

## Age at weaning of California sea lions depends on colony latitude

Martha P. Rosas-Hernández<sup>a,1,2</sup>, Claudia J. Hernández-Camacho<sup>a,\*</sup>, David Aurioles-Gamboa<sup>a,3</sup>, Andrew W. Trites<sup>b</sup>

<sup>a</sup> Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional, Laboratorio de Ecología de Pinnípedos "Burney J. Le Boeuf", 23096 La Paz, Baja California Sur, Mexico

<sup>b</sup> Marine Mammal Research Unit, Institute for the Oceans and Fisheries, University of British Columbia, V6T 1Z4 Vancouver, British Columbia, Canada

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### ABSTRACT

The age at which sea lions wean can vary significantly between years and among populations. It is an important life-history parameter that is influenced by environmental conditions and can drive changes in sea lion numbers. However, knowing when weaning begins and ends is difficult to determine. We developed a method (using Fourier analysis) to identify the lactation period from changes in the  $\delta^{15}\text{N}$  profiles of vibrissae from juvenile California sea lions—born in three colonies in Mexico. We sectioned vibrissae from 15 juvenile California sea lions (aged approximately 12 months) into 33–74 segments of similar weight. We measured  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  for each vibrissa segment and assigned dates to each one using site-specific vibrissa growth rates. We also compared the  $\delta^{15}\text{N}$  profiles that corresponded to the pup stage on the juvenile vibrissae with  $\delta^{15}\text{N}$  values of adult female vibrissae from the same colonies to validate the dietary transition from milk to fish identified by the Fourier analysis. We found that pups began supplementing their milk diet with fish at different times between colonies—ranging from 3 to 5 months old (San Esteban Island), 5–7 months old (Santa Margarita Island), and > 12 months old (Los Islotes Island). All pups were > 1 year old when weaned. The longer lactation period in Mexico contrasts with the shorter 10–11 months age at weaning recorded at northern colonies of California sea lions along the US Pacific coast (San Miguel Island). The difference in lactation duration among regions likely reflects latitudinal differences in marine productivity, and a lower nutrition quality of prey available to California sea lions in Mexico. Our study augments the limited knowledge of weaning in California sea lions and provides a means to determine weaning in other species.

### 1. Introduction

Age at weaning among sea lions and fur seals is a life-history trait that is primarily determined by environmental conditions experienced by mothers during lactation (Ferguson, 2006; Sepúlveda and Harcourt, 2021). Weaning occurs when pups have completely transferred their nutritional dependence from milk to solid foods. Age at weaning influences juvenile survival rates and birth rates (i.e., the frequency of annual births)—and thereby plays an important role in the dynamics of pinniped populations (Beauplet et al., 2005; McIntosh and Pitcher, 2021; Stearns, 1989; Trites, 2021).

The duration of lactation in sea lions and fur seals ranges from 4 months to 3 years (Riet-Sapriza, 2019). This has been determined from re-sighting known-age suckling pups, identifying stomach contents of dead animals, determining the remains of solid food in scats, and measuring stable isotope concentrations in tooth growth layers (Avery and Zinn, 2023; Bowen, 1991; Francis and Heath, 1991b; Hastings et al., 2021; Newsome et al., 2006). However, these methodologies only approximate when lactation occurs and cannot identify when the weaning process begins and ends, and what pattern it follows.

An alternative technique for reconstructing the diet history of mammals is to measure the proportions of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  along the

\* Corresponding author at: Av. Instituto Politécnico Nacional s/n Col. Playa Palo de Santa Rita Apdo. Postal 592. 23096 La Paz, B.C.S., Mexico.

E-mail addresses: [mrosas@cicese.mx](mailto:mrosas@cicese.mx) (M.P. Rosas-Hernández), [jcamacho@ipn.mx](mailto:jcamacho@ipn.mx) (C.J. Hernández-Camacho), [a.trites@oceans.ubc.ca](mailto:a.trites@oceans.ubc.ca) (A.W. Trites).

<sup>1</sup> Present address: Consejo Nacional de Humanidades, Ciencias y Tecnologías. Av. Insurgentes Sur 1582, Col. Crédito Constructor. Alcaldía Benito Juárez, C.P. 03240, Mexico City.

<sup>2</sup> Present address: Centro de Investigación Científica y de Educación Superior de Ensenada, Unidad La Paz, Laboratorio de Aeroecología Marina, 23,050 La Paz, Baja California Sur, Mexico.

<sup>3</sup> Present address: Facultad de Ingeniería Ambiental, Universidad Popular Autónoma del Estado de Puebla, 72,410 Puebla, Puebla, Mexico.

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length of their vibrissae (Lowther and Goldsworthy, 2016).  $\delta^{15}\text{N}$  reflects the trophic level of prey consumed, and can be used to assess ontogenetic changes (Elorriaga-Verplancken et al., 2013; Newsome et al., 2010) due to the 3–4 ‰ enrichment that occurs between consumer and prey or between trophic levels (DeNiro and Epstein, 1978). Tissues that are metabolically inactive after deposition (e.g., vibrissae or dentin) provide a record of successive changes of growth that represent months or years of information about diet depending on the pinniped species (Cherel et al., 2009; Hiron and Schell, 2001; Rosas-Hernández et al., 2018c). These changes can be associated with ontogenetic shifts, and used to identify the lactation period, the transition to a mixed diet, and finally weaning and adulthood (Elorriaga-Verplancken et al., 2013; Kernaléguen et al., 2012; Kernaléguen et al., 2016; Stegall et al., 2008). However, identifying when the ratio of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  begins to change is challenging.

We developed a method (using Fourier analysis) to identify dietary changes in the  $\delta^{15}\text{N}$  profiles of vibrissae taken from juvenile sea lions—and applied it to California sea lions (*Zalophus californianus*) born at three breeding colonies in Mexico. California sea lion breeding colonies occur from Año Nuevo Island and the Farallon Islands on the Channel Islands in California, USA (Bartholomew and Boolootian, 1960; Lowry and Forney, 2005) to Santa Margarita Island in the southern part of the Baja California Peninsula, and within the Gulf of California in Mexico (Fig. 1) (Le Boeuf et al., 1983; Lowry and Maravilla-Chavez, 2005; Peterson and Bartholomew, 1967). Breeding occurs from June to August, but relatively little is known about the lactation period (Heath, 1989; Odell, 1975). On the northern island of San Miguel in the United States (Fig. 1), the lactation period of known-aged individuals is 10–11

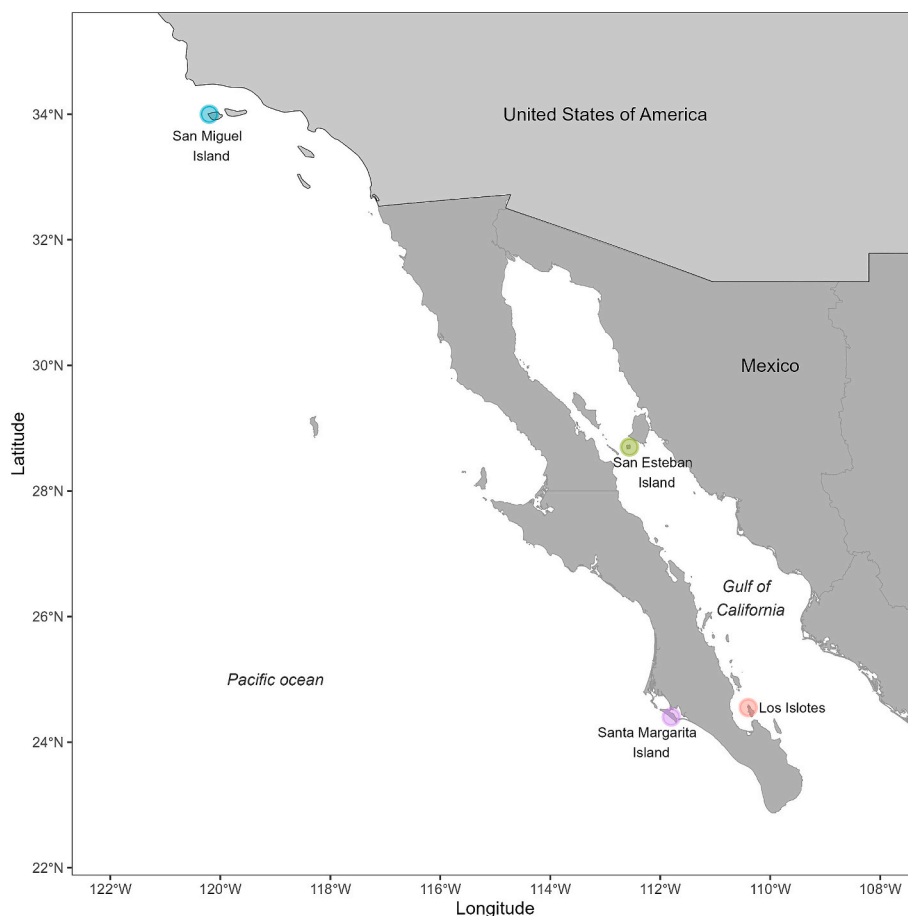
months, but can be as short as ~6 months when environmental conditions during El Niño events are dire (Harris, 2016; Melin et al., 2008; Melin et al., 2000; Odell, 1981). In contrast, lactation at Santa Margarita Island (Mexico) has been estimated to last 12–14 months based on stable isotope analysis of tooth growth layers (Newsome et al., 2006).

