

Multi-cusped postcanine teeth are associated with zooplankton feeding in phocid seals

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ABSTRACT:

Tooth morphologies often reflect diet in animals. Among marine mammals, a well-known example is krill-feeding crabeater seals (*Lobodon carcinophaga*), in which complex, comb-like postcanine teeth function as a sieve by retaining krill inside their mouth while expelling water. However, information on teeth morphology and function is scarce for other seal species. A recent bio-logging study found that Baikal seals (*Pusa sibirica*) feed on tiny pelagic amphipods at remarkably high rates with highly multi-cusped postcanine teeth, highlighting the need for comparative analyses on teeth morphologies and diets in phocid seals. Here, we quantified postcanine teeth morphology for 13 seal species based on museum skull specimens, with a particular focus on Baikal seals and their related species (genus *Pusa* and *Phoca*). The species in *Pusa*, including Baikal seals, had more specialized multi-cusped postcanine teeth than *Phoca* species, reflecting higher zooplankton proportions in their diets. Postcanine teeth of Baikal seals exhibited the highest degree of specialization among *Pusa*, even when the effect of age-related wear is controlled for. This result agrees with the highest zooplankton preference in this species. Further, we found a strong positive correlation between the degree of specialization in postcanine teeth and zooplankton reliance across phocid seal species. Our findings indicate that the functional role of multi-cusped postcanine teeth as a sieve is not limited to crabeater seals but prevail in many phocid seals feeding on zooplankton.

1. INTRODUCTION

Morphological variations of feeding apparatus (e.g., teeth, bill) across species in a clade are often associated with dietary variations. Studying such associations helps elucidate the mechanisms and processes of adaptive radiation (Jernvall et al. 1996, Slater & Friscia 2019). A well-known example is Darwin's finches in the Galapagos, where the variations in bill morphology are mechanistically linked to their primary foods (Suloway 1982). The teeth of the two Antarctic seals are also well-known examples. Crabeater seals (*Lobodon carcinophaga*), which feed almost exclusively on krill, have distinct, lattice-like (Adam & Berta, 2002) or comb-like (Hocking et al. 2017) postcanine teeth (Hückstädt et al. 2012). These complex teeth appear to function as a sieve, retaining krill in the mouth while expelling water (Klages & Cockcroft 1990). Leopard seals (*Hydrurga leptonyx*) also have multi-cusped postcanine teeth, which are considered to function for both sieving when eating krill and biting when eating marine mammals and penguins (Hocking et al. 2013). By contrast, Weddell seals (*Leptonychotes weddellii*) and Ross seals (*Ommatophoca rossii*), which are known to feed primarily on fish (Casaux et al. 1997) and cephalopods respectively (Hückstädt, 2018), do not have such specialized postcanine teeth. These examples indicate that the postcanine teeth of phocid seals (true seals) are a great model for studying the relationship between feeding morphology and dietary variations in mammals. However, previous studies have mainly focused on Antarctic seals, and little information is available for postcanine tooth morphology

and its possible link to diet in phocid seals in the northern hemisphere.

A recent study showed that Baikal seals (*Pusa sibirica*) in Lake Baikal, Russia, hunt a large number of pelagic amphipods individually in addition to fishes during dives (Watanabe et al. 2020). That study also showed that Baikal seals have highly specialized, multi-cusped postcanine teeth, suggesting that their teeth function as a sieve as in crabeater and leopard seals. However, the tooth morphology of Baikal seals and other phocid seals was assessed only visually in that study, and quantitative analyses have yet to be conducted.

