2002; Hobson et al. 2004a). Values of stable nitrogen (measured as $\delta^{15}\text{N}$) and carbon (measured as $\delta^{13}\text{C}$) in teeth and other tissues have been used to infer maternal inputs to offspring (Hobson and Sease 1998; Polischuk et al. 2001; Newsome et al. 2006). Nursing neonates are feeding at a higher trophic level than their mothers, since they are consuming proteins that have been derived from maternal tissues, resulting in elevated $\delta^{15}\text{N}$ values in tissues associated with that nursing period. Lower $\delta^{13}\text{C}$ val-

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ues are often associated with the nursing period, since carbon derived from lipid-rich milk is typically more depleted in carbon-13 compared with other sources of carbon in food webs (Polischuk et al. 2001). Weaning is thus often associated with a commensurate drop in $\delta^{15}\text{N}$ values and an increase in $\delta^{13}\text{C}$ values of tissues of young animals.

Stable isotope analyses have become an important tool for the study of population declines, particularly in those without a long history of directed and consistent biological sampling (Hobson et al. 2004a). The western stock of Steller sea lions (*Eumetopias jubatus* (Schreber, 1776); SSL) is an endangered population whose remote habitat along the Aleutian archipelago in the northern North Pacific Ocean places logistic and practical constraints on direct biological sampling and observation effort. Such an effort would have been required to be in place before a population decline to determine the causes of the decline. In addition to providing a historical measure of diet, the stable isotope data came from tissues that were laid down during 1962–1984, a period that encompassed the 1976 climate regime change in the North Pacific Ocean and a large population decline. Numerous apex predators sharing a common prey base in the North Pacific Ocean and Bering Sea underwent significant population declines during this period of climate change that are thought to have been influenced, in part, by changes in diet (Anonymous 1993; Hunt et al. 2002; DeMaster and Atkinson 2002).

The aim of this paper is to investigate age-specific changes in the patterns of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the teeth of the endangered SSL as a signal for determining the age of weaning. We explore the observed isotopic patterns as a reflection of the age distribution of weaning. We evaluate the potential relationship between temporal variability in weaning patterns, the 1976 climate regime shift, and the population decline in SSLs. In addition, we describe measurements and age-specific changes in the sizes of individual growth layer groups (GLGs) in SSL teeth, investigate them as a proxy for SSL size, and relate shifts in GLG size to the changes in stable isotope values, thereby, generating hypotheses on the determinants of weaning for SSLs.

Steller sea lion

The SSL is a large sexually dimorphic member of the family Otariidae (eared seals) living in the North Pacific Ocean and Bering Sea. SSLs breed and raise pups on sites called rookeries, which range along the Pacific coast from California to Alaska and along the Aleutian archipelago to the Sea of Okhotsk. Adult males weigh up to 1200 kg and females weigh as much as 350 kg (Loughlin et al. 1987). Based on genetic analyses and local migration patterns, the SSL population has been divided into eastern and western stocks at 144°W, at Cape Suckling, Alaska (Bickham et al. 1998a). Further genetic analysis (Bickham et al. 1998b; Baker et al. 2005; O’Corry-Crowe et al. 2006) and analyses of diet and population patterns (Sinclair and Zeppelin 2002) have established the existence of additional stocks.

Fiscus (1961) aged SSLs by assuming that their GLGs were laid down annually. His procedures followed those of Scheffer (1950), who developed the methods for northern fur seals (*Callorhinus ursinus* (L., 1758)). That one GLG represented 1 year was verified by examining the teeth of

known-age specimens (T.R. Loughlin, personal communication (2007)) in the 1970s. Annuli are deposited as inverted cones, from the outside toward the inside of the tooth. The neonatal line is a dark band formed at birth (Fiscus 1961); dentine outside of the neonatal line is fetal dentine that is formed after the fetus ossifies, probably during the last trimester of pregnancy (Scheffer and Kraus 1964).

The population of the eastern stock has been stable or slightly increasing, but the western stock decreased by about 80% during 1970–1998. Surveys of SSLs were not conducted frequently or consistently before 1975, so there is uncertainty concerning the timing of the start of the decline. Merrick et al. (1987) argue that the SSL population began to decline in the mid-1950s, coincident with the onset of large-scale bottom trawl fishing in Alaska. However, Trites and Larkin (1996) contend that the population was increasing until the mid-1970s and decreasing after that period. York et al. (1996) describe the spatial and temporal patterns in the SSL decline beginning in the early 1970s in the historical center of abundance in the eastern Aleutian Islands (Braham et al. 1980). During 1985–1990, the decline was severe in most parts of the range (York et al. 1996) and slowed by the mid-1990s. Counts of SSLs have increased somewhat since 1998. The extent and rapidity of the decline after 1985 led the National Marine Fisheries Service to list the western stock of SSL as threatened under the US Endangered Species Act in 1990 (Loughlin and York 2000) and endangered in 1997.

Population modeling by York (1994) and Pascual and Adkison (1994) implicated decreases in juvenile survival (on the order of about 20%), perhaps coupled with lesser reductions in reproductive rates, as being responsible for the declines from 1975 to 1985. Further modeling by Holmes and York (2003) suggested that juvenile and adult survivorships had severely decreased to about 40% and 85% of pre-decline levels, respectively, during the mid- to late 1980s. By the early 1990s, juvenile and adult survivorships had improved to near pre-decline estimates, but estimated fecundity was about 75% of estimated pre-decline levels.

No definitive biological cause for any phase of the decline has been widely accepted. Direct takes, mainly shooting and fishing mortalities, were implicated in the early declines (Loughlin and York 2000), but these had decreased sharply in the early 1990s. A harvest of approximately 40 000 pups during 1962–1974 had been suggested as a cause of the decline, but models from Pascual and Adkison (1994) demonstrated that this was unlikely. However, Trites and Larkin (1996) argue that the culling of pups stabilized what they believed was an increasing population in the 1960s and early 1970s. An oceanic climate regime shift in the mid-1970s was possibly a contributory cause of the decline because it could have changed prey availability for SSLs, especially for juveniles, or could have affected the prey mix available to SSLs (e.g., Anonymous 1993; Benson and Trites 2002; DeMaster and Atkinson 2002; Fritz and Hinckley 2005; Trites et al. 2007). Diet changes, occurring as a result of competition with commercial fisheries or in combination with climate shifts as evidenced by reduced body size in female SSLs (Calkins et al. 1998), have also been suggested as a factor in SSL population declines. Others have linked SSL declines to those that occurred for

northern fur seals and sea birds during the mid-1970s (Hunt et al. 2002; Sinclair et al. 2008). In a temporal–spatial analysis of both the fisheries and the SSL rookery declines, Hennen (2006) found that the decline was correlated with several measures of fishing pressure; his analysis also asserts that the conservation measures which restricted fishing near SSL rookeries after the early 1990s had a positive effect on the SSL population.