In the present study, we measured the  $\delta^{15}\text{N}$  profiles along the length of vibrissae removed from juvenile California sea lions (aged ~1 y). We then applied a Fourier analysis to the time series of  $\delta^{15}\text{N}$  values to determine change points on the vibrissae (i.e., when milk consumption began following fetal growth, and when consumption of solid food was initiated). We also compared the  $\delta^{15}\text{N}$  of young-of-the-year with  $\delta^{15}\text{N}$  values in the vibrissae of adult female California sea lions as a point of reference for prey consumption. We thus tested a method to quantitatively assess the weaning process in pinnipeds from changes in  $\delta^{15}\text{N}$  in vibrissae—and examined how the timing of weaning of California sea lions varies between three colonies in Mexico (Santa Margarita, San Esteban, and Los Islotes Islands; Fig. 1). Our study augments the limited knowledge of weaning in California sea lions and the factors that influence it—and describes a methodological approach that can be applied to determine weaning in other species.

## 2. Material and methods

### 2.1. Study area

Vibrissae were collected at three California sea lion breeding colonies in Mexico with different population sizes and distinct environmental levels of seasonality and productivity (Rosas-Hernández et al.,



**Fig. 1.** Location of San Esteban (green point) and Los Islotes (red point) Islands in the Gulf of California, Santa Margarita Island (purple point) off the southwest coast of Mexico's Baja California Peninsula and San Miguel Island (blue point) of the southwest coast of USA's. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2018a) (Fig. 1): San Esteban Island, Los Islotes Island, and Santa Margarita Island.

San Esteban Island is situated in the central region of the Gulf of California, in a marginal sea with a high evaporation rate. The major productivity in this region is driven by seasonal upwelling, which is caused by strong winds and extensive tidal mixing throughout spring and fall. The chlorophyll-*a* concentration (Chla) is  $3.54 \text{ mg m}^{-3} \pm 0.19 \text{ mg m}^{-3}$ , and the average sea surface temperature (SST) is  $23.1 \text{ }^\circ\text{C} \pm 0.48 \text{ }^\circ\text{C}$  (Fig. S1) (Salas-de-León et al., 2011; Simpson et al., 1994).

Los Islotes Island, located in the southern Gulf of California, is influenced by a mesoscale cyclonic structure referred to as a cyclonic eddy. This cyclonic structure occurs during the late spring, and is forced by the local wind field that causes upwelling and promotes high concentrations of nutrient and chlorophyll-*a* levels of  $0.94 \text{ mg m}^{-3} \pm 0.07 \text{ mg m}^{-3}$  and SST is of  $25.2 \text{ }^\circ\text{C} \pm 0.34 \text{ }^\circ\text{C}$  (Fig. S1) (Coria-Monter et al., 2017).

In contrast to San Esteban and Los Islotes Islands, Santa Margarita Island is located on the southwestern coast of the Baja California Peninsula in an area characterized by its proximity to the large coastal lagoon system of Magdalena Bay that is an important source of shallow-water prey. The productivity of waters near Santa Margarita Island depends on major seasonal upwelling during spring as well as the productive California Current System. Chlorophyll-*a* values average  $1.97 \text{ mg m}^{-3} \pm 0.22 \text{ mg m}^{-3}$ , and SST averages  $22.2 \text{ }^\circ\text{C} \pm 0.31 \text{ }^\circ\text{C}$  (Fig. S1) (Álvarez-Borrego et al., 1975; Zaytsev et al., 2003).

## 2.2. Sample collection and processing

Five juvenile California sea lions thought to be about one year old were captured at each colony ( $n = 15$ ) using hoop nets on Santa Margarita Island (June 11–12, 2011), San Esteban Island (June 23–28, 2011), and Los Islotes Island (May 05–06, 2012) (Table 1), which corresponds with the reproductive season of the species. We identified pups that turned one year old as juveniles based on their size and the date when captured relative to the breeding season. Newborn pups typically measure on average 73.7 cm (SE = 0.48) for females, and 78.3 cm (SE = 0.38) for males, while one-year-old immatures measure 119 cm (95 % CI 118.1, 120.4) for females and 122 cm (95 % CI 119.9, 124) for males (Laake et al., 2016). Juveniles were masked and chemically sedated with 5 % isoflurane, and later maintained with 3 % isoflurane. Each juvenile was weighed in a net using a tripod and a digital scale with a 100 kg capacity ( $\pm 0.1$  kg precision). Body length was measured to the nearest centimeter from the tip of the nose to the tip of the tail (belly down) with a tape-measure.

The longest mystacial vibrissa was pulled consistently from the left side of each juvenile from the root using tweezers. Each vibrissa was placed in a paper envelope labeled with the sample ID and collection date. Samples were transported to the Laboratorio de Ecología de Pinnípedos “Burney J. Le Boeuf” (“Burney J. Le Boeuf” Pinniped Ecology Laboratory) at the Centro Interdisciplinario de Ciencias Marinas (CICIMAR; Interdisciplinary Center for Marine Sciences) in La Paz, Baja California Sur, Mexico.

The total length of each vibrissa was recorded and the cuticle surrounding the root was removed to eliminate the lipids present in this layer. Each vibrissa was then washed with phosphate-free soap, distilled water, and a 2:1 chloroform-to-methanol mixture to remove any contaminants or lipid residue. A nail clipper was used to remove a segment

**Table 1**

Mean weights and lengths ( $\pm$ SD) of 15 juvenile California sea lions sampled at three breeding colonies in Mexico.

Colony	n	Collection Date	Weight (kg)	Length (cm)
Santa Margarita Island	5	June 2011	$35.09 \pm 6.09$	$117.00 \pm 7.23$
San Esteban Island	5	June 2011	$39.12 \pm 6.28$	$125.06 \pm 4.42$
Los Islotes Island	5	May 2012	$32.28 \pm 4.58$	$114.08 \pm 3.35$

from each root weighing  $1.0 \pm 0.2$  mg.

The remaining length of each vibrissa was then measured—and a subsequent segment was again removed with the nail clipper. This procedure was repeated until the entire vibrissa was cut into evenly weighed pieces. The segments weighing  $\sim 1.0 \pm 0.2$  mg were of varying lengths because vibrissae are thinner at the tip than at the root (i.e., the segments were shorter at the root and longer at the tip). The segments were stored in tin capsules for isotopic analysis (Table 2).

Due to the high costs of stable isotope analysis, we could only analyze five vibrissae per colony. However, we analyzed the entirety of the 15 vibrissae to have better detail of the isotopic changes related to diet shifts.

## 2.3. Stable isotope analysis

Determining the C and N isotopic ratios through the combustion of  $\text{CO}_2$  and  $\text{N}_2$  was carried out at the Stable Isotope Facility at the University of California at Davis, USA. The samples were analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (PDZ Europa 20–20, Sercon Ltd.) with an accuracy of  $\pm 0.2$  ‰ for both isotopes. The isotopic ratios are expressed as delta ( $\delta$ ):  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C} = 1000 * [(R_{\text{sam}}/R_{\text{std}}) - 1]$ , where  $R_{\text{sam}}$  and  $R_{\text{std}}$  are the ratios of  $^{15}\text{N}/^{14}\text{N}$  or  $^{13}\text{C}/^{12}\text{C}$  of the sample and the standard, respectively. The standards were Vienna-Pee Dee Belemnite limestone (V-PDB) for carbon and atmospheric  $\text{N}_2$  for nitrogen. Units are expressed as parts per thousand (‰). An ANOVA test was used to compare the isotopic values of  $\delta^{15}\text{N}$  between colonies.

## 2.4. Data analysis

A date was assigned to the isotopic values for each vibrissa based on the day of collection and estimated vibrissae growth rate, as discussed below. All statistical tests were performed using R 4.2.2 (R Development Core Team, 2022).

### 2.4.1. Vibrissa growth rate

The growth rate (m) of otariid vibrissae has generally been reported as linear (Hirons and Schell, 2001; Rea et al., 2015). However, this is based on the vibrissae growth of adults. Among otariids, vibrissae grow faster during the juvenile phase; and grow at a constant rate once an otariid reaches adulthood (Rogers et al., 2016). Unfortunately, no study has previously quantified vibrissae's growth rates for younger age classes of California sea lions. Thus, we estimated a growth rate for our juvenile vibrissae.