In this study, we quantified the morphology of postcanine teeth in phocid seals and examined its possible link to dietary variations. Our comparisons follow three steps with progressively extended taxonomic coverage. First, we compared the tooth morphologies of three species of the genus *Pusa* (see Fig. 1 for phylogenetic tree), including Baikal seals, ringed seals (*Pusa hispida*), and Caspian seals (*P. capsica*). All these species feed on fishes, but Baikal and ringed seals also feed on zooplankton (Goodman 2018, Hammill 2018, Miyazaki 2018). The proportion of zooplankton in the diet is particularly high in Baikal seals (Yoshii et al. 1999) compared to ringed seals (Yurkowski et al. 2016). Therefore, we predict that Baikal seals would exhibit the highest specialization in their multi-cusped postcanine teeth, followed by ringed and Caspian seals, when age-related wear is taken into account. Second, we extended our comparison by including harbor seals (*Phoca vitulina*) and spotted seals (*P. largha*). Because both of these *Phoca* species are primarily fish feeders (Härkönen 1987, Boveng et al. 2013),

we would expect that *Pusa* and *Phoca* have distinct tooth morphologies, with the former having higher specialization in multi-cusped postcanine teeth. Third, we analyzed the tooth morphology of 13 species in Phocidae (Fig. 1), including both northern and Antarctic seals. Assuming that multi-cusped teeth function as a sieve in phocid seals feeding on zooplankton, we hypothesize that the species with higher reliance on zooplankton would exhibit higher specialization in their multi-cusped postcanine teeth.

2. MATERIAL & METHODS

2.1. Data collection

We examined the specimens of seal skulls preserved at the National Museum of Nature and Science, Japan, including Baikal seals (*Pusa sibirica*) (n=45), Caspian seals (*P. capsica*) (n=36), ringed seals (*P. hispida*) (n=40, collected in Dikson, Russia), harbor seals (*Phoca vitulina*) (n=11, collected in Hokkaido, Japan), and spotted seals (*Phoca largha*) (n=14, collected in Hokkaido, Japan). For each specimen, the maxilla and mandible were photographed (Fig. 2) from the left side, except when the right side was in a better condition. In addition, eight mandible samples of ringed seals collected from Grise Fiord, Nunavut, Canada were photographed in the same manner. Quantitative age estimates based on canine teeth were available for three species of *Pusa*, but not two species of *Phoca*. Age estimate data

used here were based on the count of the growth layer groups in the dentine and cementum of longitudinal decalcified and stained sections of canine teeth (Amano et al. 2000; Hohn 2018).

For a wider comparison, skull specimens of bearded seals (*Erignathus barbatus*; n=2), leopard seals (*Hydrurga leptonyx*; n=1), crabeater seals (*Lobodon carcinophaga*; n=1), ribbon seals (*Histiophoca fasciata*; n=3), hooded seals (*Cystophora cristata*; n=2), Weddell seals (n=2), gray seals (*Halichoerus grypus*; n=2), and harp seals (*Pagophilus groenlandicus*; n=2) preserved at the museum were also photographed.

2.2. Measurements

We measured the following six parameters for *Pusa* and *Phoca* spp. from photographs by using the software ImageJ: (1) number of cusps of postcanine-3 (PC3) (Fig.1 c), representing the number of pointed features of tooth crown, (2) tooth width of PC3 (in mm, Fig.1 d), representing the maximum width of the teeth measured parallel to the tooth-jaw junction (straight line distance drawn between tooth-jaw junction of anterior and posterior edges of the teeth, shown as yellow dashed line in Fig.1 d), (3) tooth height of PC3 (in mm, Fig.1 d), representing the maximum height of the tooth measured perpendicular to the tooth-jaw junction, (4) perimeter of tooth of PC3 (in mm, Fig.1 e), representing the perimeter of the tooth along with its cusps and notches plus the length of the tooth-jaw junction, (5) perimeter of the smallest bounding rectangle of PC3 (in mm, Fig.1 f), representing the perimeter of the

smallest possible rectangle that includes the tooth, measured by the tool "Bounding rectangle" in ImageJ, and (6) gap length (in mm, Fig.1 h), representing the shortest length between PC3 and PC4, measured parallel to the tooth-jaw junction. Among five postcanine teeth on one side of the jaw, we chose PC3 and PC4 because they are least affected by age-related wear (Bethune et al. 2021). Using the parameters measured, the following three original morphological indices were calculated:

(A) Cusp index: perimeter of the smallest bounding rectangle of the tooth (measurement 5) divided by perimeter of the tooth (measurement 4). This index represents the degree of specialization in multi-cusped teeth (Fig. 3).

