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Contrasting whisker growth dynamics within the phocid lineage

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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

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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 mysticial 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)

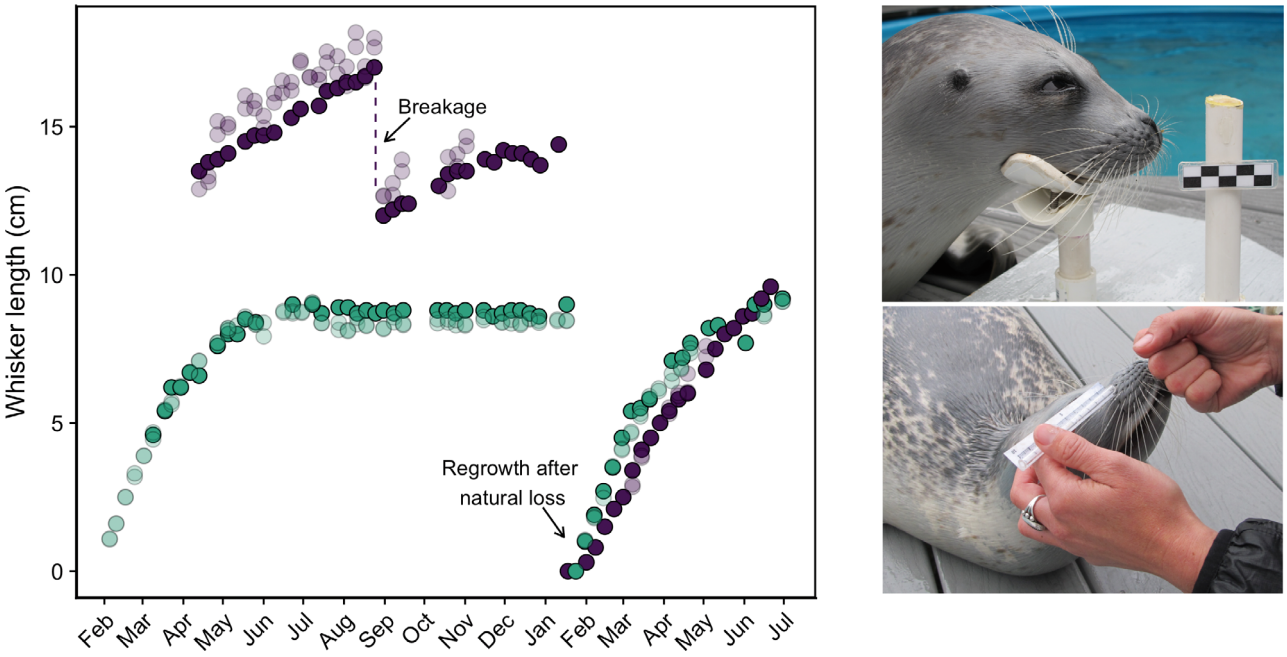


Fig. 1. Similarity between whisker measurements derived from photogrammetry (transparent dots) and direct measurement (solid dots), illustrated using whisker measurements from a single follicle for the Hawaiian monk seal (purple) and the ringed seal (green). Photographs illustrate a typical photogrammetric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