We used the length of the longest vibrissae of 100 newborn pups (June 2011) and 43 pups roughly 2 months old (August 2011) from Santa Margarita Island to estimate growth rates. The pups captured in August were different from those captured in June. Generally, pups are born between late May and early July, with peak births occurring during

**Table 2**

Isotopic values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in vibrissae of adult female California sea lions. The lactation values for each colony were calculated by adding the fractionation value of 1.6 ‰ to the  $\delta^{15}\text{N}$  values (Stricker et al., 2015).

Breeding Colony	n	$\delta^{13}\text{C}$ ‰ mean $\pm$ SD	$\delta^{15}\text{N}$ ‰ mean $\pm$ SD	Lactation expected $\delta^{15}\text{N}$ (‰)
Santa Margarita Island <sup>a</sup>	8	$-14.62 \pm 0.8$	$20.15 \pm 0.4$	$21.75 \pm 0.4$
San Esteban Island <sup>b</sup>	10	$-13.71 \pm 0.5$	$21.24 \pm 0.5$	$22.84 \pm 0.5$
Los Islotes Island <sup>c</sup>	2	$-14.55 \pm 0.2$	$21.14 \pm 0.3$	$22.74 \pm 0.3$

<sup>a</sup> Data from Rosas-Hernández et al. (2018a)).

<sup>b</sup> Data from Rosas-Hernández et al. (2018b)).

<sup>c</sup> Data from Auriolles-Gamboa et al. (2017)).

the first two weeks of June (Boness et al., 1991; García-Aguilar and Aurióles-Gamboa, 2003; Oftedal et al., 1987b).

We used the data from newborn pups and 2-month-old pups on Santa Margarita Island to estimate vibrissae growth rates ( $m$ ) during the first two months of life according to:

$$m = \frac{L_2 - L_1}{T_2 - T_1} \quad (1)$$

where  $L_1$  is the average length at  $T_1$  (June), and  $L_2$  is the average length at  $T_2$  (August). The time ( $T_i$ ) represented by each vibrissa fragment ( $i$ ) was then determined using:

$$T_i = \frac{L_i}{m} \quad (2)$$

where  $L_i$  is the distance of that segment to the base of the vibrissa and  $T_i$  is the date that corresponds to that segment based on the growth rate calculated in Eq. 1. Note that length of the vibrissae at birth reflects growth occurring during the fetal stage, and that the difference between vibrissae length at birth and at 2 months old reflects growth that occurred while pups received milk. The vibrissa growth rate for the other two colonies was assumed to be the same as that at Santa Margarita Island.

#### 2.4.2. Lactation signature

We considered dependent pups and juveniles to only consume milk, and assumed pups and juveniles in weaning transition consumed a mixed diet (milk and solid food). We constructed the  $\delta^{15}\text{N}$  time series profile of each vibrissa based on the time interval associated with each segment. Using the estimated growth rate and knowing the segment's position along the vibrissa, we assigned a date to each segment. For some dates, only a single sample (vibrissae segment) was obtained, while for other dates there were two or three segments from different vibrissae. The isotopic profile of each colony (spanning the gestation, pup and juvenile growth phases) was then obtained by applying a loess smooth (formula  $y \sim x$  of the “ggplot2” package with 95 % confidence intervals); (Wickham, 2009) to the means of the vibrissae  $\delta^{15}\text{N}$  values using R 4.2.2 (R Development Core Team, 2022).

To identify significant changes in the isotopic signature that might reflect a change in diet, we performed a Fourier analysis using the function “periods” (González-Rodríguez et al., 2015) in MatLab on the previously calculated isotopic profile (loess method). The main parameters of the Fourier harmonic components are amplitude, period, and phase. The resulting periods reflect changes in the isotopic signature, and are sequentially ordered in terms of their statistical significance (González-Rodríguez et al., 2015). The “Periods” technique is a useful tool for detecting the frequency of variation in  $\delta^{15}\text{N}$  values where well-defined oscillatory patterns in the vibrissa isotope profile are lacking, as in our case study, where the patterns of lactating are difficult to observe (Rosas-Hernández et al., 2018c). The first period was considered the time from gestation to birth, and the second as the time from nursing to the transition to consuming solid food (a mixed diet of fish and milk).

In addition to using Fourier analysis, we used a second approach to determine the duration of lactation that compared measured  $\delta^{15}\text{N}$  values with expected  $\delta^{15}\text{N}$  values derived from the  $\delta^{15}\text{N}$  concentrations in the vibrissae of adult females sampled at the same colonies (Table 2) (Aurióles-Gamboa et al., 2017; Lowther and Goldsworthy, 2016; Rosas-Hernández et al., 2018c). In the case of Santa Margarita and San Esteban Islands, females were captured at the same time as juveniles to ensure that any effect of seasonality on isotopic values would be matched with that of the juvenile vibrissae (i.e., June 2011). However, females from Los Islotes were captured in June 2008, four years prior to when the vibrissae of juveniles were taken (i.e., May 2012). In all cases, the females were not the mothers of the captured juveniles. The estimated fractionation value (1.6 ‰) between the vibrissae of mothers and pups was added to the means and standard deviations of the  $\delta^{15}\text{N}$  (Lowther

and Goldsworthy, 2016; Rosas-Hernández et al., 2018c; Stricker et al., 2015). The isotopic information we considered for this analysis started at 71 mm measured from the tip to the root because this is the length of the vibrissae of the newborn pups and thus contained information on the gestation period.

### 3. Results

A mean of 37 vibrissa segments were analyzed for each juvenile California sea lion ( $n = 558$  segments). Mean vibrissa lengths were  $12.3 \pm 1.3$  cm from San Esteban Island,  $11.2 \pm 0.5$  cm from Los Islotes Island, and  $11.9 \pm 5.7$  cm from Santa Margarita Island (Table 3). Mean stable isotope concentrations ranged from  $-13.46 \pm 1.1$  ‰ to  $-14.68 \pm 0.4$  ‰ for  $\delta^{13}\text{C}$ , and from  $22.56 \pm 1.8$  ‰ to  $23.08 \pm 0.56$  ‰ for  $\delta^{15}\text{N}$  for the three colonies (Table 3, Fig. 2). Significant differences were found between the mean  $\delta^{13}\text{C}$  ( $F_{2, 555} = 336.6$ ,  $p < 0.001$ ) and mean  $\delta^{15}\text{N}$  ( $F_{2, 555} = 155.2$ ,  $p < 0.001$ ) values of the vibrissae from the three colonies.

#### 3.1. Vibrissa growth rate

The mean length of the California sea lion vibrissae of newborn pups collected at Santa Margarita Island in June 2011 was  $70.2 \pm 6$  mm. The length of the vibrissae collected from California sea lion pups at Santa Margarita Island in August 2011 was  $81.5 \pm 6$  mm. Thus, the vibrissae grew an average of  $11.3$  mm over the first 60 days of life at an estimated rate of  $0.19$  mm  $\text{d}^{-1}$ .

#### 3.2. Lactation signature

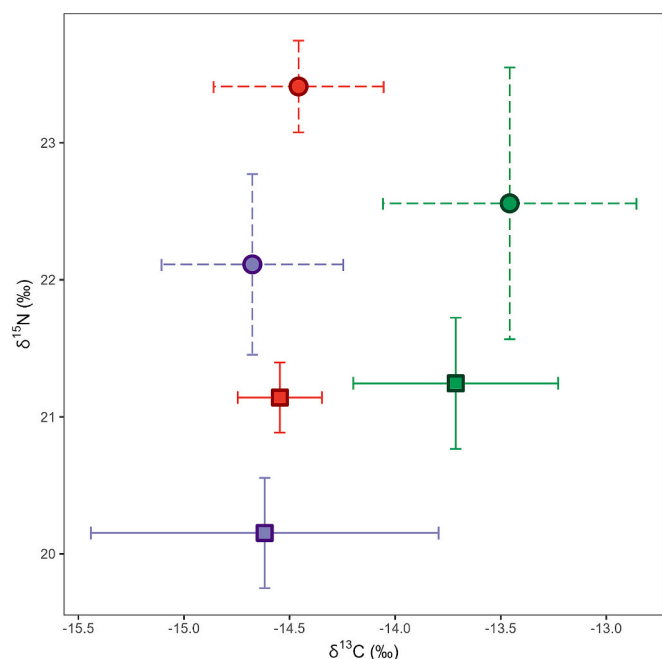
The Fourier analysis revealed two major periods in the  $\delta^{15}\text{N}$  isotopic pattern (from root to tip) at different lengths along the vibrissae that

**Table 3**

Summary of the vibrissae of 15 juvenile California sea lions collected at three breeding colonies, showing total lengths and mean ( $\pm$  SD) isotopic values of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  for all vibrissa segments analyzed.