SSL diet has been consistently monitored only since the late 1980s. Like most apex predators in the northern North Pacific Ocean and Bering Sea, SSLs eat mainly fishes and cephalopods (Beamish et al. 1999; Sinclair and Zeppelin 2002). It is not known if diet shifts were concurrent with SSL population declines beginning during the climate regime shift of the mid-1970s as was the case for other monitored apex predators (Sinclair et al. 2008), but the mix of available prey did change and small forage fishes were less likely to be found (Brodeur et al. 1999). There does, however, appear to be a strong link between population and diet patterns in SSLs to the degree that subpopulations can be discriminated by diet patterns (Sinclair and Zeppelin 2002). No matter the driving mechanism, an alteration in the availability or mix of prey (e.g., Benson and Trites 2002; Fritz and Hinckley 2005) might be expected to have the most severe impact on juvenile SSLs feeding on their own for the first time.

Stable isotopes, growth, and the biology of weaning

SSLs give birth to a single pup in the late spring or early summer. In contrast with other otariid pinnipeds, such as the northern fur seal, or phocids, such as the harbor seal (*Phoca vitulina* L., 1758), which tend pups for a matter of months prior to weaning, SSLs nurse their pups at least through their first 6 months and have been observed nursing pups for up to 3 years (Chumbley et al. 1997). Although the age at weaning is variable, most are thought to be weaned by their 3rd or 4th year (Pitcher and Calkins 1981). Using telemetry, Merrick and Loughlin (1997) suggested that diving patterns of some yearlings in the late spring were probably indicative of weaning. Using on-land observations of attendance behavior, Trites et al. (2006) found evidence of late-spring weaning and asserted that most male pups wean at age 2 years and that about 50% of female pups wean by age 1 year with the remainder at age 2 years, although no estimates of variance were provided.

Hobson et al. (2004b) reported that mean $\delta^{15}\text{N}$ (Table 1) values decreased significantly with age. They were highest in GLG-1; on average, they were 3.6% less in GLG-2 and a further 3% less in GLG-3, with no significant change from GLG-3 to GLG-4. Conversely, Hobson et al. (2004b) found that $\delta^{13}\text{C}$ values increased with age. They were lowest in GLG-1; they increased 5.3% in GLG-2, and further increased (another 1.9%) in GLG-3; as with $\delta^{15}\text{N}$ values, they found no significant difference in $\delta^{13}\text{C}$ values in GLG-3 and GLG-4. Hobson et al. (2004b) hypothesized that these patterns were a signal for weaning.

If stable isotopic signatures are evidence of weaning, the patterns in GLGs 1–4 should vary in a manner consistent with the biology of weaning with a change in the stable isotope patterns in GLG-2 and GLG-3 along a continuum between GLG-1 and GLG-4. Since pups occupy a higher

Table 1. Sample sizes, means, and standard deviations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in each growth layer group (GLG) of teeth from Steller sea lions (*Eumetopias jubatus*) (from Hobson et al. 2004b).

GLG	<i>n</i>	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)	
		Mean	SD	Mean	SD
1	113	–13.786	0.680	18.731	0.519
2	113	–13.050	0.577	18.064	0.658
3	113	–12.808	0.464	17.582	0.568
4	107	–12.831	0.476	17.510	0.451

trophic level than their mothers, if the isotopic signatures are evidence of weaning, then we expect (i) a decrease in $\delta^{15}\text{N}$ with age, within individuals, because weaning implies a decrease in trophic level; (ii) an increase in $\delta^{13}\text{C}$ with age, within individuals, because weaning with its associated drop in lipid levels and the consumption of solid foods should be associated with higher $\delta^{13}\text{C}$ values; and (iii) consistency in the patterns of change in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ with the observed rates from marked animals during nursing.

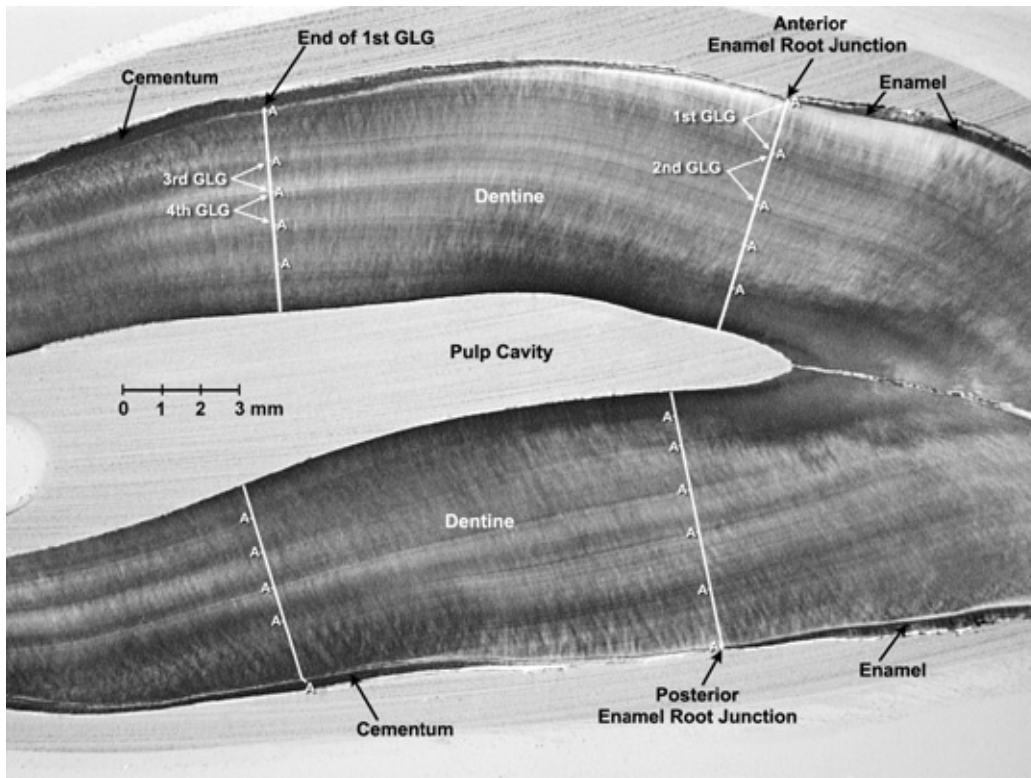
King et al. (2007) have shown that the length of the exposed canine tooth combined with the width of the diastema can be used in the field as a reasonable predictor of the age of SSLs up to 2 years of age. However, to our knowledge, there are no published studies showing a relationship between tooth size and body size in individual pinnipeds, although theory predicts that such a relationship is plausible (Peters 1983). Information on body size would be useful in investigating hypotheses on the determinants of weaning in SSLs, particularly if animals that wean at a younger age grew faster in their 1st year than older weaning animals. In the absence of body-size information from the same animals whose teeth were sampled for this study, we compare the tooth growth rates to body-size growth rates from previously published cross-sectional studies in Calkins et al. (1998) and Winship et al. (2001). In addition, we investigate the relationships among the width of the GLGs and their stable isotope values, and examine their possible relationship to the biology of weaning.