(B) Gap ratio: gap length (measurement 6) divided by tooth width (measurement 2). This index represents relative spacing in postcanine tooth row (Fig. 3).

(C) Width-height ratio: tooth width (measurement 2) divided by tooth height (measurement 3). This index represents relative width, with higher index indicating flatter shapes.

These indices characterize tooth shapes and spacings independently of teeth and jaw sizes, allowing cross-species comparisons.

2.3. Statistical Analysis

Step 1: *Pusa* spp.

The effects of species and aging on the three morphological indices and number of

cusps were evaluated by model selection of Generalized Linear Model (GLM) with age and species as explanatory variables. Species were converted into dummy variables prior to the analysis. Interactions between age and species were taken into consideration. Gaussian distribution was assumed, and identity link function was fitted for cusp index, gap ratio, and width-height ratio, whereas Poisson distribution was assumed, and log link function was fitted for number of cusps. The best fit models were determined based on Akaike Information Criteria (AIC). Model selection was performed by *MuMIn* package v. 1.47.5 of software R v. 4.2.1.

Step 2: *Pusa* and *Phoca* spp.

Age estimates were available only for *Pusa* spp. Therefore, in the comparisons of *Pusa* and *Phoca* spp., data for the individuals of 2~10 years in age were selected for *Pusa*. For *Phoca*, the individuals without obvious tooth wear were selected. This data selection is because (a) individuals of < 2 years old often have different diets from adults (Kato 1982, Bengtsson et al. 2020), and (b) tooth wear is most apparent in the individuals of >10 years old (Stirling, 1969). The sample sizes of maxilla and mandible used in this analysis were 14, 13, 10, 34, and 12 for Baikal, Caspian, harbor, ringed and spotted seals, respectively.

Boxplots of number of cusps, cusp index, gap ratio and width-height ratio were created using *ggplot2* package v. 3.4.2 of R. Jitter plot was also created for number of cusps. Comparison between mandible vs maxilla, and male vs female were conducted by Wilcoxon

rank sum test ($\alpha = 0.05$). For cross-species comparison, Steel-Dwass test were used due to relatively small sample sizes.

Principal Component Analysis (PCA) was performed using tooth width, tooth height, number of cusps, gap length, cusp index, gap ratio, and width-height ratio with *stats* package v. 4.3.0 of R. All variables were standardized by setting average and standard deviation at 0 and 1, respectively, prior to the analysis. Principal component 1 and Principal component 2 were used for PCA plot, and each species' principal component scores were plotted by *factoextra* package v. 1.0.7 of R. Vectors were also used to show principal component loadings of each variable, and 68% confidence ellipse were plotted for each species.

Step 3: Trends in Phocidae

To assess the relationships between tooth morphology and importance of zooplankton in diet in phocid seals, we used average values of cusp index, gap ratio, width-height ratio, and number of cusps of each species. As in Step 2, specimens of 2-10 years old were used for *Pusa* spp. (for which age estimates were available), and specimens with obvious wear were omitted for *Phoca* species. As no specimens of non-*Pusa* or non-*Phoca* species showed obvious wear, all samples were used for the analysis.

Two indices were calculated for each seal species to quantify the importance of zooplankton in their diet: frequency of occurrence (FO) of zooplankton (%) from stomach

content analysis, and proportion of zooplankton (%) in diet from a stable isotope mixing model. For the former, FO of amphipods and krill was collected from the literature and averaged separately across studies. Higher values were used as a representative of FO of zooplankton for each species (Table. S5).