Colony	ID	Vibrissa length (mm)	Number of segments	Segments analyzed	$\delta^{15}\text{N}$ ‰ mean $\pm$ SD	$\delta^{13}\text{C}$ ‰ mean $\pm$ SD
San Esteban Island	SE1	115	55	54	22.02 $\pm$ 0.84	-13.39 $\pm$ 0.52
	SE2	135	63	63	23.10 $\pm$ 0.57	-13.62 $\pm$ 0.61
	SE3	133	53	25	22.49 $\pm$ 0.71	-13.42 $\pm$ 0.61
	SE4	120	57	29	22.13 $\pm$ 1.20	-13.33 $\pm$ 0.54
	SE5	106	47	24	23.08 $\pm$ 0.56	-13.44 $\pm$ 0.73
Los Islotes Island	LI1	112	48	47	23.61 $\pm$ 0.23	-14.46 $\pm$ 0.21
	LI2	107	49	25	23.32 $\pm$ 0.24	-14.38 $\pm$ 0.41
	LI3	110	33	17	23.28 $\pm$ 0.40	-14.41 $\pm$ 0.32
	LI4	105	52	52	23.18 $\pm$ 0.28	-14.67 $\pm$ 0.42
	LI5	116	51	26	23.67 $\pm$ 0.22	-14.13 $\pm$ 0.42
Santa Margarita Island	SM1	139	74	74	22.30 $\pm$ 0.49	-14.66 $\pm$ 0.25
	SM2	111	43	21	22.40 $\pm$ 0.63	-14.68 $\pm$ 0.35
	SM3	102	46	46	21.57 $\pm$ 0.61	-14.28 $\pm$ 0.39
	SM4	150	61	31	22.10 $\pm$ 0.75	-15.11 $\pm$ 0.36
	SM5	116	49	24	22.40 $\pm$ 0.47	-14.93 $\pm$ 0.39





**Fig. 2.** Mean and standard deviation of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of vibrissae from juvenile (dots and dashed lines) and adult female (square) California sea lions from San Esteban Island (green), Los Islotes Island (red), and Santa Margarita Island (purple). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

differed significantly between colonies (Table 4).

At San Esteban Island, the periods identified occurred at 57 and 88 mm ( $r^2 = 0.984$ ,  $p < 0.001$ ), which suggests that lactation began at 57 mm (~05-27-2010) and lasted 13.7 months (411 days). However, some individuals began consuming a mixed diet at 88 mm (~ 10-28-2010), which means they consumed nothing but milk for the first 5.4 months; and transitioned to solid food for the next ~8 months.

At Los Islotes Island, the Fourier analysis only identified a single period at 46 mm (~ 05-31-2011;  $r^2 = 0.770$ ,  $p < 0.001$ ), which suggests that lactation occurred for more than 12.3 months (368 days). However, it is not known when the transition to solid food would have begun, or for how long it would have occurred.

Finally, at Santa Margarita Island, two periods were identified at 71 mm (~ 05-06-2010) and 115 mm (~ 12-12-2010;  $r^2 = 0.943$ ,  $p < 0.001$ ). They indicate that the pups consumed only milk for 8.36 months, and transitioned to fish over the next 5 months. Thus, the duration of lactation at this colony was 13.9 months.

**Table 4**

Lactation period represented by juvenile California sea lion vibrissae from San Esteban Island (SE), Los Islotes Island (LI), and Santa Margarita Island (SM) determined from the observed vibrissa length, and the growth rate and expected length based on a Fourier analysis. The length analyzed corresponds to the isotopic signal representing lactation. Time is the time represented in the vibrissa, and period corresponds to the length at which the Fourier analysis detected a significant change in the isotopic profile. Expected length is the period corresponding to nursing based on the Fourier analysis.

Colony	Total length (mm)	Observed		Expected		
		Length analyzed (mm)	Time (d)	Period (mm)	Expected length (mm)	Time (d)
SE	135	64	337	73	62	326
LI	116	45	237	75	41	216
SM	150	79	416	85	56	295

### 3.3. Lactation estimation

The duration of lactation as determined by the vibrissae of the juvenile California sea lions in Mexico varied between colonies. At Santa Margarita Island, vibrissae included more days of trophic information because the vibrissae were longer than those from the other colonies. In contrast, the vibrissa from Los Islotes Island provided information spanning a shorter time frame (Table 3), while the  $\delta^{15}\text{N}$  isotopic pattern in the vibrissae of juveniles from San Esteban Island suggests that lactation at this colony lasted longer than 11 months (based on the reference values from adult females and the expected values for nursing pups).

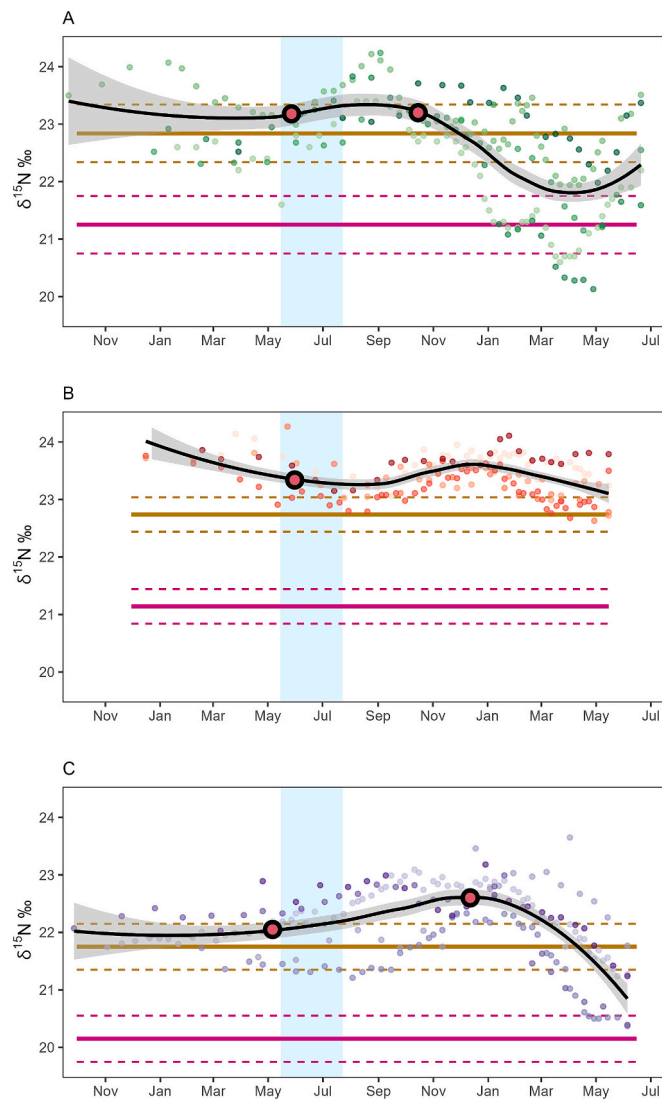
The vibrissae of the juveniles collected at San Esteban Island indicate that they only consumed milk during the first 2.5 months (~ 75 days, between 71 and 85 mm of the vibrissae). However, it is possible that they could have only consumed milk for their first 4 months (i.e., 1.5 months longer) had they been born in June rather than in August (Fig. 3A) (García-Aguilar and Aurióles-Gamboa, 2003). The subsequent decline in  $\delta^{15}\text{N}$  values suggests that the pups at San Esteban Island began a mixed diet as part of a transition that lasted over 8.6 months (~ 258 days). Finally, the isotopic pattern showed an increase in the last 10 mm of the vibrissa (~ 1.8 months), suggesting that the individuals at San Esteban Island continued consuming milk. This final increase in the isotopic pattern was influenced by three of the vibrissae that had values between the reference isotopic signatures for lactation and adult females. These three juveniles had a mixed diet, while the other two individuals had more impoverished values than those of the adult females (Fig. 3A).

The vibrissae of the juveniles from Los Islotes Island provided trophic information spanning 8 months. The  $\delta^{15}\text{N}$  pattern of these vibrissae suggests that these juveniles primarily consumed milk during this time (based on the reference values from females). However, the time at Los Islotes Island can be extended to 12 months if juveniles were born in June and not October, the month in which changes in the diet began to appear (Fig. 3B). According to the reference values, individuals consumed only milk during 8–12 months, although three juveniles showed values that suggest the integration of solid food into their diet. However, these values are still very enriched with respect to the reference values of the adult females at this colony, indicating that the proportion of milk in the diet was higher.

Finally, the vibrissae of the juvenile California sea lions from Santa Margarita Island contained 14 months of information about the lactation period. During the first 11.4 months (339 days, between 71 and 135 mm of the vibrissae), the isotopic values fell within the reference range for nursing pups. Thus, we assumed the diet of these juveniles was milk-based. In the following 2.6 months (between 135 and 150 mm of the vibrissae), the  $\delta^{15}\text{N}$  values were less enriched, but still exceeded the reference values of the adult female California sea lions, suggesting these individuals consumed a mixed diet. Based on the  $\delta^{15}\text{N}$  values, which did not fall within the reference values of the adult females (Fig. 3C), the nursing period at Santa Margarita Island lasted more than 14 months.