Materials and methods

Tooth sampling, preparation, and measurement

In this study, we selected upper canine teeth from 113 SSL females that were taken incidentally in fisheries (Fig. 1). We used teeth from females for two reasons. First, we were interested in understanding effects on females that might partially explain the large population decrease; second, we wanted to eliminate any potential source of variability across gender. The teeth were collected by fisheries observers during 1976–1986 for species verification and age assessment. A spectrum of ages was sampled so that the available year classes would include the period of the initial large decline of the western stock of SSLs and a mid-1970s oceanic regime shift, which had been implicated as a possible factor in the decline. Two independent readers determined the age of the tooth, and the birth year for each animal was back-calculated by subtracting the animal's age from the collection year. We then selected teeth from ap-

Fig. 1. Longitudinal thin section of the upper canine tooth of a female Steller sea lion (*Eumetopias jubatus*). The enamel, cementum, and annual growth layer groups (GLGs) in the dentine are indicated. Standardized areas of measurement at the enamel root junction and the terminus of the first GLG are also indicated.



proximately five SSLs per available birth year for thin sectioning, dentine extraction, and measurement of GLGs. All selected teeth were from SSLs taken between Cape Suckling (144°W) and the Shumagin Islands (160°W) in the Gulf of Alaska. Mean stable isotope values from these teeth were reported in Hobson et al. (2004b).

Tooth sections were mounted on 2 inch \times 3 inch (27.4 mm \times 76.2 mm) glass slides and polished, then electronic images were taken using a digital camera mounted on a microscope. A polarizing filter was used to enhance GLG definition and images were captured under 4 \times magnification. GLGs on each tooth image were marked and measured in two places along both the anterior and the posterior halves of the tooth image. Lines were drawn perpendicularly across the growth layers at the enamel root junction, and again at the point where the first growth layer terminated in the root (Fig. 1). This method permitted two measurements of the first growth layer and a maximum of four measurements of the second, third, and fourth layers, depending on the definition of the layers and quality of the image. Using electronic images as aides, growth layers were also marked on the remaining portion of the tooth. The extraction of dentine for the stable isotope analysis was described in Hobson et al. (2004b). A total of 10 mg of dentine was then extracted from each of the first 4 GLGs with a 1 mm engraving burr attached to a flexi-shaft Dremel³ tool.

Stable isotope extractions

Isotopic analyses of teeth followed methods described in Hobson and Sease (1998) and Hobson et al. (2004b), and we summarize them for completeness. The protein component of dentine was analyzed for stable nitrogen isotope ratios. Dentine samples were combusted at approximately 1200 °C using continuous-flow isotope ratio mass spectrometry (CFIRMS) involving a Europa 20:20 IRMS interfaced with a Robo Prep combustion system. The stable carbon isotope ratios of the inorganic fraction were obtained by reacting powdered dentine samples with concentrated (100%) phosphoric acid. The evolved CO₂ was sampled using either a breath sampler interfaced with a VG OPTIMA dual inlet or a Europa 20:20 CFIRMS. Stable isotope ratios were expressed in parts per thousands (‰) relative to the Vienna Pee Dee Belemnite or air standards for carbon and nitrogen, respectively (Hobson and Sease 1998).

Statistical methods

Hobson et al. (2004b) used Friedman's test (Hollander and Wolfe 1973) to assess significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ across the GLGs, and we used this same test to compare size differences in the tooth width across the GLGs. We used this test to control for potential year-to-year correlation in the width of GLGs within individual SSLs. Friedman's test assumes that the data arise from a

³Reference to trade names does not imply endorsement by the National Marine Fisheries Service, National Oceanic and Atmospheric Administration.

complete randomized block design with a single observation in each block. In our case, each sampled animal is its own block and the null hypothesis is that there is no difference in the outcome variables in each GLG. If the null hypothesis was rejected, we determined which levels were different using multiple comparison procedures outlined in Hollander and Wolfe (1973).

Discriminant analysis (Morrison 1967; Venables and Ripley 2002) is a statistical method for separating groups and for classifying other data as more similar to one of the established groups. We used discriminant analysis to determine which GLG-2 and GLG-3 samples had isotopic values that were more similar to those in GLG-1 (from nursing animals) or GLG-4 (from probably weaned animals). We fitted a linear discriminant function (LDF) to the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ patterns in GLG-1 and GLG-4. We then applied that function to the GLG-2 and GLG-3 data and classified them as more similar to GLG-1 or GLG-4. Since linear discriminant analysis can produce biased results if the normality and covariance matrix assumptions are not satisfied, we verified that the LDF was adequate by also fitting a robust version of the discriminant function (Venables and Ripley 2002) and checking that it was not substantially better than the simple discriminant function. In addition, it is well known that the rate of correct classification may be artificially high if one uses all data to fit a LDF and then applies the fitted function to the same data (e.g., Venables and Ripley 2002). To determine if the classification rate of our discriminant analysis was substantially biased, we simulated the classification rate of the LDF by randomly splitting the sample in half, using one part of the data for estimating the function and the other for classification. We repeated this process 1000 times and compared these classification rates with that of the original discriminant function.