The relative contribution of potential prey proportion (zooplankton) in seals' diet was estimated using Markov Chain Monte Carlo (MCMC) methods using the package *simmr* v. 0.5.0 in R. This method incorporates the uncertainty of trophic enrichment factors, mixtures, and sources (Parnell et al. 2010). The *simmr* MCMC was run for each seal species at 10,000 iterations, a burn-in of 1000, thinned by 10 and with 4 chains of MCMC. We used known diet tissue discrimination factors for relevant tissues (skin: $\Delta^{15}\text{N} = 2.3\text{‰}$, $\Delta^{13}\text{C} = 2.8\text{‰}$; muscle: $\Delta^{15}\text{N} = 2.4\text{‰}$, $\Delta^{13}\text{C} = 1.3\text{‰}$; blood: $\Delta^{15}\text{N} = 1.7\text{‰}$, $\Delta^{13}\text{C} = 1.7\text{‰}$) (Hobson et al. 1996). Before running the *simmr* MCMC, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope data of seal species and their prey were collected from the literature (see Table. S6 and Table. S9 for stable isotope data used in this analysis). As the representatives of each seal species' prey, the top three prey species based on FO from stomach content analysis were selected. In addition to that, we selected either amphipods or krill as a representative of zooplankton based on their FO. The mean and standard deviation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of each seal species were used to generate random numbers that follow a normal distribution with the *rnorm* function available in R. Result of Gelman-Rubin diagnostics of running the *simmr* MCMC were 1 for all seals and prey, which means no

convergence issues were detected.

We used Phylogenetic Generalized Least Squares (PGLS) models using *caper* package v. 1.0.1 of R to assess whether morphological indices are related to FO and proportion of zooplankton while controlling for the effect of phylogeny. A phylogenetic tree (Fig. 1) was created using the published phylogenetic relationships among species (Fulton & Strobeck 2010) based on mitochondrial DNA sequence with maximum likelihood method. However, phylogenetic signal (λ) was 0 for both diet indices and all morphological indices, meaning that our results were essentially based on the ordinary least squares regressions. Using *MuMIn* package v. 1.47.5 of R, the morphological indices (number of cusps, cusp index, gap ratio, and width-height ratio) that best explain diet indices were determined based on Akaike Information Criteria (AIC). When multiple models were within $\Delta AIC < 2$ of the lowest AIC models, we considered the model with the fewest number of variables as the best model (Leroux 2019). All explanatory variables were standardized by setting average and standard deviation at 0 and 1, respectively, prior to the model selection analysis. *ggplot2* package v. 3.4.2 of R was used to visualize the relationship between cusp index and the two diet indices.

3. RESULTS

3.1. *Pusa* spp.

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Based on AIC criteria, the best model explaining cusp index of both jaws, and number of cusps and gap ratio of maxilla, had age and species as explanatory variables (see Table. 1 and Table. S1). The coefficient of Caspian seal and Baikal seal were not discriminated in the best model for width-height ratio of maxilla. The best model explaining mandible number of cusps and width-height ratio had age, Caspian seal, and their interaction. The best model for mandible gap ratio had age, ringed seal, and their interaction.

According to the best models selected, in all *Pusa* species, number of cusps and cusp index of both jaw decreased with age (number of cusps: $Coefficient = -1.96 \times 10^{-2}$, $P < 0.001$ for maxilla, $Coefficient = -1.44 \times 10^{-2}$, $P < 0.001$ for mandible; cusp index: $Coefficient = -4.01 \times 10^{-3}$, $P < 0.001$ for maxilla, $Coefficient = -4.47 \times 10^{-3}$, $P < 0.001$; see Fig.3 a, b). Baikal seals had higher cusp index and greater number of cusps than the other two species in maxilla and mandible ($P < 0.001$) even when age was taken into account. Gap ratio of maxilla of the three species increased with age ($Coefficient = 1.02 \times 10^{-2}$, $P < 0.001$), and the gap ratio of Caspian seals and ringed seals were higher than Baikal seals in both jaws ($P < 0.001$) even when age was taken into account. Width-height ratio of Baikal seals and ringed seals increased with age in maxilla ($Coefficient = 5.23 \times 10^{-3}$, $P < 0.006$), and the gap ratio of Baikal seals were smaller than ringed seals in maxilla ($P < 0.006$).

3.2. *Pusa* and *Phoca* spp.