## 4. Discussion

The age at weaning has a significant influence on the population dynamics of sea lions (Trites, 2021) but is a difficult life-history parameter to determine. We developed an analytical method to document the weaning process from changes in the stable isotope ratios laid down in the vibrissa of pups and juveniles as they grew. The Fourier analyses we applied proved to be a rigorous means to identify when milk consumption and the transition to solid food began, as well as when weaning is complete. This analytical approach to quantify the weaning process can be readily applied to other species of mammals but requires knowing or estimating vibrissa growth rates. It can also be used to gain insights into the prey base available to support mothers and their



**Fig. 3.** General pattern of the  $\delta^{15}\text{N}$  signature along vibrissae from juvenile California sea lions from: A) San Esteban Island, B) Los Islotes Island, and C) Santa Margarita Island (black line and 95 % CI gray shadow). The blue shading represents birth period according to [García-Aguilar and Aurióles-Gamboa \(2003\)](#), which started from the length 71 mm. The magenta line represents the mean and standard deviation (dotted lines) of the isotopic values of adult female vibrissae for each colony. The purple line represents the mean, and standard deviation (dotted lines) of the expected lactation values from the fractionation of 1.6 ‰ ([Stricker et al., 2015](#)) applied to the female values. Red circles represent periods determined by Fourier analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

weaned offspring.

#### 4.1. Whisker growth rates

California sea lions are generally considered to be pups until 1 year of age and are classified as juveniles for the next 2 to 3 years ([Ofstedal et al., 1987a, 1987b](#)). We categorized the California sea lions we sampled as juveniles based on the size of the animals and the dates when captured. We also collected the whiskers relative to peak numbers of California sea lion births that usually occur during the last two weeks of June ([García-Aguilar and Aurióles-Gamboa, 2003](#)). At San Esteban and Santa Margarita Islands, sampling occurred in June, so the individuals were about 1 year old; while the individuals we captured in May at Los Islotes

Island were not yet 1 year old.

We estimated that the pup whiskers ( $\sim 2$  months) grew at a rate of  $0.19 \text{ mm d}^{-1}$ , which is close to the growth rate reported for older pups and yearlings from 5 to 22 months of age, as shown for the Steller sea lions (*Eumetopias jubatus*) ([Rea et al., 2015](#)). This is more than twice the estimated vibrissa growth rate of adult female California sea lions of  $0.08 \text{ mm}$  ([McHuron et al., 2016](#); [Rosas-Hernández et al., 2018c](#)). Vibrissae grow faster during the early stages of life ([Rogers et al., 2016](#)), and decrease with age as rates of body growth slow. Decreases in growth rates can also be caused by reduced caloric intake when mothers can no longer produce sufficient milk to meet the daily needs of their offspring, and nursing animals begin to supplement their diet with solid foods that have a lower caloric content than milk ([Aurióles-Gamboa, 1988](#); [Donohue et al., 2002](#)).

The vibrissa segments removed for stable isotope analysis need to be assigned appropriate growth rates to know at what age they appeared in the whisker. This is important given that erroneous growth rates will lead to incorrect conclusions about the chronology of the trophic information inferred from the stable isotope signatures. Thus, understanding the growth rates of vibrissae at different stages of development is necessary to properly infer trophic feeding levels from stable isotopes measured in vibrissae.

#### 4.2. The Fourier method to determine the weaning process.

The Fourier approach is an effective technique for identifying periodic patterns in  $\delta^{15}\text{N}$  profiles. The phenomenon of periodicity has been employed to investigate the growth of vibrissae in several pinniped species by virtue of its correlation with established environmental occurrences ([Cherel et al., 2009](#); [Kernaléguen et al., 2012](#); [Rosas-Hernández et al., 2018c](#)). In relation to our research, the periods identified by the Fourier approach were not characterized as alterations in the environment. Instead, they served as valuable indicators for elucidating the potential timing of births within each colony, as well as the corresponding shifts in their dietary patterns. The reference points we used were derived from the birth dates documented for California sea lions from various colonies, together with the corresponding data on nursing and weaning durations. Otherwise, it would have been challenging to properly interpret the detected periods of isotopic signatures ([Fig. 3](#)).

#### 4.3. Age at weaning

Attendance records from lactating California sea lions instrumented with VHF radio transmitters and from pups that had been marked and resighted over a year in San Miguel Island, California, have shown that California sea lion pups wean between 9 and 11 months at breeding colonies in the United States ([Harris, 2016](#); [Melin et al., 2000](#); [Odell, 1981](#)). Most pups in the United States are weaned abruptly from the end of April to the end of May. This period overlaps with a phase of high ocean productivity in the California Current Ecosystem ([Harris, 2016](#)).

In Mexico, stable isotope studies on tooth dentin have shown pups to wean between 12 and 14 months of age at Santa Margarita Island ([Newsome et al., 2006](#)). This estimate from teeth is similar to our vibrissae-based estimates even though different hard parts were used. At Santa Margarita Island, the lactation period lasted more than 14 months; and was more than 13 months in some pups at San Esteban Island. At Los Islotes Island, duration of lactation exceeded 12 months based on the enriched isotopic profiles toward the root of the vibrissae, which suggests the sea lions using this site mainly consumed milk, and had not begun transitioning to fish when their vibrissae were sampled.

The  $\delta^{15}\text{N}$  information obtained from the vibrissae provide finer details about the weaning process of California sea lion pups in Mexico than could be obtained from teeth. The vibrissae contained identifiable periods, such as the transition to fish, and showed that the lactation period at the three colonies we studied (San Esteban Island, Los Islotes

Island, Santa Margarita Island) lasts longer than 14 months. They further show that the lactation period of California sea lions is longer at lower latitudes where environmental seasonality is not as marked as it is at higher latitudes.

It has been argued that short lactation periods, as occur for pinnipeds in Arctic and subarctic waters, are preferred due to the strong seasonality, severe weather, and relatively stable annual conditions that occur at high latitudes (Oftedal, 2011; Oftedal et al., 1987a). However, the California sea lion habitat ranges from tropical to subtropical latitudes (from  $\sim 23^{\circ}\text{N}$  to  $45^{\circ}\text{N}$ ) and does not experience such marked seasonality. Instead, California sea lions are more likely to be subjected to unpredictable environmental oscillations (e.g., El Niño) that may alter the abundance or accessibility of prey that in the most extreme situations terminates the nursing period (Oftedal et al., 1987a). Such environmental oscillations tend to have greater negative effects on the California sea lion colonies on the western coast of the continent than those in the Gulf of California (Elorriaga-Verplancken et al., 2016; Melin et al., 2008; Melin et al., 2000) where oceanographic conditions are more conducive to high productivity (Álvarez-Borrego and Lara-Lara, 1991). Thus, sea lions in the Gulf of California are more likely to be able to access prey during warm water events and continue to nurse their young for more than 14 months.

#### 4.4. Prolonged lactation

Producing milk to support the growth of neonates is the most energetically expensive activity mammals undertake (Gittleman and Thompson, 1988; Pond, 1977). As such, mothers should wean their young as soon as their offspring can sustain themselves on solid food. Thus, latitudinal differences in the ages of weaning between breeding colonies of California sea lions likely reflect differences in marine productivity and the quality and quantity of prey available to support juvenile sea lions.

The prolonged duration of lactation among California sea lions on both coasts of the Baja California Peninsula contrasts with patterns observed in the United States. This is most likely explained by differences in the bathymetries and regional environmental conditions that affect the diversity and availability of prey species in each region (Caudron, 1997; Melin et al., 2008; Melin et al., 2000; Van Parijs, 2003). California sea lions consume a greater diversity of species consisting largely of schooling fish and benthic species in the Gulf of California than in California near the Channel Islands where schooling fish and squid dominate the diets (Pozas 2022, Lowry et al. 2022). However, diets have been noted to shift in both regions toward more benthic and demersal species, and fewer epipelagic species when anomalously high sea-surface temperatures occur. Benthic and demersal species tend to have less lipid than epipelagic species, which are adequate to sustain adult sea lions, but may not contain sufficient calories to support the rapid body growth and survival of young animals (Trites, 2021).

All species of sea lions display plasticity in the age at which they wean their offspring (Goldsworthy, 2006; Trites, 2021). While the optimum life history strategy should be to produce and wean a pup each year, mothers at many breeding colonies are known to keep their pups for an extra one or two years (Trites, 2021; Villegas-Amtmann et al., 2017). In the case of California sea lions, some females are known to nurse a newborn and a juvenile at the same time (Francis and Heath, 1991a; Hernández-Camacho et al., 2021; Fig. 4). This has also been observed among fur seals and sea lions breeding on the Galapagos Islands, although many of the newborns die because they are unable to compete with one-year-old pups for milk (Trillmich and Wolf, 2008).

Prolonged lactation is likely an adaptive life-history strategy that ensures the dependent juvenile can continue growing on a diet of milk until they are big enough with sufficient stomach capacity to wean and subsist only on a diet of lower quality prey. Extended maternal investment may also help pups contend with seasonally reduced food availability when it would be difficult for young animals to find food on their



Fig. 4. Female California sea lions nursing her pup and juvenile at the same time. Photo taken in Los Islotes, Island B.C.S July 2020.

own. Spending more time suckling on land may also reduce the risk of pups being preyed on by sharks and killer whales (Trillmich and Wolf, 2008).