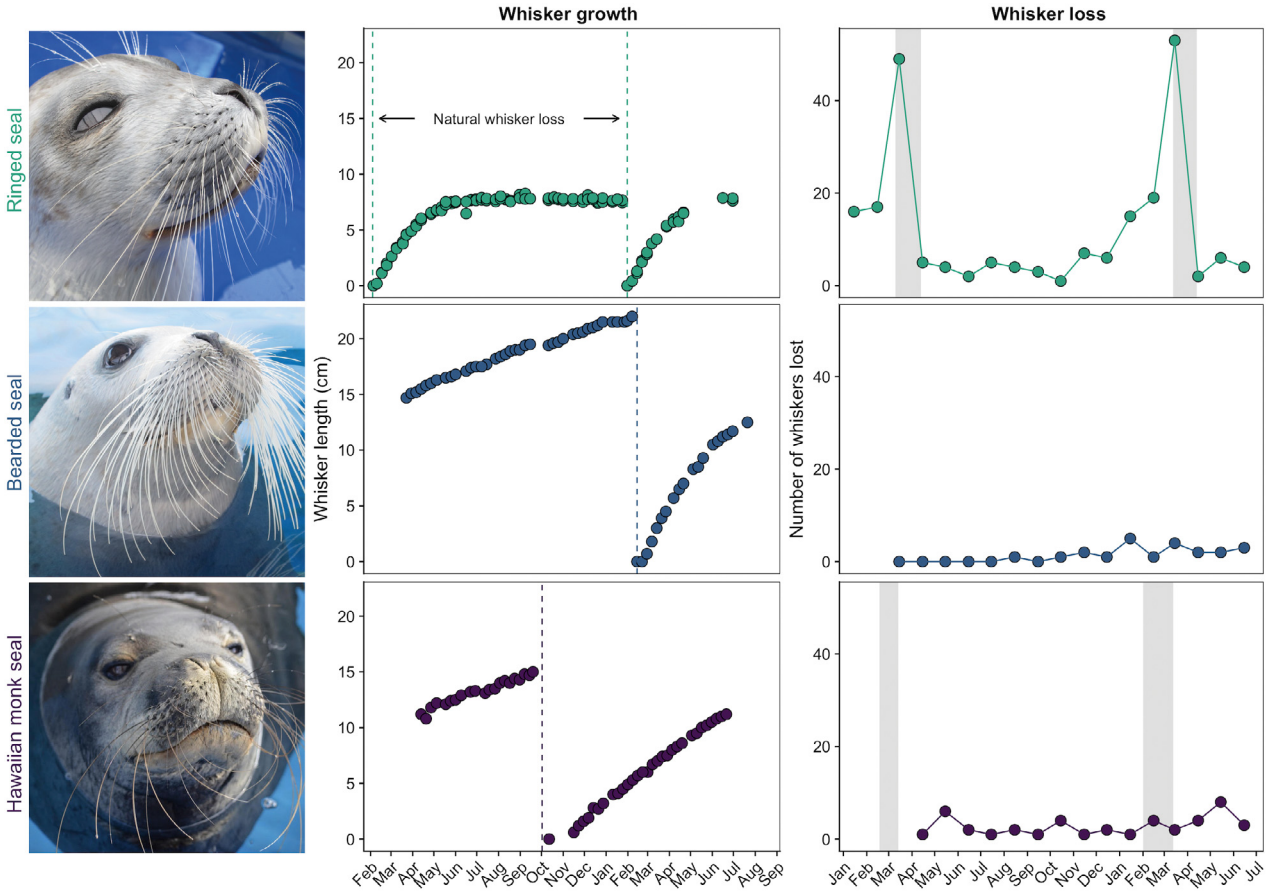


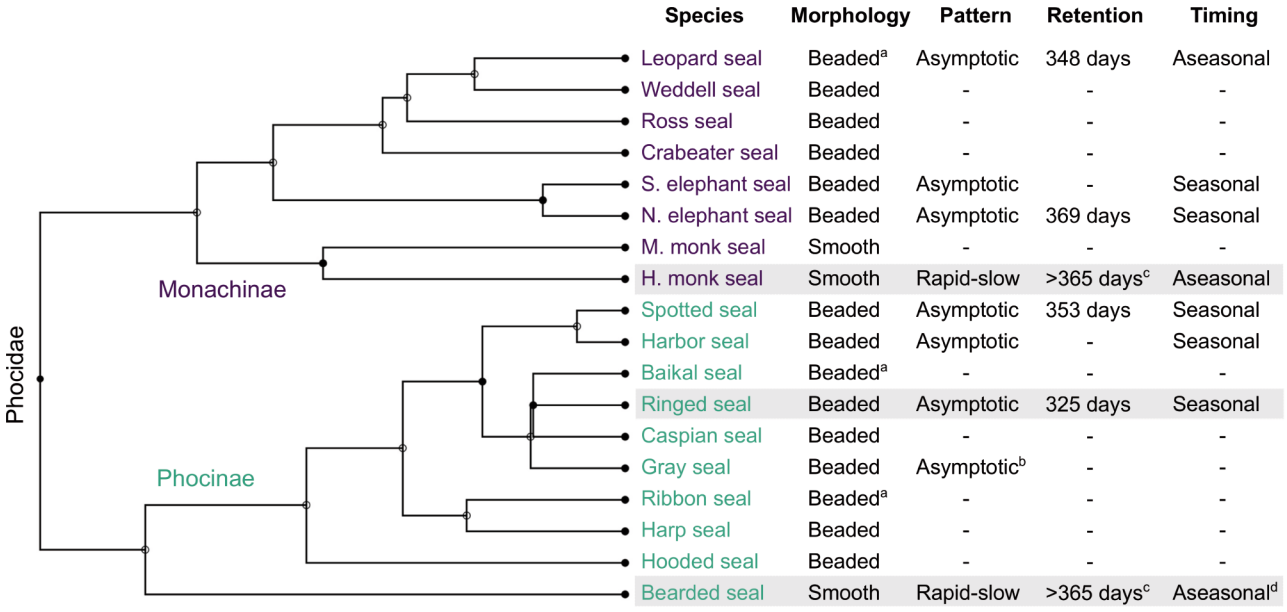
Fig. 2. Images of whisker beds (left), typical growth patterns (center), and temporal patterns of loss (right) for the ringed seal, bearded seal, and Hawaiian monk seal. Growth patterns are illustrated by measurements collected at a single follicle for each seal, highlighting the disparity in growth 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: $\chi = 10.6$, $p_{sim} = 0.25$; 2017: $\chi = 8$, $p_{sim} = 0.16$). 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.

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