Baikal seals had a significantly higher cusp index than the other four species in both maxilla and mandible. No significant difference was found in any other pairs of the five species in both maxilla and mandible. Baikal seals had a significantly greater number of cusps in maxilla, but not mandible, than other four species. Baikal seals and two *Phoca* species (harbor and spotted seals) had a significantly lower gap ratio than Caspian and ringed seal in both maxilla and mandible. *Pusa* species (Baikal, ringed, and Caspian seals) had a significantly higher width-height ratio than *Phoca* species (harbor and spotted seals) in both maxilla and mandible (See Table. S2 for more details.)

Teeth in the mandible had a significantly higher cusp index than those in maxilla in *Pusa* species and harbor seals (Fig. 5a, Table. S2). Similar to cusp index result, mandible had a significantly greater number of cusps than those in maxilla in ringed, Caspian, and spotted seals (Fig. 5b, Table. S2). The teeth in the mandible had a significantly lower gap ratio than those in the maxilla in *Pusa* species (Fig. 5b, Table. S2). *Width-height ratio* was lower for teeth in the mandible than those in maxilla in both Baikal and Caspian seals (Fig. 5d, Table. S2). No significant differences in number of cusps and width-height ratio were found between sex, except for number of cusps for spotted seals and width-height ratio for ringed seals (Fig. S3, Table. S3).

PCA showed that postcanine tooth morphologies of five species of *Pusa* and *Phoca* can be grouped into three clusters: Baikal vs *Phoca* (harbor and spotted) vs ringed & Caspian

seals (Fig. 6). Principal Component 1 (PC-1) explained 56.0% of variance, and Principal Component 2 (PC-2) explained 19.5% of variance, which summed up to 75.5% cumulative proportion of variance (see Table. S9). Ringed seals and Caspian seals had highest PC-1 scores and intermediate PC-2 scores (Fig. 6). The two *Phoca* species had lowest PC-2 scores and low PC-1 scores, while Baikal seal had low PC-1 score and highest PC-2 score.

3.3. Trends in Phocidae

The best model explaining zooplankton FO had cusp index and gap ratio as explanatory variables. Variance Inflation Factor (VIF) of each variable in this model was less than 10, suggesting no multi-collinearity between the variables (Akinwande et al. 2015). In this model, cusp index had the highest Standardized Partial Regression Coefficient (SPRC) followed by gap ratio, indicating that cusp index is the most influential variable (Table. 2).

The best model explaining zooplankton proportion (estimated from Stable Isotope mixing model) had cusp index and width-height ratio (Table. 2) as explanatory variables. VIF of each variable in this model was less than 10. Cusp index had the highest SPRC followed by width-height ratio, indicating that cusp index is the most influential variable. Width-height ratio had a negative SPRC score, indicating that the seal species with higher width-height ratio have lower zooplankton proportion (Table. 3). Relationships between cusp index and diet indices are shown in Fig. 7. Species with higher cusp index also had higher zooplankton FO (Fig. 7a)

and proportion of zooplankton (Fig. 7b). The slopes of regression lines for both zooplankton FO ($Adjusted R^2 = 0.541$) and proportion of zooplankton ($Adjusted R^2 = 0.513$) were statistically significant ($P = 0.014$ and $P = 0.005$, respectively).

4. DISCUSSION

Our analysis quantitatively showed that (1) Baikal seals have the most specialized multi-cusped postcanine teeth among northern seals, and (2) specialized multi-cusped postcanine teeth are associated with the proportion of zooplankton in the diet of phocid seals.