We used generalized linear models with binomial errors to analyze the yearly changes in the proportion of SSLs estimated to be still nursing in their 2nd year and to assess if there were changes coincidental with the timing of a North Pacific climate regime shift. The sample was divided into groups of years so that there were at least 10 SSLs in each group. The years 1976–1977 were grouped together, because we were interested in comparing SSLs that were yearlings or pups at the time of the regime shift with SSLs from other time periods.

We compared the sizes of tooth GLGs to the published growth curves in Calkins et al. (1998) and Winship et al. (2001) by fitting linear and logarithmic allometric equations of GLG tooth width as a function of body size (Reiss 1989). We used linear models to compare the width of specific GLGs in potentially weaned or nursing animals to determine whether it was likely that faster growing individuals had weaned at a younger age and to examine how this relationship changed over time.

We used the open-source statistical package R (Ihaka and Gentleman 1996; R Development Core Team 2006) for all analyses. For the discriminant analysis, we followed Venables and Ripley (2002; online material available from <http://www.stats.ox.ac.uk/pub/MASS4> [accessed March 2006]) and used the R package, MASS, available from <http://www.r-project.org/> [accessed March 2006] within the VR bundle.

Results

Stable isotope values in GLG-1 to GLG-4

Complete samples of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and age estimates from GLG-1 to GLG-4 were available for 107 animals; an additional 6 animals had complete samples from GLG-1 to GLG-3. Unless stated, all analyses are for the set of 107 complete observations. For the population (Table 1), the mean $\delta^{15}\text{N}$ in GLG-4 was 1.2‰ less than in GLG-1, whereas the mean $\delta^{13}\text{C}$ in GLG-4 was 0.9‰ higher than in GLG-1.

Discriminant analysis

The isotopic signatures of GLG-1 and GLG-4 appear well separated (Fig. 2). When all data were used, 97% of all samples were correctly classified by the LDF. The robust LDF classified one additional datum correctly. We simulated the performance of the linear discriminant analysis with a Monte-Carlo experiment of the classification rate. In 1000 simulations, at least 93% of the observations were correctly classified, and 95% of the simulations correctly classified 94%–99% of the observations. These results suggested that the ordinary LDF was adequate for separating the GLG-1 and GLG-4 stable isotope values. Thus, in the remainder of the paper, we use only the ordinary LDF.

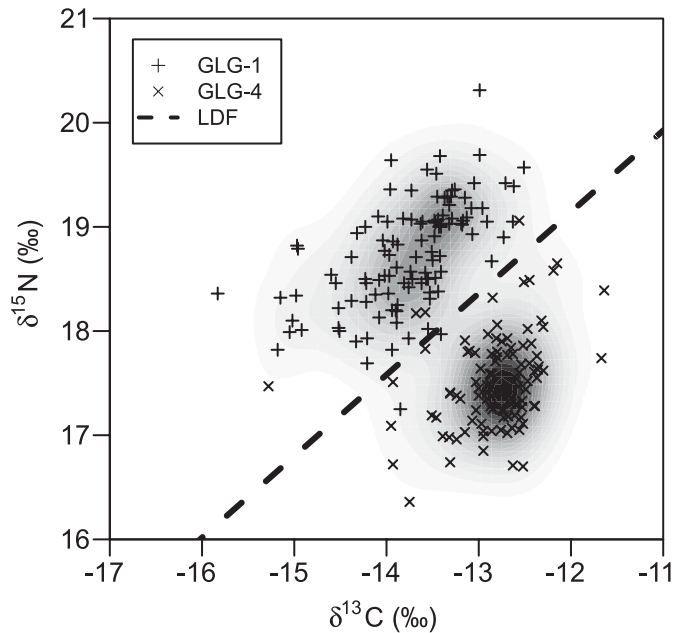
When we applied the LDF to the GLG-2 and GLG-3 data (Fig. 3), a majority of (approximately 60%) GLG-2 samples were classified as GLG-4 and even more (approximately 90%) GLG-3 samples were classified as GLG-4. The details of the classification (Tables 2A–2C) indicate that 103 of 107 samples (or 96% of all complete samples) had profiles that were consistent with our hypotheses on how the isotopic signatures should behave if they are a signal for weaning. Two profiles were not consistent with the notion that the signatures are a signal for single-point weaning (i.e., the discriminant analysis predicted that the animals were “nursing” after a gap of 1 year or more of “not nursing”). There were two profiles whose signatures in GLG-1 were classified as more similar to GLG-4; one animal was classified as never nursing during its first 4 years and the other as nursing only in its 2nd year. Among the 101 animals that the discriminant function classified as “weaned” by their 4th year (Table 2C), 60% were weaned by the end of their 1st year, another 30% by the end of their 2nd year, and another 8% in their 3rd year. The results suggest that a small number of animals ($\leq 2\%$) could still be nursing in their 4th year.

Mean values in Table 1 were computed for the entire sample and do not take into account that animals weaned at different ages would be expected to have different isotopic profiles. For those animals classified by the LDF as being weaned by age 2, the $\delta^{15}\text{N}$ values decreased by 1.1‰ and the $\delta^{13}\text{C}$ values increased by 1.0‰ between GLG-1 and GLG-2 (Table 3). Similarly, the other groups had decreases in $\delta^{15}\text{N}$ and increases in $\delta^{13}\text{C}$ in the year following their estimated weaning (Table 3). The isotope values appeared stable after the estimated weaning age.

