Vol. 634: 231–236, 2020
https://doi.org/10.3354/meps13204

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published January 23

NOTE

Contrasting whisker growth dynamics within the phocid lineage

Elizabeth A. McHuron[1,3,*], Terrie Williams[1], Daniel P. Costa[1], Colleen Reichmuth[2]

[1]Department of Ecology and Evolution, University of California Santa Cruz, Santa Cruz, CA 95060, USA
[2]Institute of Marine Sciences, University of California Santa Cruz, Santa Cruz, CA 95060, USA

[3]*Present address:* Joint Institute for the Study of the Atmosphere and Ocean, University of Washington, Seattle, WA 98115, USA

ABSTRACT: The use of biochemical analyses of whiskers to address ecological and physiological questions requires an understanding of whisker growth dynamics. To expand comparative data for phocid seals, we report fine-scale growth patterns, retention times, and temporal patterns of whisker loss for 3 captive seals using direct and photogrammetric methods. The ringed seal *Pusa hispida*, bearded seal *Erignathus barbatus*, and Hawaiian monk seal *Neomonachus schauinslandi* all showed rapid regrowth following whisker loss, with maximum growth rates of 0.15 to 0.20 cm d^{-1}. After this initial growth period, tissue deposition rates contrasted between the smallest species — the ringed seal — and the other 2 species. Ringed seal whiskers exhibited an asymptotic growth pattern typical of other phocids, whereas growth of bearded and monk seal whiskers continued at a slow, linear rate until shedding. The ringed seal had a seasonal pattern of whisker loss that coincided with the timing of the annual pelage molt, whereas there was no temporal pattern of whisker loss for the other 2 species. The rapid-to-slow growth of bearded and monk seal whiskers is unique within the phocid lineage, along with the presence of smooth rather than undulated whiskers in these species. In light of phylogenetic differences in growth and shedding patterns, extrapolation of whisker growth to related species requires careful consideration.

KEY WORDS: Vibrissae · Bearded seal · Ringed seal · Monk seal · Biochemical analyses

1. INTRODUCTION

Ecological and physiological studies of marine predators increasingly rely on biochemical analyses of animal tissues to overcome challenges associated with observing and sampling species with cryptic aquatic and/or migratory habits (Ramos & González-Solís 2012, Fleming et al. 2018). For pinnipeds (seals, sea lions, and walruses), whiskers represent a promising archival tissue because they encode a longitudinal record of biochemical features that can be used to infer temporal changes in foraging behavior and physiological status during the period of tissue growth (e.g. Kernaléguen et al. 2012, Karpovich et al. 2019). Information on whisker growth dynamics are needed to appropriately design and interpret results of such studies, yet these data are still lacking for many species. Recent efforts to remedy this have revealed divergent whisker growth patterns between otariid (sea lions and fur seals) and phocid (true seals) pinnipeds, as well as considerable interspecific variability in whisker growth characteristics among phocid seals (Beltran et al. 2015, Lübcker et al. 2016, McHuron et al. 2016, 2019, Rogers et al. 2016, Smith et al. 2018). This variability raises uncertainty about extrapolating growth characteristics to related species, necessitating

*Corresponding author: emchuron@uw.edu

a broader understanding of whisker growth dynamics within the phocid lineage.

Here we describe whisker growth dynamics for ringed seals *Pusa hispida*, bearded seals *Erignathus barbatus*, and Hawaiian monk seals *Neomonachus schauinslandi*, 3 phocids that inhabit disparate environments, use different foraging strategies (Dehn et al. 2007, Wilson et al. 2017), and are phylogenetically distant (Berta et al. 2018). We conducted serial photogrammetry and direct whisker measurements with captive individuals to describe whisker growth patterns, growth rates, retention times, and shedding patterns. The measured parameters will inform future research on these 3 species and, by considering them in a comparative context, provide insight into the derivation of species-typical traits and the appropriate extrapolation of whisker growth patterns for data-deficient species.

2. MATERIALS AND METHODS

Whisker measurements were collected from 2 juvenile male bearded seals, 1 adult female ringed seal, and 1 adult male Hawaiian monk seal housed at Long Marine Laboratory at the University of California Santa Cruz (Table 1). One bearded seal was subsequently removed from the study, but we present preliminary data from this individual as confirmatory evidence for the patterns observed. Whisker measurements were collected using photogrammetry and direct measurements of individual whiskers. Seals were trained using operant methods and positive (fish) reinforcement to participate in data collection. Measurements were conducted at weekly intervals depending on scheduling constraints and animal motivation (Table 1). Photographs were taken of each mystical whisker bed at a fixed distance and angle using a rigid mounted Canon Powershot G12 with embedded scale bar (Fig. 1). For direct measurements, we slid each whisker into an acrylic tube affixed to a scale bar that allowed us to measure the straightened length (to the nearest mm) from the muzzle to the whisker tip (Fig. 1). We selected 4 to 8 whiskers for each seal that were measured throughout the entire study (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m634p231_supp.pdf). As additional whiskers were lost by the bearded and monk seal, their regrowth was monitored through direct measurement. The position of missing or emerging whiskers was noted during each session using whisker bed maps (Fig. S1). Photogrammetric measurements of each whisker were determined using Image J software (https://imagej.nih.gov/ij/) and were broadly similar to direct measurements (Fig. 1). For reasons detailed in the Supplement (Text S1), we used the photogrammetric measurements for the ringed seal and direct measurements for the other 2 species in all analyses.