The lactation period of otariids ranges from 4 months in northern fur seals (*Callorhinus ursinus*) and Antarctic fur seals (*Arctocephalus gazella*), to as long as 3 years in the case of Steller sea lions (*Eumetopias jubatus*) and Galapagos fur seals (*Arctocephalus galapagoensis*) (Sepúlveda and Harcourt, 2021). Differences in lengths of lactation appear to be linked to environmental conditions, with extended lactation more common for species living where resource availability is inconsistent or uncertain. The Galapagos fur seal and sea lion are among the species facing the greatest challenges due to living in an unpredictable oceanic system with lower productivity and less seasonal variation compared to otariids living at higher latitudes (Villegas-Amtmann et al., 2017). The low chlorophyll concentrations in the Galapagos ranging between  $0.25$  and  $1.0\text{ mg m}^{-3}$  limit prey availability and forces young to rely on milk for longer periods until they can forage independently (Riofrío-Lazo and Páez-Rosas, 2021; Villegas-Amtmann et al., 2017). In contrast, our study colonies of California sea lions were located at higher latitudes in areas of greater productivity with chlorophyll concentrations exceeding  $1\text{ mg m}^{-3}$  (Fig. S1).

The natural change in diet in California sea lion pups occurs between the reproductive and non-reproductive seasons as the pup transitions to becoming an independent juvenile and begins to supplement their milk diet with fish (Labrada-Martagón et al., 2005; Melin et al., 2008). Milk has a much higher energy density than fish and is easier to digest and assimilate than solid food (Trites, 2021; Trites et al., 2006; Winship et al., 2002). Thus, supplementing milk with fish would be ill advised if the fish takes up limited stomach capacity and reduces the net energy a pup assimilates. On the other hand, transitioning to fish that are high in lipid as the quality and quantity of milk a mother produces declines would greatly benefit a pup (Trites, 2021).

Mothers frequently nurse pups older than 1 year, and are commonly observed nursing pups and juveniles at the same time at California sea lion colonies in the Gulf of California and at Santa Margarita Island (Hernández-Camacho et al., 2021). In contrast, females at US colonies (such as at Santa Barbara and San Nicolas Islands) have been reported nursing California sea lions older than 1 year, but in the absence of a pup (Melin et al., 2008; Melin et al., 2000). Mothers may be more likely to continue nursing juveniles if they do not give birth to a newborn. It is possible that California sea lions abort fetuses in years when prey-quality has been low—as appears to occur for Steller sea lions (Trites, 2021)—allowing them to nurse the previous season's pups longer and increase the probability of their pup surviving and passing their genes to



future generations.

Increases and decreases in California sea lion numbers at breeding colonies in Mexico and the United States may be related in large part to the quantity and quality of prey available to them (Adame et al., 2020; Pelayo-González et al., 2021). Prey abundance can have direct effects on the survival of all age classes, particularly young animals—while changes in the nutritional density of available prey can alter birth rates by altering age at weaning and the interval between births. Thus, systematically monitoring the age at weaning using stable isotopes in vibrissae can provide valuable insights into the diets of sea lions, and the factors that drive their population dynamics.

## 5. Conclusions

The age at which pups separate from their mother's milk is a significant aspect of mammalian life history. However, determining this age can be challenging, particularly for species living in remote or inaccessible areas. Fortunately, age at weaning can be indirectly determined from the trophic information contained in the sequential stable isotopes stored in growing vibrissae. Our analysis of vibrissae revealed that California sea lions wean at about 1 year of age in Mexico. The isotope profiles also revealed that pups in Mexico begin incorporating fish into their milk diet between the ages of 3 and 12 months. This lactation phase is significantly longer in Mexico compared to the northern colonies along the Pacific coast of the United States, which suggests that the prey needed by juvenile sea lions to physically develop is of lower quality compared to northern regions.

## CRedit authorship contribution statement

**Martha P. Rosas-Hernández:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Claudia J. Hernández-Camacho:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **David Aurióles-Gamboa:** Writing – review & editing, Visualization, Methodology, Investigation, Conceptualization. **Andrew W. Trites:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Claudia Janetl Hernandez-Camacho reports financial support was provided by SEMARNAT Secretariat of the Environment and Natural Resources. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2024.152059>.

## References

- Adame, K., Elorriaga-Verplancken, F.R., Beier, E., Acevedo-Whitehouse, K., Pardo, M.A., 2020. The demographic decline of a sea lion population followed multi-decadal sea surface warming. *Sci. Rep.* 10, 10499. <https://doi.org/10.1038/s41598-020-67534-0>.
- Álvarez-Borrego, S., Lara-Lara, J.R., 1991. The physical environment and primary productivity of the Gulf of California. In: Paul Dauphin, J., Simoneit, B.R.T. (Eds.), *The Gulf and Peninsular Province of the Californias*. American Association of Petroleum Geologists, Tulsa, Okla., U.S.A., pp. 555–567. <https://doi.org/10.1306/M47542C26>.
- Álvarez-Borrego, S., Galindo-Bect, L., Chee-Barragán, A., 1975. Características hidroquímicas de Bahía Magdalena. *BCS. Cienc. Mar.* 2, 94–110. <https://doi.org/10.7773/cm.v2i2.285>.
- Aurióles-Gamboa, D., 1988. *Behavioral Ecology of California Sea Lions in the Gulf of California*. Ph. D. dissertation, Ecology and Evolutionary Biology Department, University of California, Santa Cruz, CA, p. 188.
- Aurióles-Gamboa, D., Silverberg, N., Aguirre-Bahena, F., 2017. Possible relation between enrichment of  $\delta^{15}\text{N}$  in the top predator *Zalophus californianus* and the expansion of the oxygen minimum zone. *Mar. Biol.* 164, 157. <https://doi.org/10.1007/s00227-017-3189-7>.
- Avery, J.P., Zinn, S.A., 2023. Extraordinary diversity of the pinniped lactation triad: lactation and growth strategies of seals, sea lions, fur seals, and walruses. *Anim. Front.* 13, 93–102. <https://doi.org/10.1093/af/vfad037>.
- Bartholomew, G.A., Booloottian, R.A., 1960. Numbers and population structure of the pinnipeds on the California Channel Islands. *J. Mammal.* 41, 366–375. <https://doi.org/10.2307/1377495>.
- Beauplet, G., Barbraud, C., Chambellant, M., Guinet, C., 2005. Interannual variation in the post-weaning and juvenile survival of subantarctic fur seals: influence of pup sex, growth rate and oceanographic conditions. *J. Anim. Ecol.* 74, 1160–1172. <https://doi.org/10.1111/j.1365-2656.2005.01016.x>.
- Boness, D.J., Oftedal, O.T., Ono, K.A., 1991. The effect of El Niño on pup development in the California Sea lion (*Zalophus californianus*) I. Early postnatal growth. In: Trillmich, F., Ono, K.A. (Eds.), *Pinnipeds and El Niño: Responses to Environmental Stress*. Springer, Berlin Heidelberg, Berlin, Heidelberg, pp. 173–179. [https://doi.org/10.1007/978-3-642-76398-4\\_19](https://doi.org/10.1007/978-3-642-76398-4_19).
- Bowen, W.D., 1991. Behavioural ecology of pinnipeds neonates. In: Renouf, D. (Ed.), *The Behaviour of Pinnipeds*. Springer, Dordrecht, pp. 66–117. [https://doi.org/10.1007/978-94-011-3100-1\\_3](https://doi.org/10.1007/978-94-011-3100-1_3).
- Caudron, A., 1997. Pinnipeds social systems: a review. *Mammalia* 61, 153–160. <https://doi.org/10.1515/mamm.1997.61.2.153>.
- Cherel, Y., Kernaléguen, L., Richard, P., Guinet, C., 2009. Whisker isotopic signature depicts migration patterns and multi-year intra- and inter-individual foraging strategies in fur seals. *Biol. Lett.* 5, 830–832. <https://doi.org/10.1098/rsbl.2009.0552>.
- Coria-Monter, E., Monreal-Gómez, M.A., de León, D.A.S., Durán-Campos, E., Merino-Ibarra, M., 2017. Wind driven nutrient and subsurface chlorophyll-a enhancement in the bay of La Paz, gulf of California. *Estuar. Coast. Shelf Sci.* 196, 290–300. <https://doi.org/10.1016/j.ecss.2017.07.010>.
- DeNiro, M.J., Epstein, S., 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochim. Cosmochim. Acta* 42, 495–506. [https://doi.org/10.1016/0016-7037\(78\)90199-0](https://doi.org/10.1016/0016-7037(78)90199-0).
- Donohue, M., Costa, D., Goebel, E., Antonelis, G., Baker, J., 2002. Milk intake and energy expenditure of free-ranging northern fur seal, *Callorhinus ursinus*, pups. *Physiol. Biochem. Zool.* 75, 3–18. <https://doi.org/10.1086/338284>.
- Elorriaga-Verplancken, F., Aurióles-Gamboa, D., Newsome, S.D., Martínez-Díaz, S.F., 2013.  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in dental collagen as a proxy for age- and sex-related variation in foraging strategies of California Sea lions. *Mar. Biol.* 160, 641–652. <https://doi.org/10.1007/s00227-012-2119-y>.
- Elorriaga-Verplancken, F.R., Sierra-Rodríguez, G.E., Rosales-Nanduca, H., Acevedo-Whitehouse, K., Sandoval-Sierra, J., 2016. Impact of the 2015 El Niño-southern oscillation on the abundance and foraging habits of Guadalupe fur seals and California Sea lions from the San Benito archipelago, Mexico. *PLoS One* 11, e0155034. <https://doi.org/10.1371/journal.pone.0155034>.
- Ferguson, S.H., 2006. The influences of environment, mating habitat, and predation on evolution of pinniped lactation strategies. *J. Mamm. Evol.* 13, 63–82. <https://doi.org/10.1007/s10914-005-9003-1>.
- Francis, J., Heath, C., 1991a. The effects of El Niño on the frequency and sex ratio of suckling yearlings in the California Sea lion. In: Trillmich, F., Ono, A. (Eds.), *Pinnipeds and El Niño*, 1st ed. Springer, Berlin, pp. 193–201.