Width of GLGs

Complete samples of width measurements of GLG-1 to GLG-4 were available for 35 SSLs at the anterior enamel root junctions and for 53 SSLs at the posterior enamel root

Fig. 2. Relationships between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in GLG-1 and GLG-4 of teeth from Steller sea lions with the estimated joint probability density function and the linear discriminant function (LDF) that best separated GLG-1 and GLG-4 superimposed on the figure.



junction (Tables 4A, 4B). Complete samples of measurements of GLG-2 to GLG-4 were available for 76 SSLs at the anterior secondary location and for 81 SSLs at the posterior secondary location (Tables 4C, 4D). The width of GLG-1 at the secondary locations was zero because of the measurement point for this location is defined as the location where GLG-1 meets the enamel (Fig. 1).

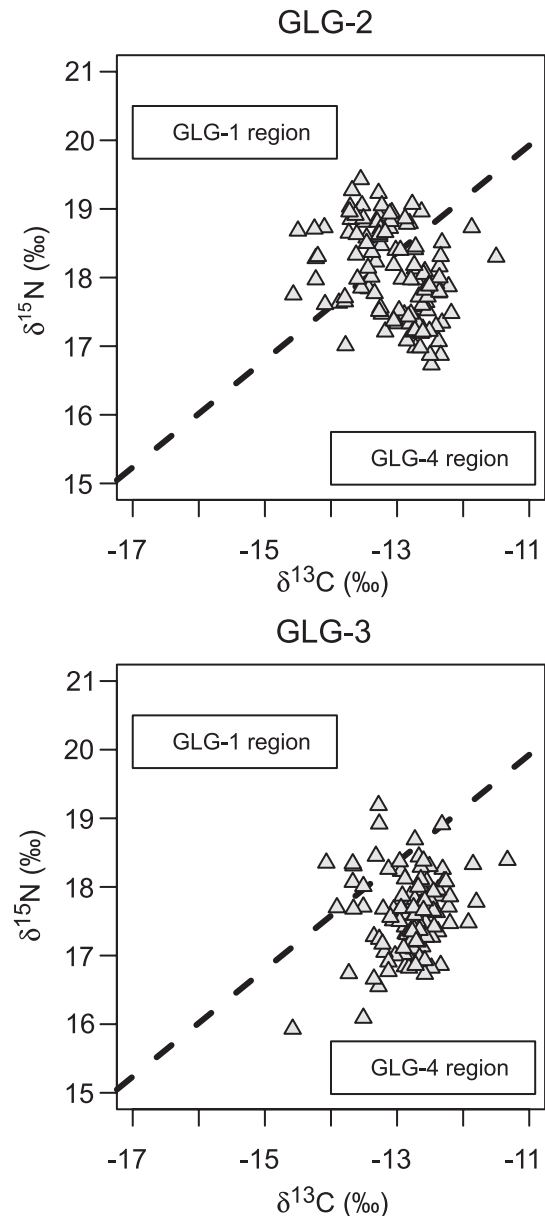
The measurements at all four locations were correlated with each other (correlation coefficients were between 0.7 and 0.9). In all cases, individual GLG widths (Table 4) decreased significantly from one GLG to the next ($P < 0.001$). The relationships between the cumulative GLG width (the mean of the anterior and posterior enamel root junction measurements) and the ventral standard body length from Calkins et al. (1998) and standard body length from Winship et al. (2001) were linear (corrected $r^2 = 0.99$ and 0.86 , respectively). The relative contribution of the width of GLG-1 to the total growth through the 4th year averaged 32.5%; this decreased to 26.1% in GLG-2, 22.4% in GLG-3, and 19.0% in GLG-4. These compare with relative size contributions of ventral standard length in the first 4 years (calculated from Calkins et al. 1998), of 30.7%, 27.1%, 23.2%, and 18.9% in years 1–4, respectively.

GLG size, the regime shift, and age at weaning

Except for those cohorts that were pups or yearlings at the beginning of the North Pacific regime shift, the proportion of animals classified as nursing into their 2nd year increased ($P = 0.02$ from approximately 0.35 to 0.52 (Fig. 4) during 1960–1983. In contrast, the observed proportion of animals still nursing past their 1st year was only 0.23 during the time of the regime shift, which is less ($P < 0.01$) than the predicted value of 0.45 based on the trend from the remaining data.

The mean width in GLG-1 was less ($P < 0.01$) in animals

Fig. 3. Relationships between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in GLG-2 and GLG-3 of teeth from Steller sea lions with the linear discriminant function (LDF) that best separated GLG-1 and GLG-4 superimposed on the figure (as in Fig. 2). Points lying above the discriminant line were classified as more similar to GLG-1 and those below were classified as more similar to GLG-4. Approximately 60% of GLG-2 and approximately 90% of GLG-3 samples were classified as similar to GLG-4 (“probably weaned”) samples.



classified as nursing at age 2 years than those classified as weaned at age 2 years. However, in GLG-2, the mean width was larger ($P < 0.01$) in the nursing animals. The total width of the first two growth layers was no different in those that were weaned or nursing at age 2 years. Since the tooth size measurements appear to scale to body length, this also suggests that (i) weaned animals were probably longer at the end of their 1st year than animals that continued to nurse, (ii) those that continued to nurse grew faster in their 2nd year, and (iii) by the end of the 2nd year, there was no size

Table 2. Discriminant analysis results of isotopic signatures of teeth from Steller sea lions.

GLG-1	GLG-2	GLG-3	GLG-4	<i>n</i>	Interpretation
(A) Logically possible, but not consistent with single point weaning					
1	4	4	1	1	Weaned before 2nd year, but nursing in the 4th year
1	1	4	1	1	Weaned before 3rd year but nursing in the 4th year
				2	Total
(B) Not possible					
4	4	4	4	1	Never nursed
4	1	4	4	1	Nursing only in the 2nd year
				2	Total
(C) Consistent with single point weaning					
1	1	1	1	2	Not weaned by the 4th year
1	4	4	4	62	Weaned before the 2nd year
1	1	4	4	31	Weaned before the 3rd year
1	1	4	4	8	Weaned before the 4th year
				103	Total

Note: Numbers of SSLs whose isotopic signatures in GLGs 1–4 were classified as being similar to GLG-1 (1) or GLG-4 (4).

Table 3. Mean, standard deviation, and sample size of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in GLG-1 to GLG-4 of teeth from Steller sea lions.