We used exploratory plots of whisker length vs. time to determine the most appropriate analysis of whisker growth rates for each species. For the ringed seal, a von Bertalanffy growth function was used to describe the growth of each whisker following the methods of Beltran et al. (2015). We also calculated growth rates during the initial regrowth phase following whisker loss as described in Text S1. Growth rates for the other seals were calculated as the difference between consecutive measurements divided by the time interval, differentiating growth rates that occurred within the first 100 d of regrowth following loss from those that occurred prior to loss (or were never lost) or after the first 100 d. We estimated the retention times and loss date for each whisker to determine how frequently whiskers were shed and whether there was a temporal pattern to whisker loss; for details, see the methods in the Supplement (Text S1). A chi-squared analysis was used to determine whether the frequency of whisker loss varied among months for each year. Statistical analyses

Table 1. Demographic and summary data for each seal including study duration, number of sampling events, number of whisker follicles per bed, number of measured whiskers, and the number of whisker measurements. The number of measurements was derived from photogrammetry (ringed seal) or direct measurements (bearded, monk seals). –: not measured

Species	Sex	Age class	Duration (d)	Sampling events	Follicles	Measured whiskers	Measurements
Ringed seal	Female	Adult	497	67	53	104	7061
Bearded seal	Male	Juvenile	513	65	>110[a]	17	613
Bearded seal	Male	Juvenile	51	6	–	13	41
Hawaiian monk seal	Male	Adult	494	55	40–45[a]	30	811

[a]These species had 1 to 4 chin whiskers, either along the mandible (monk seal) or offset from the dorsal midline (bearded seal)

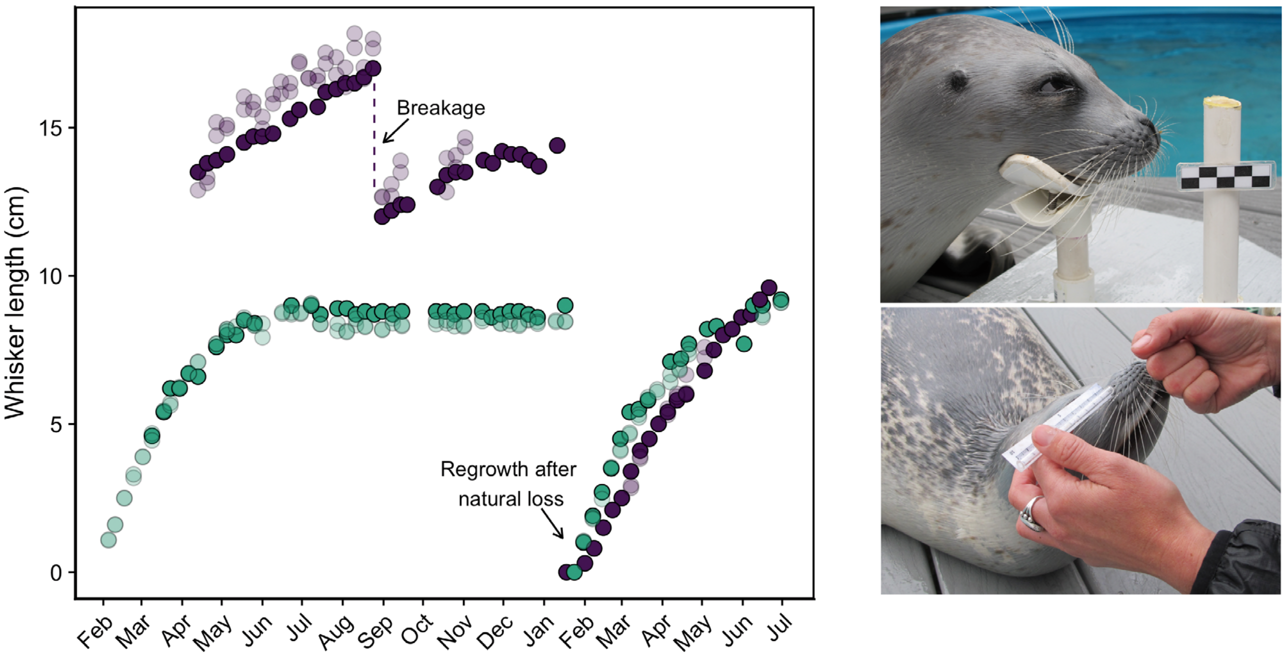


Fig. 1. Similarity between whisker measurements derived from photogrammetry (transparent dots) and direct measurement (solid dots), illustrated using whisker measurements from a single follicle for the Hawaiian monk seal (purple) and the ringed seal (green). Photographs illustrate a typical photogrammetric image (upper right) and collection of direct measurements (lower right)

were conducted using R software v.3.4.1 (www.R-project.org/). Variability around mean estimates represents the SD.

3. RESULTS

The ringed seal's whiskers exhibited rapid growth following loss (Fig. 2), with mean growth rates during this period of 0.04 to 0.15 cm d^{-1} (Table S1). Growth effectively slowed to zero as whiskers reached their asymptote (1.0–8.9 cm) with average K values of 0.041 ± 0.022 d^{-1} (0.018–0.099, Table S1). Based on comparisons with direct measurements (n = 4 whiskers, 5.9–9.0 cm), the growth model using photogrammetric measurements underestimated asymptotic lengths by 0.5 cm. On average, it took whiskers 37 d (10–76 d) and 79 d (20–164 d) to reach 75% and 95% of their asymptotic length, respectively. A total of 218 whiskers were lost across 497 d; shedding events were observed between 1 and 3 times for every whisker follicle. The average whisker retention from the growth model was 325 ± 62 d (140–370 d). Once lost, it took an average of 5.6 ± 2.9 d until reemergence; the exception to this was 1 whisker that was prematurely lost due to trauma that took ~1 mo to reemerge. There was a significant temporal pattern to whisker loss (2016: χ = 196.3, df = 11, p < 0.001; 2017: χ = 110.2, df = 5, p < 0.001), with loss increasing from January to the peak in March (Fig. 2).