- Francis, J.M., Heath, C.B., 1991b. Population abundance, pup mortality, and copulation frequency in the California Sea lion in relation to the 1983 El Niño on San Nicolas Island. In: Trillmich, F., Ono, K.A. (Eds.), Pinnipeds and El Niño. Responses to environmental stress. Springer-Verlag, Berlin, pp. 193–201. [https://doi.org/10.1007/978-3-642-76398-4\\_13](https://doi.org/10.1007/978-3-642-76398-4_13).
- García-Aguilar, M.C., Aurióles-Gamboa, D., 2003. Breeding season of the California Sea lion (*Zalophus californianus*) in the Gulf of California. Mexico. Aquat. Mamm. 29, 67–76. <https://doi.org/10.1578/016754203101024086>.
- Gittleman, J.L., Thompson, S.D., 1988. Energy allocation in mammalian reproduction. Am. Zool. 28, 863–875.
- Goldsworthy, S.D., 2006. Maternal strategies of the New Zealand fur seal: evidence for interannual variability in provisioning and pup growth strategies. Aust. J. Zool. 54, 31–44.
- González-Rodríguez, E., Villalobos, H., Gómez-Muñoz, V.M., Ramos-Rodríguez, A., 2015. Computational method for extracting and modeling periodicities in time series. Open J. Stat. 5, 604. <https://doi.org/10.4236/ojs.2015.56062>.
- Harris, J.D., 2016. Estimation of an Unobservable Transition: From Dependence to Weaning in the California Sea Lion (*Zalophus californianus*). Master's thesis. University of Washington <http://hdl.handle.net/1773/35587>.
- Hastings, K.K., Johnson, D.S., Pendleton, G.W., Fadely, B.S., Gelatt, T.S., 2021. Investigating life-history traits of Steller Sea lions with multistate hidden Markov mark-recapture models: age at weaning and body size effects. Ecol. Evol. 11, 714–734. <https://doi.org/10.1002/ece3.6878>.
- Heath, C.B., 1989. The behavioral ecology of the California Sea lion, *Zalophus californianus*. Ph.D. dissertation, ecology and evolutionary biology department. University of California, Santa Cruz, California, p. 275 pp.
- Hernández-Camacho, C.J., Pelayo-González, L., Rosas-Hernández, M.P., 2021. California Sea lion (*Zalophus californianus*, lesson 1828). In: Heckel, G., Schramm, Y. (Eds.), Ecology and Conservation of Pinnipeds in Latin America. Springer Nature, Switzerland AG, pp. 119–143. [https://doi.org/10.1007/978-3-030-63177-2\\_7](https://doi.org/10.1007/978-3-030-63177-2_7).
- Hirons, A.C., Schell, D.M., St. Aubin, D.J., 2001. Growth rates of vibrissae of harbor seals (*Phoca vitulina*) and Steller Sea lions (*Eumetopias jubatus*). Can. J. Zool. 79, 1053–1061. <https://doi.org/10.1139/z01-055>.
- Kernaléguen, L., Cazelles, B., Arnould, J.P., Richard, P., Guinet, C., Cherel, Y., 2012. Long-term species, sexual and individual variations in foraging strategies of fur seals revealed by stable isotopes in whiskers. PLoS One 7, e32916. <https://doi.org/10.1371/journal.pone.0032916>.
- Kernaléguen, L., Dorville, N., Ierodiakonou, D., Hoskins, A.J., Baylis, A.M.M., Hindell, M.A., Semmens, J., Abernathy, K., Marshall, G.J., Cherel, Y., Arnould, J.P.Y., 2016. From video recordings to whisker stable isotopes: a critical evaluation of timescale in assessing individual foraging specialisation in Australian fur seals. Oecologia 180, 657–670. <https://doi.org/10.1007/s00442-015-3407-2>.
- Laake, J.L., Melin, S.R., Orr, A.J., Greig, J.P., Prager, K., DeLong, R.L., Harris, J.D., 2016. California Sea lion sex- and age-specific morphology. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-312, 21. <https://doi.org/10.7289/V5/TM-AFSC-312>.
- Labrada-Martagón, V., Aurióles-Gamboa, D., Martínez-Díaz, S.F., 2005. Natural and human disturbance in a rookery of the California Sea lion (*Zalophus californianus californianus*) in the Gulf of California, Mexico. Latin Am. J. Aquat. Mammals 4, 175–185. <https://doi.org/10.5597/lajam00080>.
- Le Boeuf, B.J., Aurióles, D., Condit, R., Fox, C., Gisinier, R., Romero, R., Sinsel, F., 1983. Size and distribution of the California Sea lion population in Mexico. Proc. Calif. Acad. Sci. 43, 77–85.
- Lowry, M.S., Forney, K.A., 2005. Abundance and distribution of California Sea lions (*Zalophus californianus*) in central and northern California during 1998 and summer 1999. Fish. Bull. 103, 331–343. <https://doi.org/10.25923/6qhf-0z55>.
- Lowry, M.S., Maravilla-Chavez, O., 2005. Recent abundance of California Sea lions in western Baja California, Mexico and the United States. In: Garcelon, V.D., Schwemm, C. (Eds.), Proceedings of the Sixth California Islands Symposium. Institute for Wildlife Studies, Ventura, pp. 94–106.
- Lowry, S.M., Nehasil, S.E., Moore, J.E., 2022. Spatio-temporal diet variability of the California sea lion *Zalophus californianus* in the southern California Current Ecosystem. MEPS 692, 1–21. <https://doi.org/10.3354/meps14096>.
- Lowther, A.D., Goldsworthy, S.D., 2016. When were the weaners weaned? Identifying the onset of Australian sea lion nutritional independence. J. Mammal. 97, 1304–1311. <https://doi.org/10.1093/jmammal/gyw106>.
- McHuron, E., Walcott, S., Zeligs, J., Skrovan, S., Costa, D., Reichmuth, C., 2016. Whisker growth dynamics in two North Pacific pinnipeds: implications for determining foraging ecology from stable isotope analysis. Mar. Ecol. Prog. Ser. 554, 213–224. <https://doi.org/10.3354/meps11793>.
- McIntosh, R.R., Pitcher, B.J., 2021. The enigmatic life history of the Australian sea lion. In: Campagna, C., Harcourt, R. (Eds.), Ethology and Behavioral Ecology of Otariids and the Odobenid. Springer Nature, Switzerland, pp. 557–585. <https://doi.org/10.1007/978-3-030-59184-7>.
- Melin, S.R., DeLong, R.L., Thomason, J.R., Vanblaricom, G.R., 2000. Attendance patterns of California Sea lion (*Zalophus californianus*) females and pups during the non-breeding season at San Miguel Island. Mar. Mamm. Sci. 16, 169–185. <https://doi.org/10.1111/j.1748-7692.2000.tb00911.x>.
- Melin, S.R., DeLong, R.L., Siniff, D.B., 2008. The effects of El Niño on the foraging behavior of lactating California Sea lions (*Zalophus californianus californianus*) during the nonbreeding season. Can. J. Zool. 86, 192–206. <https://doi.org/10.1139/z07-132>.
- Newsome, S.D., Koch, P.L., Etnier, M.A., Aurióles-Gamboa, D., 2006. Using carbon and nitrogen isotope values to investigate maternal strategies in northeast pacific otariids. Mar. Mamm. Sci. 22, 556–572. <https://doi.org/10.1111/j.1748-7692.2006.00043.x>.
- Newsome, S.D., Clementz, M.T., Koch, P.L., 2010. Using stable isotope biogeochemistry to study marine mammal ecology. Mar. Mamm. Sci. 26, 509–572. [10.1111/j.1748-7692.2009.00354.x](https://doi.org/10.1111/j.1748-7692.2009.00354.x).
- Odell, D.K., 1975. Breeding biology of the California Sea lion, *Zalophus californianus*. Rapports et Procès-verbaux des Réunions Conseil International pour l'Exploration de la Mer 169, 374–378.
- Odell, D.K., 1981. California Sea lion *Zalophus californianus* (Lesson, 1828). Handbook of marine mammals 1, 67–97.
- Oftedal, O.T., 2011. Lactation: land mammal species comparisons, encyclopedia of animal science, Second Edition. Taylor & Francis 664–666.
- Oftedal, O.T., Boness, D.J., Tedman, R.A., 1987a. In: Genoways, H.H. (Ed.), The Behavior, Physiology, and Anatomy of Lactation in the pinnipedia. Current mammalogy Springer, Boston, MA, pp. 175–245. [https://doi.org/10.1007/978-1-4757-9909-5\\_6](https://doi.org/10.1007/978-1-4757-9909-5_6).
- Oftedal, O.T., Iverson, S.J., Boness, D.J., 1987b. Milk and energy intakes of suckling California Sea lion *Zalophus californianus* pups in relation to sex, growth, and predicted maintenance requirements. Physiol. Zool. 60, 560–575.
- Pelayo-González, L., Hernández-Camacho, C.J., Aurióles-Gamboa, D., Gallo-Reynoso, J. P., Barba-Acuña, I.D., Godínez-Reyes, C., Ramírez-Delgado, D., Ávalos-Téllez, R., Rubio-Rodríguez, U., Villalobos, H., 2021. Effect of environmental variables on the number of births at California sea lion (*Zalophus californianus*) rookeries throughout the Gulf of California, Mexico. Aquat. Conserv. Mar. Freshwat. Ecosyst. 31, 1730–1748. <https://doi.org/10.1002/aqc.3545>.
- Peterson, R.S., Bartholomew, G.A., 1967. The natural history and behavior of the California Sea lion. The American Society of Mammalogist. Special publication No. 1, 1–79.
- Pond, C.M., 1977. The significance of lactation in the evolution of mammals. Evolution 177–199.
- Pozas Franco, A.L., 2022. The influence of diet quality on the divergent population trends of California sea lions (*Zalophus californianus*) in the Channel Islands and the Gulf of California. Master's thesis. The University of British Columbia. <http://hdl.handle.net/2429/83295>.
- R Development Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rea, L.D., Christ, A.M., Hayden, A.B., Stegall, V.K., Farley, S.D., Stricker, C.A., Mellish, J. A.E., Maniscalco, J.M., Waite, J.N., Burkanov, V.N., 2015. Age-specific vibrissae growth rates: a tool for determining the timing of ecologically important events in Steller Sea lions. Mar. Mamm. Sci. 31, 1213–1233. <https://doi.org/10.1111/mms.12221>.
- Riet-Sapriza, F.G., 2019. Lactation strategies and milk composition in pinnipeds. In: M'Hamdi, N. (Ed.), Lactation in Farm Animals-Biology, Physiological Basis, Nutritional Requirements, and Modelization. IntechOpen, London, United Kingdom. <https://doi.org/10.5772/intechopen.85386>.
- Riofrío-Lazo, M., Páez-Rosas, D., 2021. Galapagos Sea lions and Fur seals, adapted to a variable world. In: Campagna, C., Harcourt, R. (Eds.), Ethology and Behavioral Ecology of Otariids and the Odobenid. Springer International Publishing, Cham, pp. 643–661. [https://doi.org/10.1007/978-3-030-59184-7\\_30](https://doi.org/10.1007/978-3-030-59184-7_30).
- Rogers, T.L., Fung, J., Slip, D., Steindler, L., O'Connell, T.C., 2016. Calibrating the time span of longitudinal biomarkers in vertebrate tissues when fine-scale growth records are unavailable. Ecosphere 7, e01449. <https://doi.org/10.1002/ecs2.1449>.
- Rosas-Hernández, M.P., Aurióles-Gamboa, D., Hernández-Camacho, C.J., 2018a. Differences in the isotopic niche and trophic position of female California Sea lions (*Zalophus californianus*) in distinct oceanographic conditions. Aquat. Mamm. 44. <https://doi.org/10.1578/AM.44.4.2018.374>.
- Rosas-Hernández, M.P., Hernández-Camacho, C.J., Aurióles-Gamboa, D., 2018b. Specialized feeding habits of adult female California Sea lions *Zalophus californianus*. Mar. Mamm. Sci. <https://doi.org/10.1111/mms.12603>.
- Rosas-Hernández, M.P., Hernández-Camacho, C.J., González-Rodríguez, E., Aurióles-Gamboa, D., 2018c. Vibrissae growth rate in California Sea lions based on environmental and isotopic oscillations. PLoS One 13, e0204641. <https://doi.org/10.1371/journal.pone.0204641>.
- Salas-de-León, D.A., Carbajal, N., Monreal-Gómez, M.A., Gil-Zurita, A., 2011. Vorticity and mixing induced by the barotropic M2 tidal current and zooplankton biomass distribution in the Gulf of California. J. Sea Res. 66, 143–153. <https://doi.org/10.1016/j.seares.2011.05.011>.
- Sepúlveda, M., Harcourt, R.G., 2021. Maternal behavior in otariids and the walrus. In: Campagna, C., Harcourt, R. (Eds.), Ethology and Behavioral Ecology of Otariids and the Odobenid. Springer Nature, Switzerland, pp. 51–61. <https://doi.org/10.1007/978-3-030-59184-7>.
- Simpson, J., Souza, A., Lavin, M., 1994. Tidal mixing in the Gulf of California. In: Beven, K.J., Chatwin, P.C., Millbank, J.H. (Eds.), Mixing and Transport in the Environment. John Wiley, New York, pp. 170–182.
- Stearns, S.C., 1989. Trade-offs in life-history evolution. Funct. Ecol. 3, 259–268.
- Stegall, V.K., Farley, S.D., Rea, L.D., Pitcher, K.W., Rye, R.O., Kester, C.L., Stricker, C.A., Bern, C.R., 2008. Discrimination of carbon and nitrogen isotopes from milk to serum and vibrissae in Alaska Steller Sea lions (*Eumetopias jubatus*). Can. J. Zool. 86, 17–23. <https://doi.org/10.1139/z07-115>.
- Stricker, C.A., Christ, A.M., Wunder, M.B., Doll, A.C., Farley, S.D., Rea, L.D., Rosen, D.A., Scherer, R., Tollit, D.J., 2015. Stable carbon and nitrogen isotope trophic enrichment factors for Steller Sea lion vibrissae relative to milk and fish/invertebrate diets. Mar. Ecol. Prog. Ser. 523, 255–266. <https://doi.org/10.3354/meps11205>.
- Trillmich, F., Wolf, J.B., 2008. Parent-offspring and sibling conflict in Galápagos fur seals and sea lions. Behav. Ecol. Sociobiol. 62, 363–375.
- Trites, A.W., 2021. Behavioral insights into the decline and natural history of Steller Sea lions. In: Campagna, C., Harcourt, R. (Eds.), Ethology and Behavioral Ecology of