GLG	$\delta^{15}\text{N}$ (‰)		$\delta^{13}\text{C}$ (‰)		<i>n</i>
	Mean	SD	Mean	SD	
Age 1					
1	18.735	0.507	-13.706	0.669	62
2	17.645	0.430	-12.747	0.456	62
3	17.346	0.473	-12.732	0.464	62
4	17.408	0.410	-12.800	0.431	62
Age 2					
1	18.770	0.490	-13.742	0.460	31
2	18.556	0.379	-13.460	0.498	31
3	17.708	0.407	-12.748	0.347	31
4	17.554	0.385	-12.773	0.299	31
Age 3					
1	18.851	0.491	-13.741	0.467	8
2	18.914	0.354	-13.584	0.278	8
3	18.375	0.362	-13.400	0.271	8
4	17.864	0.487	-12.874	0.581	8

Note: The statistics were calculated separately by estimated age of weaning for the 101 animal in Table 2, which the discriminant analysis classified as being weaned by the beginning of their 4th year.

difference. Except for animals born near the time of the regime shift, the width of GLG-1 in weaned animals decreased significantly over the course of the study ($P = 0.04$) (Fig. 5); there was no significant trend ($P = 0.15$) in nursing animals. The mean width of GLG-1 in the weaned animals for the 1975–1976 cohorts was 8.2% higher ($P < 0.01$) than the predicted value based on the trend from the remaining data.

The combination of the trends in Fig. 5 indicates that GLG-1 size in nursing and weaned animals converged during our study. Furthermore, the relationship between that size difference and the proportion of animals nursing into their 2nd year (Fig. 6) suggests that (except for the cohorts born

Table 4. Sample size and width (mean and SD) of GLGs at four locations in teeth of Steller sea lions.

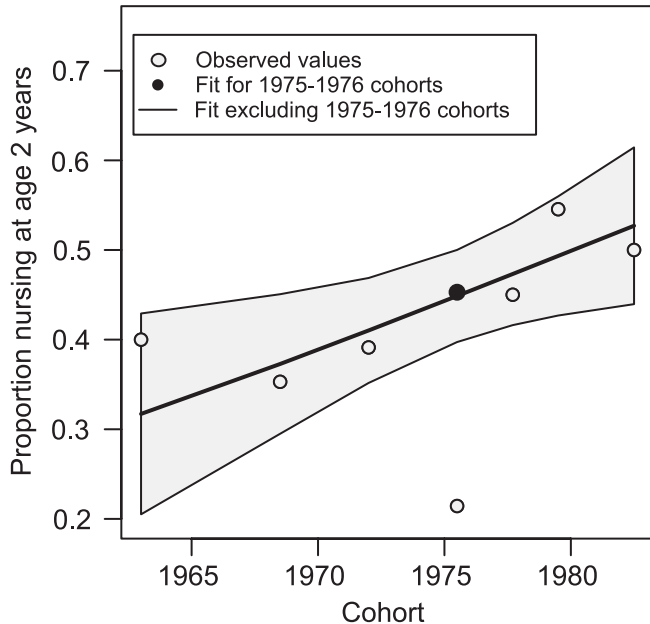
GLG	<i>n</i>	Width (mm)	
		Mean	SD
(A) Anterior enamel root junction			
1	109	1.346	0.251
2	107	1.078	0.244
3	83	0.910	0.153
4	35	0.735	0.156
(B) Posterior enamel root junction			
1	110	1.407	0.233
2	110	1.131	0.246
3	100	0.997	0.171
4	53	0.878	0.132
(C) Anterior secondary junction			
1	0		
2	106	1.131	0.264
3	97	0.939	0.161
4	76	0.860	0.178
(D) Posterior secondary junction			
1	0		
2	108	1.207	0.268
3	101	0.995	0.191
4	81	0.819	0.140

near the time of the North Pacific regime shift) a larger mean difference in GLG-1 width of weaned and nursing animals is associated with a smaller proportion of animals nursing into the 2nd year. The 1975–1976 cohorts again stand out in this relationship; based on the GLG-1 width difference between weaned animals and those still nursing, they would be predicted to have had more than 1.5 times their members still nursing at age 2 years (38%) instead of the observed 23%.

Discussion

Our analyses build a case that the stable isotope signa-

Fig. 4. Estimated portion of Steller sea lion pups that were nursing at age 2 years. The rate increased ($P < 0.02$) except for the 1975–1976 cohorts, which were pups and yearlings at the beginning of the North Pacific regime shift. The observed rate for the 1975–1976 cohorts (0.23) was significantly less ($P < 0.01$) than the predicted rate of 0.45 based on regression using the remainder of the data. The shaded area is the approximate 95% interval for the regression.

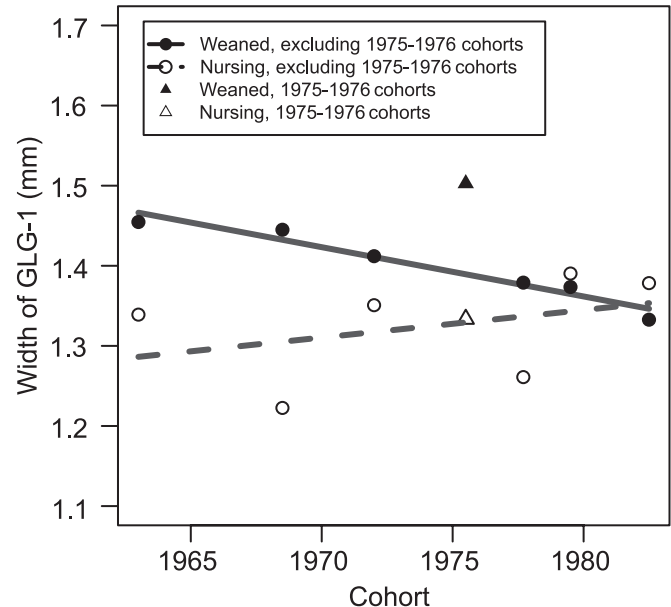


tures in the teeth of SSLs are a weaning signature. Our results suggest that (i) the age of weaning in SSLs varies over time, (ii) almost all individuals were weaned before the end of their 3rd year, and (iii) there was a change in weaning or survival patterns during the North Pacific climate regime shift.