The bearded seal's whiskers showed rapid initial growth following loss (Fig. 2), with mean growth rates of 0.03 to 0.12 cm d^{-1} ($\bar{x}$ = 0.08 ± 0.03 cm d^{-1}) and maximum rates up to 0.20 cm d^{-1} during the first 100 d of regrowth (Table S2). This initial growth rate slowed but continued linearly until a whisker was shed ($\bar{x}$ = 0.04 ± 0.01 cm d^{-1}). Maximum lengths of measured whiskers ranged from 3.0 to 22.2 cm. Measurements from the second bearded seal validated this growth pattern, with slow growth of existing whiskers ($\bar{x}$ = 0.02 – 0.06 cm d^{-1}) and rapid linear growth in newly emerged whiskers ($\bar{x}$ = 0.05–0.15 cm d^{-1}). The bearded seal that completed the 513 study days lost 22 whiskers, with no temporal component to the shedding pattern in either year (2016: χ = 9.0, p_{sim} = 0.70; 2017: χ = 3.82, p_{sim} = 0.66; Fig. 2). It should be noted that this individual had an unusual and extended pelage molt. There were no whiskers that completed a full growth cycle (loss-regrowth-loss), indicating that the retention time of a single whisker was >1.4 yr.

The monk seal's whiskers had a growth pattern similar to that shown by the bearded seal (Fig. 2), with initial mean growth rates between 0.03 and 0.10 cm d^{-1} ($\bar{x}$ = 0.07 ± 0.02 cm d^{-1}, max. = 0.17 cm d^{-1}) that slowed to an average rate of 0.05 cm d^{-1} until the

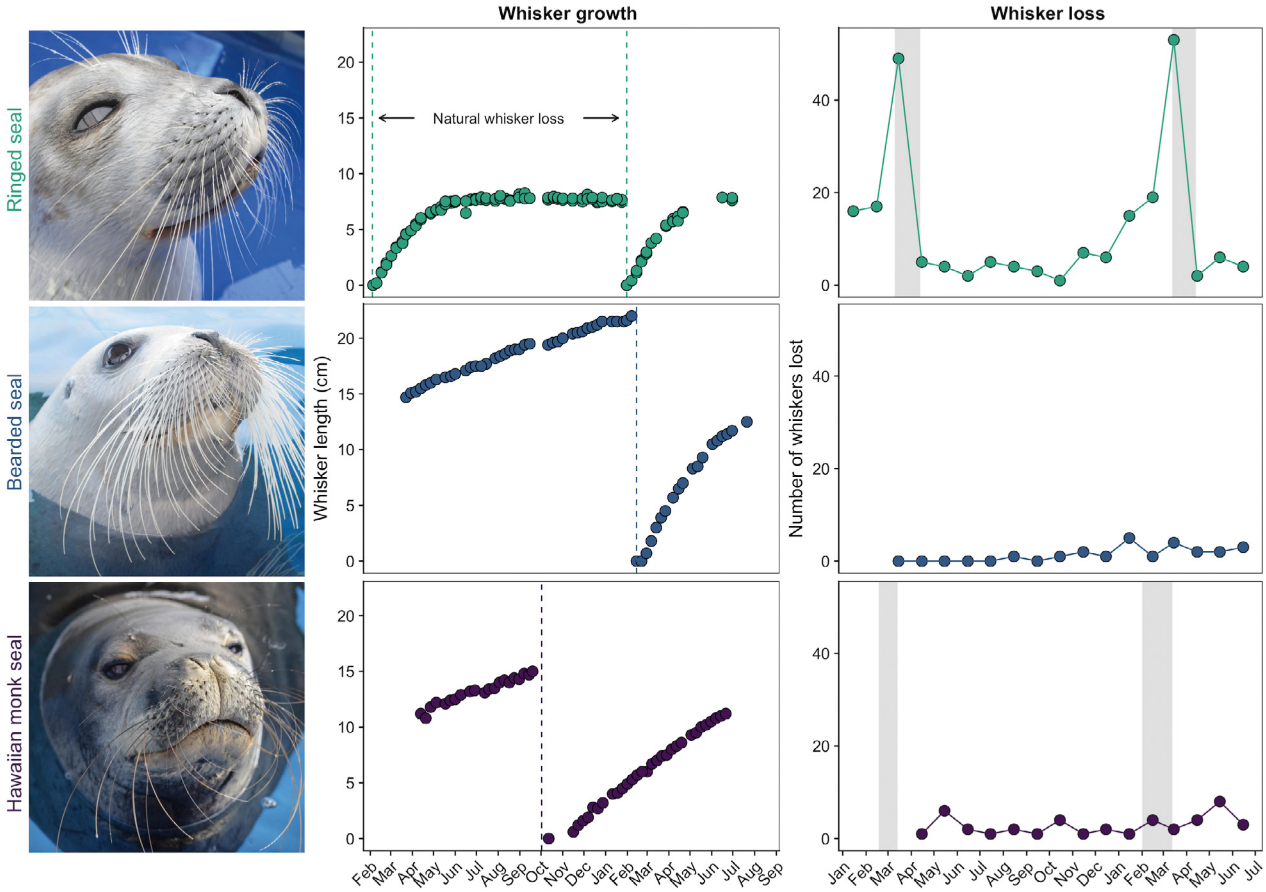


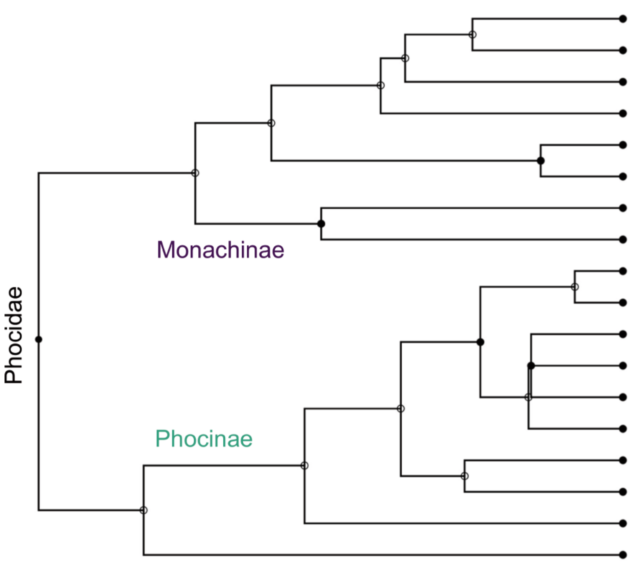
Fig. 2. Images of whisker beds (left), typical growth patterns (center), and temporal patterns of loss (right) for the ringed seal, bearded seal, and Hawaiian monk seal. Growth patterns are illustrated by measurements collected at a single follicle for each seal, highlighting the disparity in growth between the ringed seal and the other 2 species. The ringed seal lost most whiskers around the time of the pelage molt (denoted by the shaded regions); there was no temporal trend for the other 2 seals