- Otariids and the Odobenid. Ethology and behavioral ecology of marine mammals. Springer, Cham, pp. 489–519. [https://doi.org/10.1007/978-3-030-59184-7\\_23](https://doi.org/10.1007/978-3-030-59184-7_23).
- Trites, A.W., Porter, B.P., Deecke, V.B., Coombs, A.P., Marcotte, M.L., Rosen, D.A., 2006. Insights into the timing of weaning and the attendance patterns of lactating Steller Sea lions (*Eumetopias jubatus*) in Alaska during winter, spring, and summer. *Aquat. Mamm.* 32, 85.
- Van Parijs, S., 2003. Aquatic mating in pinnipeds—a review. *Aquat. Mamm.* 29, 214–226. <https://doi.org/10.1578/016754203101024167>.
- Villegas-Amtmann, S., McDonald, B.I., Páez-Rosas, D., Aurióles-Gamboa, D., Costa, D.P., 2017. Adapted to change: low energy requirements in a low and unpredictable productivity environment, the case of the Galapagos Sea lion. *Deep-Sea Res. II Top. Stud. Oceanogr.* 140, 94–104.
- Wickham, H., 2009. *ggplot2: Elegant Graphics for Analysis*. Springer-Verlag, New York.
- Winship, A.J., Trites, A.W., Rosen, D.A., 2002. A bioenergetic model for estimating the food requirements of Steller Sea lions *Eumetopias jubatus* in Alaska, USA. *Mar. Ecol. Prog. Ser.* 229, 291–312.
- Zaytsev, O., Cervantes-Duarte, R., Montante, O., Gallegos-García, A., 2003. Coastal upwelling activity on the Pacific shelf of the Baja California peninsula. *J. Oceanogr.* 59, 489–502. <https://doi.org/10.1023/A:1025544700632>.