There is potential for bias in the interpretations. If teeth were sectioned at an angle, so that one (or more GLGs) was missed, we might have mistaken GLG-2 for GLG-1 or fetal dentine for GLG-1. This scenario would have caused a sample thought to be from GLG-1 to have been from another part of the tooth, and thus to have had an isotopic signature more similar to GLG-4. This factor could explain the results for the samples from the two animals that were predicted not to have been nursing in their 1st year (Table 2). Samples from another two animals were not consistent with the idea of “single point” weaning (Table 2). At face value, the discriminant analysis predicts that they skipped nursing for a year or more and resumed nursing in their 4th year. To our knowledge, this has not been documented in field studies. One would expect that a mother SSL would stop lactating if her young had weaned; if the young SSL skipped nursing for a year or more and then resumed nursing, it possible that the mother had given birth to another pup and that the older offspring had resumed nursing.

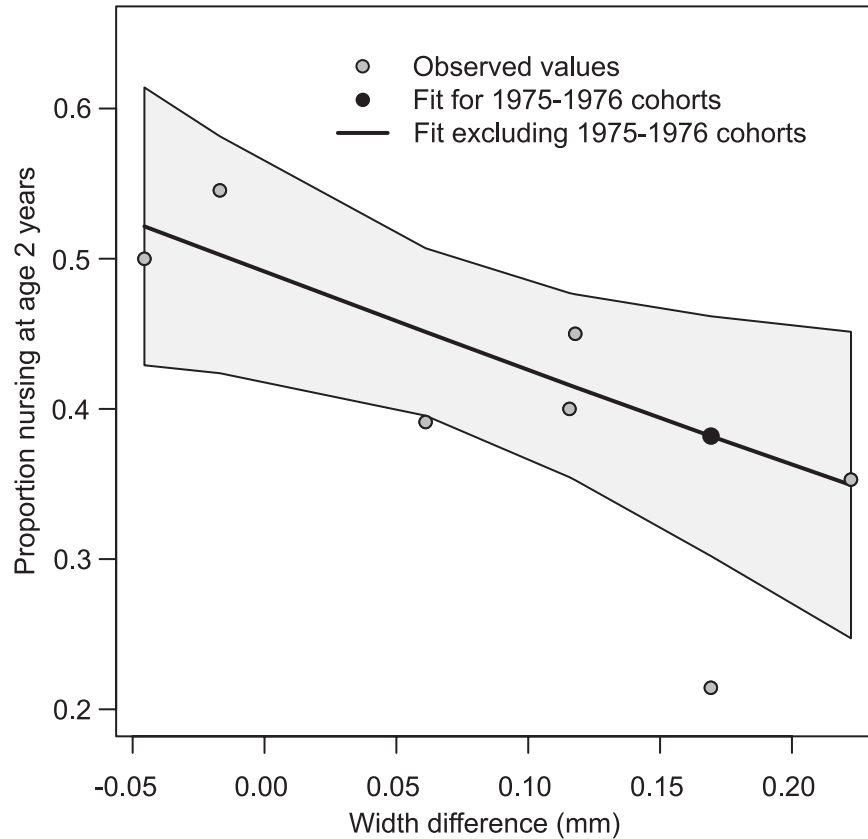
We must also ask if any wild diet that SSLs consume could have produced the different stable isotope values that we observed in GLG-1 and GLG-4. The $\delta^{13}\text{C}$ signature is affected by water mass and proximity to shore (Hobson et al. 2004b). This may have been especially important in the

Fig. 5. Mean width of GLG-1 for those Steller sea lions “weaned” and still “nursing” at age 2 years. Each point represents a mean that was calculated over a group of cohorts. The GLG width in the weaned animals decreased (except for the 1975–1976 cohorts, which were pups and yearlings at the beginning of the North Pacific regime shift) approximately 8% during the study. There was no significant trend in the width of GLG-1 in animals that were still nursing in their 2nd year.



regime shift years when SSLs may have been foraging in different water masses, eating new prey, or seeking their usual prey in different locations. It is also possible that prey for adult females changed during regime shift, so what looks like weaning may in fact be a different signature coming from the nursing mother. However, we think this is unlikely. The prey items listed in Sinclair and Zeppelin (2002), mostly fishes and cephalopods, could not have caused these differences because they would have required the diets of young SSLs to have changed to higher ^{15}N and lower ^{13}C . Since ^{15}N and ^{13}C are positively correlated in the food web, such a change would seem unlikely as an increase in ^{15}N would also cause an increase in ^{13}C . Predation upon nursing marine mammals by juvenile SSLs could account for the pattern (e.g., Muir et al. 1995). Gentry and Johnson (1981) observed older juvenile male SSLs eating northern fur seal pups at St. George, Alaska. Such a behavior among 2- or 3-year-old animals could explain the prediction from the discriminant analysis that two animals resumed nursing after a hiatus of a year or more. However, our sample consisted of only females, and Gentry and Johnson (1981) did not observe female SSLs eating northern fur seals; this behavior was not reported at St. Paul Island, only 65 km from St. George Island. The male SSLs that were observed consuming northern fur seals were large juveniles, about 400–500 kg (R. Gentry, personal communication (2007)), which according to age-size keys (Winship et al. 2001) makes them approximately 7 or 8 years old. Thus, we do not think that predation upon nursing marine mammals by young SSLs is a likely explanation of the stable isotope patterns that we observed.

Fig. 6. The difference in mean GLG-1 width of weaned and nursing Steller sea lions versus the proportion estimated to still be nursing at age 2 years. A linear model based on all cohorts except the 1975–1976 cohorts and a shaded area defining the 95% confidence interval of the fitted model are also shown.



Age-at-weaning figures provided by Trites et al. (2006) were only approximate. Our estimated distribution of age at weaning from the discriminant analysis is similar but perhaps somewhat older than that reported for females in Trites et al. (2006). This effect could be due to different methods in the two studies. Their results were from an observational study with some animals lost to follow-up; in fact, they suggest that their estimated ages at weaning may be biased on the low side because of this effect. Animals dropping out of the study could bias the estimated age at weaning if later weaning animals were not available for resighting as frequently as those weaned at a younger age or if nursing pups travel with their mothers and move to other rookeries or haul out more frequently than weaned pups. Our results suggest that age at weaning can change over time. The duration of time covered by our two studies was very different: the Trites et al. (2006) study ranged over 3 years and our study ranged over 20 years. We expect to see greater variation in a study conducted over a longer time period. In spite of all these differences, the distributions of age at weaning appear similar.