whisker was shed (Table S2). Maximum lengths of the measured whiskers ranged from 1.9 to 22.1 cm. The monk seal lost 42 whiskers over 494 d (Fig. 2), with no temporal component to the shedding pattern (2016: χ = 10.6, p_{sim} = 0.25; 2017: χ = 8, p_{sim} = 0.16). There was only 1 whisker that completed a full growth cycle during the study interval, with a retention time of 377 d.

4. DISCUSSION

This study contributes data on whisker growth dynamics for 3 additional species, bringing the available data to half of the extant species within the phocid family (Fig. 3). The bearded and Hawaiian monk seals displayed a previously undocumented whisker growth pattern for phocids, which consisted of rapid initial growth followed by slower, linear growth until the time of whisker loss. This pattern is intermediate to the asymptotic growth pattern characteristic of the ringed seal and other phocids that show a terminal or non-growth resting phase and the relatively slow, linear whisker growth exhibited by otariids (McHuron et al. 2016). We documented both aseasonal and seasonal whisker loss patterns, corroborating the findings of Rogers et al. (2016) that at least 2 distinct shedding patterns exist within the phocid lineage. The ringed seal, which is the smallest phocid, exhibited the shortest whisker retention time of all phocids studied to date, indicating that physiological factors mediated by body size may play a role in whisker growth dynamics.

The apparent disparity in whisker growth patterns among phocids raises the question of whether the rapid-to-slow pattern is a primitive or derived trait. Bearded and monk seals are not closely related within the phocid lineage, but they both occupy basal positions within their respective subfamilies (Berta et al. 2018; Fig. 3). They are also the only phocids confirmed to have smooth rather than undulated or 'bearded' whiskers, which may reflect functional dif-



Species	Morphology	Pattern	Retention	Timing
Leopard seal	Beaded[a]	Asymptotic	348 days	Aseasonal
Weddell seal	Beaded	-	-	-
Ross seal	Beaded	-	-	-
Crabeater seal	Beaded	-	-	-
S. elephant seal	Beaded	Asymptotic	-	Seasonal
N. elephant seal	Beaded	Asymptotic	369 days	Seasonal
M. monk seal	Smooth	-	-	-
H. monk seal	Smooth	Rapid-slow	>365 days[c]	Aseasonal
Spotted seal	Beaded	Asymptotic	353 days	Seasonal
Harbor seal	Beaded	Asymptotic	-	Seasonal
Baikal seal	Beaded[a]	-	-	-
Ringed seal	Beaded	Asymptotic	325 days	Seasonal
Caspian seal	Beaded	-	-	-
Gray seal	Beaded	Asymptotic[b]	-	-
Ribbon seal	Beaded[a]	-	-	-
Harp seal	Beaded	-	-	-
Hooded seal	Beaded	-	-	-
Bearded seal	Smooth	Rapid-slow	>365 days[c]	Aseasonal[d]

[a]Assumed per King (1983) due to lack of species-specific description. [b]Study was only 5 mo long. [c]Minimum retention time. [d]Seal had unusual pelage molt during study duration

Fig. 3. Comparative summary of whisker growth dynamics and phylogenetic relationships among phocid seals, including whisker morphology, growth pattern, mean retention time, and timing of whisker loss. Dashes represent data gaps. Species are color-coded by subfamily, and those evaluated in this study are highlighted in gray. S.: southern; N.: northern; M.: Mediterranean; H.: Hawaiian. See Table S3 in the Supplement for data sources. Phylogeny from TimeTree (www.timetree.org)

ferences related to foraging ecology (Ginter et al. 2012, Dehnhardt et al. 2014). While a phylogenetic perspective suggests that the rapid-to-slow whisker growth pattern may be a basal trait for phocids, it remains possible that it is an adaptation to compensate for whisker abrasion or breakage that occurs during search and capture of benthic prey (Fay 1982, Wilson et al. 2017).

Our findings underscore the importance of long-term studies (>1 yr) to fully capture whisker growth dynamics and highlight the value of captive animals in providing data that are largely unattainable from wild individuals. While the within-individual metrics are robust, the conclusions are based on observations from a single representative of each species and similarities in whisker growth dynamics in captive and wild animals has not been confirmed. As such, future captive studies that encompass a range of sex- and age-classes as well as wild studies to corroborate captive findings would bolster understanding of growth dynamics in these species. Our emerging understanding of phocid whisker growth dynamics suggests that the amount of biochemical information recorded within a whisker ranges widely across species. In the absence of species-specific data, extrapolation from a phocid of similar size, foraging strategy, whisker morphology, and phylogenetic position may be the best approach. Although using whiskers to infer past status of individual seals presents challenges, these archival tissues encode a wealth of meaningful data that can be properly translated using data from individuals studied in human care.

Acknowledgements. This project was made possible by the support of animal trainers and volunteers at Long Marine Laboratory. Caroline Casey, Jenna Lofstrom, Beau Richter, Courtney Ribeiro-French, and Traci Kendall contributed greatly to data collection. Research was conducted under authorization from the National Marine Fisheries Service (permits 18902, 19590), with approval from the Institutional Animal Care and Use Committee of the University of California Santa Cruz. Funding was provided in part by NOAA's Alaska Pinnipeds Program (NA16NMF4390027 to C.R.), the Joint Industry Programme on Sound and Marine Life (JIP 22 7-23 to D.P.C. and C.R.), and the Office of Naval Research (N00014-17-1-2737 to T.W.).

LITERATURE CITED

Beltran RS, Connolly Sadou M, Condit R, Peterson SH, Reichmuth C, Costa DP (2015) Fine-scale whisker growth measurements can reveal temporal foraging patterns from stable isotope signatures. Mar Ecol Prog Ser 523:243–253

Berta A, Churchill M, Boessenecker RW (2018) The origin and evolutionary biology of pinnipeds: seals, sea lions, and walruses. Annu Rev Earth Planet Sci 46:203–228

Dehn LA, Sheffield GG, Follmann EH, Duffy LK, Thomas DL, O'Hara TM (2007) Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. Polar Biol 30:167–181

Dehnhardt G, Hanke W, Wieskotten S, Krüger Y, Miersch L (2014) Hydrodynamic perception in seals and sea lions. In: Bleckmann H, Mogdans J, Coombs SL (eds) Flow sensing in air and water. Springer, Berlin, p 127–146

Fay FH (1982) Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. North Am Fauna 74:1–279

Fleming AH, Kellar NM, Allen CD, Kurle CM (2018) The utility of combining stable isotope and hormone analyses for marine megafauna research. Front Mar Sci 5: 1–15

Ginter CC, DeWitt TJ, Fish FE, Marshall CD (2012) Fused traditional and geometric morphometrics demonstrate pinniped whisker diversity. PLOS ONE 7:e34481

Karpovich SA, Skinner JP, Kapronczai LA, Smith JA, Janz DM (2019) Examination of relationships between stable isotopes and cortisol concentrations along the length of phocid whiskers. Mar Mamm Sci 35:395–415

Kernaléguen L, Cazelles B, Arnould JPY, 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

King JE (1983) Seals of the world, 2nd edn. Cornell University Press, Ithaca, NY

Lübcker N, Condit R, Beltran RS, de Bruyn PJN, Bester MN (2016) Vibrissal growth parameters of southern elephant seals *Mirounga leonina*: obtaining fine−scale, time−based stable isotope data. Mar Ecol Prog Ser 559: 243–255

McHuron EA, Walcott SM, Zeligs J, Skrovan S, Costa DP, 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

McHuron EA, Holser RR, Costa DP (2019) What's in a whisker? Disentangling ecological and physiological isotopic signals. Rapid Commun Mass Spectrom 33:57–66

Ramos R, González-Solís J (2012) Trace me if you can: the use of intrinsic biogeochemical markers in marine top predators. Front Ecol Environ 10:258–266

Rogers TL, Fung J, Slip D, Steindler L, O'Connell TC (2016) Calibrating the time span of longitudinal biomarkers in vertebrate tissues when fine-scale growth records are unavailable. Ecosphere 7:1–22

Smith J, Karpovich S, Breed GA, O'Brien DM (2018) Morphological characteristics of harbor seal (*Phoca vitulina*) whiskers and their use in dietary reconstruction using stable isotope ratios. Can J Zool 96:1255–1263

Wilson K, Littnan C, Halpin P, Read A (2017) Integrating multiple technologies to understand the foraging behaviour of Hawaiian monk seals. R Soc Open Sci 4:160703

Editorial responsibility: Peter Corkeron, Woods Hole, Massachusetts, USA

Submitted: July 22, 2019; Accepted: November 21, 2019
Proofs received from author(s): January 10, 2020

Contrasting whisker growth dynamics within the phocid lineage

Elizabeth A. McHuron[1,3*], Terrie Williams[1], Daniel P. Costa[1], Colleen Reichmuth[2]

[1]Department of Ecology and Evolution, University of California Santa Cruz, Santa Cruz, CA 95060

[2]Institute of Marine Sciences, University of California Santa Cruz, Santa Cruz, CA 95060

[3]Present address. Joint Institute for the Study of the Atmosphere and Ocean, University of Washington, Seattle, WA 98115

*corresponding author: emchuron@uw.edu

Supplement. Additional description of methodology

Photogrammetric measurements of each whisker were determined using Image J software (https://imagej.nih.gov/ij/). We analyzed two photographs per whisker bed, which resulted in between 0 and 2 measurements per whisker for each session depending on the visibility of the whisker base and tip. Sadou et al. (2014) reported that photogrammetric measurements of post-mortem seals were within 1 mm of the actual length assuming standardized geometric relationships between the camera and whisker bed. Our data generally supported the reliability of this method, but measurement accuracy appeared dependent on the positioning of the whisker with respect to the camera (Fig. 1), and absolute differences between the two methods were smallest when the whisker was shorter. Photogrammetry was an ineffective method for the bearded seals because the large number of whiskers and their length and proximity on the whisker bed made it difficult to discern the base and tip of all but a few whiskers in photographs. We were able to obtain direct measurements easily from the bearded and monk seal because they displayed no aversion to having their whiskers handled. The ringed seal tolerated direct measurement but was more sensitive to whisker handling; her whiskers were also shorter, slender, and transparent, making it difficult to obtain accurate measurements for all but the longest whiskers. As a result, we opted to use the photogrammetric measurements in all further analyses for the ringed seal, and the direct measurements of whisker length for the bearded and monk seals.