Our estimates could be biased because our sample consists of animals that survived to at least 4 years of age. If a longer period of nursing conveys survival benefits, then we expect that the mean age at weaning would be biased on the high side. On the other hand, if the situation is similar to that of the Galápagos fur seal, *Arctocephalus galapagoensis* Heller, 1904 (Horning and Trillmich 1999), a shorter

nursing period could indicate better foraging conditions for both mothers and juveniles, and thus be associated with higher juvenile survival. Better foraging conditions may not necessarily be defined by more or better prey so much as more accessible prey. In the case of northern fur seals, better foraging conditions are created by close proximity of the rookery sites to the continental shelf edge. Faster pup growth is achieved under these conditions in part, because the mother spends less time away feeding and more time attending to her pup (Antonelis et al. 1997).

No direct work on the determinants of weaning for SSLs has been done. Particularly, it has not been previously documented if a shortage of food results in less attendance to pups by adult females, or greater attendance as described for other otariids. In the Galápagos fur seal, Horning and Trillmich (1999) found that faster growing pups were weaned earlier and that the period of maternal dependence was less if foraging conditions for juveniles were good. In the subantarctic fur seal, (*Arctocephalus tropicalis* (J.E. Gray, 1872)), Beauplet et al. (2005) found that early survival was positively influenced by pre-weaning growth rates and environmental conditions considered beneficial for post-weaning survival (measured by oceanic conditions near the study site). Our finding, the width of GLG-1 was greater in animals that were not nursing in their 2nd year, suggests that faster growing pups wean earlier. Our comparison of the combined width of GLG-1 and GLG-2 indicated that weaned animals in their 2nd year grew more slowly than

those that continued to nurse; however, by the end of the 2nd year, there was no difference between the two groups.

Our analysis indicates that the proportion of animals nursing into their 2nd year increased during our study period (1960–1983). If adult females that nursed their pups into their 2nd or 3rd year were less likely to give birth or to successfully raise their new pups into the 2nd year, then the consequence is a decrease in either fecundity or juvenile survival in the population. That result is consistent with the modeling work of York (1994) and Pascual and Adkison (1994), who suggested that SSL juvenile survival and possibly fecundity decreased during 1975–1985. Our result, the width of GLG-1 was greater in animals not nursing in their 2nd year, suggests that faster growing pups wean earlier. Our comparison of the combined width of GLG-1 and GLG-2 indicated that weaned animals in their 2nd year grew more slowly than those that continued to nurse; however, by the end of the 2nd year, there was no difference between the two groups.

The greatly reduced rate of nursing at age 2 years for 1975–1976 cohorts (Fig. 4) indicates that the beginning of the regime shift presented environmental changes great enough to affect the life histories of young SSLs and their mothers. The combination of reduced nursing and the abrupt increase in the width of GLG-1 in the same cohorts (Fig. 5) suggests that smaller animals suffered greater mortality than in the other years, and that the higher mortality rates for smaller animals appear to have affected both those that weaned and those that continued to nurse.

The 1975–1976 regime shift was important but perhaps not the only significant factor documented in our analysis that had the potential to affect SSL demography. Throughout the period covered by our study, something else occurred that caused a significant increase in age at weaning (Fig. 4) and changed the relative size of animals that were weaned or continued nursing in their 2nd year (Fig. 5). The result of this change was a convergence in the 1st year growth of the two groups by the end of the period covered by the study. The response owing to the regime shift was important but was an additional “blip” on a long-term change (Figs. 4, 5, 6). We hypothesize that these results are consistent with a change in relative mortality of weaned pups and those that continued to nurse. Theory suggests that a reduction in available resources for adult female mothers can cause a response that could be characterized as a switch from a “live-fast” to a “live-slow” life history (Promislow and Harvey 1990). The cause of such a change could be a density-dependent response to reduced prey availability that could have been caused by a reduction in SSL carrying capacity as a result of competition with fishing or some unknown factor. Newsome et al. (2007) found a significant decrease in $\delta^{13}\text{C}$ over the last 60 years in the teeth of northern fur seals; a decrease in $\delta^{13}\text{C}$ was also reported in SSL teeth by Hobson et al. (2004b) over a shorter time period. Newsome et al. (2007) attribute this change to a long-term decrease in primary productivity in the Gulf of Alaska and the Bering Sea; such a decrease in primary productivity could explain our results. We also should not overlook the possibility that we are observing either a direct or a residual effect of shooting large numbers of SSL pups during 1963–1972, which negatively affected the quality of females in the

breeding population. If that harvest differentially selected larger weaned pups, it could explain both the decrease in size of weaned pups and the increase in the rate of nursing that we observed among the survivors of the harvest. Such a demographic hangover was an unexpected effect observed in the northern fur seal population following a commercial harvest of females from 1956 to 1968 (York and Hartley 1981; Trites and York 1993). Managers of northern fur seals had predicted that reproductive rates would increase in a density-dependent fashion if they reduced the population, and the same number of subadult males would be harvested from a smaller breeding population (Anonymous 1955). However, contrary to expectations, the harvest never rebounded following the planned herd reduction (York and Hartley 1981). Even more puzzling was the result that age at first reproduction actually increased, juvenile survival decreased (York 1983), and overall reproductive rates decreased (Trites and York 1993) in the cohorts that were subject to the female harvest. Thus, it is possible that our documented changes in SSLs and those previously documented in northern fur seals might have resulted from the selective killing of “high-quality” females by both processes. The large-scale shooting of SSL females in the late 1970s until the early 1990s could have also had that effect and possibly prolonged this process until the late 1990s if high-quality females were differentially killed.

We believe that the techniques described in our paper have great potential. It may be possible to construct tooth-ring chronologies, which is similar to tree-ring chronologies, that could provide us a history of weaning age and growth in young SSLs. These techniques could provide a link between the biological and the demographic factors used to explain the SSL decline. A stable isotopic analysis of fetal dentine, laid down in the last trimester of pregnancy, could provide additional information on the changing contribution of maternal quality through time. It is our hope that these studies go forward with the analysis of more recent samples.

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