We used exploratory plots of whisker length vs. time to determine the most appropriate analysis of whisker growth rates for each species. A von Bertalanffy growth function was used to describe growth of the ringed seal whiskers

$$L_t = L_\infty \cdot (1 - e^{-K(t-t_0)})$$

where the length of a single whisker at time *t* can be predicted from the asymptotic length (L_∞), a curvature constant (*K*) that describes how quickly a whisker reaches L_∞, and the time of initial growth (t_0). We used the growth model described in Beltran et al. (2015), which accepts multiple measurements per follicle (per timestep) and accounts for sequential shedding events from a single follicle to estimate these parameters and the retention time (lifespan) of each whisker. As described in McHuron et al. (2016), this model underestimated *K* when whisker lengths decreased due to breakage or measurement error that resulted in consistent underestimation of whisker lengths. For the ten whiskers where this occurred, we identified this transition point using length vs. time plots and excluded the measurements from each whisker that occurred after the transition, which always occurred after the whisker entered the non-linear phase of growth. We did calculate a linear growth rate for each whisker using all whisker measurements that occurred following loss that were less than 75% of the estimated asymptotic length. Growth rates were calculated from consecutive measurements; these were averaged to provide one measurement per whisker shedding cycle and then further averaged across multiple shedding cycles (when applicable). The growth of both the bearded and monk seal whiskers was non-linear but did not appear to include a resting phase of limited or no growth. For these species, we calculated growth rates of consecutive measurements as the length difference divided by the time difference, differentiating growth rates that occurred within the first 100 days of regrowth following loss from those that occurred prior to loss (or were never lost) or after the first 100 days. We excluded negative growth rates from these calculations, as they reflect wear, breakage, or measurement error and not actual growth. For all seals, a whisker length of zero was only assigned once at the first observation of loss (when applicable) to avoid artificially inflated growth rates if the whisker took more than one week to remerge.

A loss date was assigned to each shedding event using data from visual observations; whiskers that were present in one week and missing the following week were assumed to be lost on the day of observation of the empty follicle. The ringed seal frequently lost whiskers between two sampling events, where the old whisker was present at the first sampling event and a newly emerged whisker was present at the next sampling event. For these cases, we assigned a loss data that was one day after the first sampling event.

Figure S1. Example of whisker bed maps for each species used to measure whiskers and identify the position of lost or newly emerged whiskers. Rows are designated by letters, whereas columns are designated by numbers.

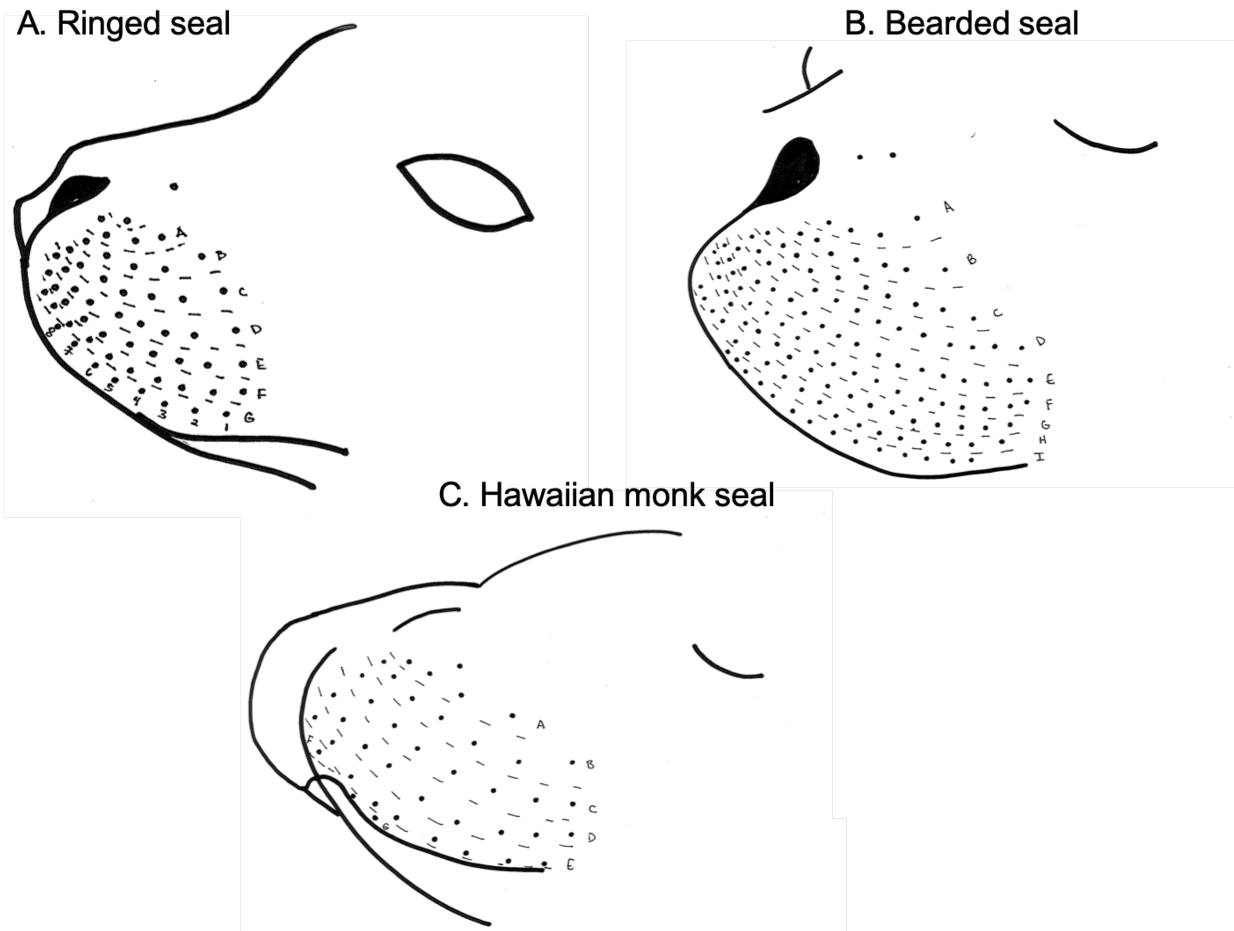


Table S1. Whisker growth dynamics and estimated asymptotic length for individual ringed seal whiskers. Note that the number of whiskers with output from the growth model differs slightly from the number of measured whiskers in Table 1 because not all whiskers had sufficient measurements to run the growth model.

Whisker	K (d^{-1})	Growth rate (cm day^{-1})	Asymptotic length (cm)	
			1st	2nd
LB1	0.059	0.09	3.3	2.8
LC1	0.022	0.06	5.4	4.7
LC2	0.046	0.07	3.0	3.2
LC3	0.093	0.11	2.3	2.2
LD1	0.024	0.09	7.0	7.5
LD2	0.032	0.08	4.9	5.4
LD3	0.039	0.08	3.7	3.5
LD4	0.097	0.15	2.7	2.8
LE1	0.018	0.08	8.7	8.8
LE2	0.026	0.09	6.4	6.7
LE3	0.033	0.10	5.0	5.2
LE4	0.047	0.10	4.0	4.3
LE5	0.073	0.13	3.1	3.2
LE6	0.054	0.07	2.5	2.9
LF1	0.021	0.09	8.7	8.7
LF2	0.024	0.10	7.5	7.7
LF3	0.028	0.09	6.1	6.0
LF4	0.041	0.11	4.8	5.1
LF6	0.042	0.08	3.5	3.6
LF7	0.045	0.07	2.7	2.6
LG1	0.021	0.09	7.9	8.2
LG2	0.024	0.09	6.8	6.9
LG3	0.025	0.08	5.7	5.8
LG4	0.030	0.08	4.5	4.8
LG5	0.041	0.08	3.3	3.5
RB1	0.034	0.06	3.4	3.1
RB3	0.072	0.04	1.1	1.0
RC1	0.025	0.06	5.2	4.7
RC2	0.032	0.06	3.2	3.1
RC3	0.099	0.10	2.0	2.0
RC4	0.088	0.07	1.6	1.7

RD1	0.020	0.07	7.1	7.0
RD2	0.032	0.08	4.8	4.7
RD3	0.033	0.06	3.9	3.7
RE1	0.019	0.09	8.6	8.4
RE2	0.032	0.11	6.2	6.3
RE3	0.056	0.13	4.6	4.6
RE4	0.049	0.11	3.9	4.1
RE5	0.063	0.12	3.1	3.4
RE6	0.091	0.13	2.5	2.6
RF1	0.019	0.09	8.8	8.9
RF2	0.023	0.09	7.7	7.6
RF3	0.029	0.10	6.2	6.3
RF4	0.032	0.09	5.0	4.9
RF5	0.046	0.10	3.9	4.1
RF6	0.049	0.08	3.5	3.1
RG1	0.021	0.09	7.9	8.0
RG2	0.021	0.08	7.1	7.2
RG3	0.026	0.08	5.5	5.5
RG4	0.036	0.09	4.6	4.8
RG5	0.041	0.08	3.4	3.5

Table S2. Mean whisker growth rates of the bearded and Hawaiian monk seals during the initial 100 days of regrowth following natural loss and all other time periods. Bolded whiskers are those where measurements were collected throughout the entire study interval; data collection for all other whiskers began at initiation of regrowth following loss. Maximum measured whisker lengths are also shown. Note that the number of whiskers with growth rates may be less than the number of whiskers measured as shown in Table 1 because not all whiskers had sufficient measurements to calculate robust growth rates.

Seal	Whisker	Growth rates (cm day^{-1})		Max. length (cm)
		Initial regrowth	All other	
Bearded seal 1	LB1	0.06	0.07	4.3
Bearded seal 1	**LC1**	NA	0.03	12.0
Bearded seal 1	**LD1**	0.08	0.04	16.8
Bearded seal 1	**LE1**	0.11	0.03	22.0
Bearded seal 1	**LF1**	0.11	0.05	21.9
Bearded seal 1	LG1	0.10	0.05	13.2
Bearded seal 1	LG11	0.03	0.03	3.0
Bearded seal 1	RB1	0.06	NA	3.2
Bearded seal 1	**RC1**	0.07	0.02	13.5
Bearded seal 1	**RD1**	0.09	0.04	17.8
Bearded seal 1	RD2	0.10	NA	6.1
Bearded seal 1	**RE1**	0.09	0.04	21.0
Bearded seal 1	RE2	0.10	NA	4.5
Bearded seal 1	RE3	0.03	0.05	9.0
Bearded seal 1	**RF1**	0.11	0.04	22.2
Bearded seal 1	RG1	0.09	0.04	12.5
Bearded seal 1	RI1	0.12	NA	3.5
Bearded seal 2	LB1	0.07	NA	3.7
Bearded seal 2	LE1	NA	0.06	13.5
Bearded seal 2	RB1	0.05	NA	1.0
Bearded seal 2	RC1	NA	0.02	11.0
Bearded seal 2	RC2	0.14	NA	2.8
Bearded seal 2	RH2	0.15	NA	6.5
Hawaiian monk seal	**LB1**	0.08	0.05	15.0
Hawaiian monk seal	**LC1**	0.09	0.05	20.0
Hawaiian monk seal	**LD1**	0.09	0.05	22.1
Hawaiian monk seal	LE2	0.08	0.04	7.5
Hawaiian monk seal	LE3	0.08	0.05	17.6

Hawaiian monk seal	RA3	0.03	0.02	2.6
Hawaiian monk seal	**RB1**	0.07	0.04	17.0
Hawaiian monk seal	RB2	0.07	0.05	7.8
Hawaiian monk seal	RB3	0.05	0.04	10.2
Hawaiian monk seal	RB4	0.05	0.04	8.9
Hawaiian monk seal	RB5	0.03	0.03	4.0
Hawaiian monk seal	**RC1**	0.08	0.06	16.5
Hawaiian monk seal	**RD1**	0.05	0.07	17.1
Hawaiian monk seal	RD2	0.10	0.07	14.5
Hawaiian monk seal	RD3	0.09	0.05	19.0
Hawaiian monk seal	RD6	0.07	NA	4.1
Hawaiian monk seal	RD7	0.05	NA	4.0
Hawaiian monk seal	RE1	0.07	0.07	16.5
Hawaiian monk seal	RE3	0.08	0.06	16.0
Hawaiian monk seal	RE4	0.08	0.05	13.3
Hawaiian monk seal	RE7	0.05	NA	1.9

Table S3. Sources for phocid whisker morphology and growth dynamics data presented in Fig. 3 in the main text. Dashes represent data gaps.

Species	Morphology	Growth dynamics
Monachinae		
Leopard seal[a]	King 1983	Rogers et al. 2016
Weddell seal	Ginter Summarell et al. 2015	-
Ross seal	King 1969, N. Lübcker pers. comm.	-
Crabeater seal	King 1983, L. Hückstädt pers. comm.	-
S. elephant seal	Ling 1966	Lübcker et al. 2016
N elephant seal	Murphy et al. 2013	Beltran et al. 2015, McHuron et al. 2019
M. monk seal[b]	King 1956	-
H. monk seal[b]	King & Harrison 1961	This study
Phocinae		
Spotted seal	Ginter et al. 2012	McHuron et al. 2016
Harbor seal	Ginter et al. 2012, Murphy et al. 2013	Zhao & Schell 2004, Smith et al. 2018, C. Reichmuth unpubl. data
Baikal seal[a]	King 1983	-
Ringed seal	Ginter et al. 2012	This study
Caspian seal	Ognev 1935	-
Gray seal	Ognev 1935, Ginter et al. 2010	Greaves et al. 2004
Ribbon seal[a]	King 1983	-
Harp seal	Ognev 1935, Ginter et al. 2010	-
Hooded seal	Ginter et al. 2010	-
Bearded seal	Ognev 1935, Ginter et al. 2010	This study

[a] Whisker morphology assumed based on statements in King (1993) due to lack of species-specific description
[b] Allen (1890) noted that the now extinct Caribbean monk seal also had smooth whiskers

Literature Cited

Allen JA (1890) The West Indian seal (*Monachus tropicalis* Gray). Bull Am Museum Nat Hist 2:1–34.

Beltran R, Connolly Sadou M, Condit R, Peterson S, Reichmuth C & Costa D (2015) Fine-scale whisker growth measurements can reveal temporal foraging patterns from stable isotope signatures. Mar Ecol Prog Ser 523:243–253.

Ginter CC, DeWitt TJ, Fish FE & Marshall CD (2012) Fused traditional and geometric morphometrics demonstrate pinniped whisker diversity. PLoS One 7:e34481.

Ginter CC, Fish FE & Marshall CD (2010) Morphological analysis of the bumpy profile of phocid vibrissae. Mar Mammal Sci 26:733–743.

Ginter Summarell CC, Ingole S, Fish FE & Marshall CD (2015) Comparative analysis of the flexural stiffness of pinniped vibrissae. PLoS One 10:e0127941.

Greaves DK, Hammill MO, Eddington JD, Pettipas D & Schreer JF (2004) Growth rate and shedding of vibrissae in the gray seal, *Halichoerus grypus*: a cautionary note for stable isotope diet analysis. Mar Mammal Sci 20:296–304.

King JE (1983) Seals of the world, Second. Cornell University Press: Ithaca, NY.

King JE (1969) Some aspects of the anatomy of the Ross seal, *Ommatophoca rossi* (Pinnipedia: Phocidae). Br Antarct Surv Sci Reports 63:1–54.

King JE (1956) The monk seals (genus *Monachus*). Bull Am Museum Nat Hist 3:201–256.

King JE & Harrison R. (1961) Some notes on the Hawaiian monk seal. Pacific Sci 15:282–293.

Ling JK (1966) The skin and hair of the southern elephant seal, *Mirounga leonina* (Linn.) 1. The facial vibrissae. Aust J Zool 14:855–866.

Lübcker N, Condit R, Beltran R, de Bruyn N & Bester M (2016) Vibrissal growth parameters of southern elephant seals *Mirounga leonina*: obtaining fine–scale, time–based stable isotope data. Mar Ecol Prog Ser 559:243–255.

McHuron EA, Holser RR & Costa DP (2019) What's in a whisker? Disentangling ecological and physiological isotopic signals. Rapid Commun Mass Spectrom 33:57–66.

McHuron EA, Walcott SM, Zeligs J, Skrovan S, Costa DP & 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.

Murphy CT, Eberhardt WC, Calhoun BH, Mann KA & Mann DA (2013) Effect of angle on flow-induced vibrations of pinniped vibrissae. PLoS One 8:e69872.

Ognev S. (1935) Mammals of the U.S.S.R and adjacent countries. Volume 3 Carnivora (Fissipedia and Pinnipedia). Translated from Russian by the Israel Program for Scientific Translations: Glavpushnina, Moscow-Leningrad.

Rogers TL, Fung J, Slip D, Steindler L & O'Connell TC (2016) Calibrating the time span of longitudinal biomarkers in vertebrate tissues when fine-scale growth records are unavailable. Ecosphere 7:1–22.

Sadou MC, Beltran RS & Reichmuth C (2014) A calibration procedure for measuring pinniped vibrissae using photogrammetry. Aquat Mamm 40:213–218.

Smith J, Karpovich S, Breed GA & O'Brien DM (2018) Morphological characteristics of harbor seal (*Phoca vitulina*) whiskers and their use in dietary reconstruction using stable isotope ratios. Can J Zool 96:1255–1263.

Zhao L & Schell D (2004) Stable isotope ratios in harbor seal *Phoca vitulina* vibrissae: effects of growth patterns on ecological records. Mar Ecol Prog Ser 281:267–273.