4.1. Within *Pusa* comparison

Our analysis showed that Baikal seals have the most specialized postcanine teeth among the three species of *Pusa*. Unlike the previous study (Watanabe et al. 2020), we quantitatively analyzed tens of samples for each species with the effect of age-related wear taken into account. All tooth morphological indices decreased with age, highlighting the importance of age effects in cross-species comparison of tooth morphologies. Most pinniped species rarely masticate prey (Jones et al. 2013), although Australian sea lions (*Neophoca cinerea*) and Australian fur seals (*Arctocephalus pusillus doriferus*) were shown to chew in captive experiments (Hocking et al., 2017a, 2014). Therefore, teeth might have worn due to

occlusion rather than mastication (Loch & Simões-Lopes 2013). Highly specialized multi-cusped postcanine teeth in Baikal seals presumably help the species to catch and consume small pelagic amphipods individually at a high rate (as observed by seal-borne video cameras) without drinking excessive water (Watanabe et al. 2020). Pelagic amphipods in Lake Baikal are highly abundant (Didorenko et al. 2021) and form dense swarms (Naumova et al. 2020), making them an easy target for Baikal seals. According to stable isotope mixing model diet analysis, fish (*Comephorus* spp.) and amphipods (*Macrohectopus branickii*) were primary food for Baikal seals (Yoshii et al. 1999). Similarly, highly complex, multi-cusped postcanine teeth of crabeater seals are thought to function as a sieve, retaining krill in the mouth while expelling water during foraging. Although the diet of ringed seals also includes zooplankton, the proportion of zooplankton in diets is higher for Baikal seals based on isotope mixing model ($\bar{x} = 46.6 \pm 6\%$ for Baikal and 11~31% for ringed seals). This is consistent with previous studies reporting the consumption of a wide variety of prey including a high proportion of fishes and some zooplankton by ringed seals (Yurkowski et al. 2020). FO of amphipods have not been investigated yet for Caspian seals. However, higher accumulation of Hg than Cd was reported in Caspian seals, a phenomenon seen in the predators that feed more on fishes than invertebrates (Watanabe et al. 2002). Taken together, we suggest that highly specialized multi-cusped postcanine teeth of Baikal seals are associated with their higher reliance on pelagic amphipods than ringed and Caspian seals.

4.2. Comparison of *Pusa* and *Phoca*

We revealed that postcanine teeth morphology of *Pusa* and *Phoca* species can be classified into three groups: Baikal seals (*Pusa*) vs ringed and Caspian (*Pusa*) vs *Phoca* species. Baikal seals frequently feed on zooplankton, whereas ringed and Caspian seals only partially rely on zooplankton. *Phoca* species are generally fish feeders (Frost & Burns 2018, Teilmann & Galatius 2018). Three *Phoca* species have wider (i.e., tooth width is greater than tooth height) postcanine teeth with narrower spacing than ringed and Caspian seals. These features might prevent teeth breakage and are thus important for the species that bite prey such as fishes (Ydesen et al. 2014). Having wider teeth might also lower the risk of tooth tip breakage (Evans & Sanson 1998). Moreover, previous studies on seals showed that pierce-feeders tend to have narrower tooth spacing than suction feeders (Churchill & Clementz 2015), and that the species feeding on tough prey tend to have wider teeth (Evans & Sanson 1998).

We found no significant sex differences in tooth morphologies for all five species we examined. This result is consistent with the previous study reporting no sexual dimorphism in *Pusa* or *Phoca* species, as well as limited variation in diet between sexes (Mesnick & Ralls 2018). Interestingly, almost all tooth morphological indices were different between maxilla and mandible in *Pusa*, but not in *Phoca*. This difference may be associated with the difference in feeding modes and prey types.

4.3. Trends in Phocidae

We found that the reliance on zooplankton is positively associated with the degree of specialization in multi-cusped postcanine teeth in phocid seals. We acknowledge that our sample size is small except for five species of *Phoca* and *Pusa*, and future studies should expand the dataset. Our finding suggests that specialized multi-cusped postcanine teeth are useful when feeding on small prey such as pelagic amphipods (Baikal seals) and krill (crabeater and leopard seals). Captive experiments showed that leopard seals with highly specialized multi-cusped postcanine teeth were able to retain small-chopped fish in the mouth, whereas California sea lions (*Zalophus californianus*), which lack multi-cusped postcanine teeth, could not (Hocking et al. 2013). Effectiveness of highly specialized multi-cusped teeth is also supported by the observation that a leopard seal had >10,000 freshly caught krill in the stomach (Lowry et al. 1988).

We also showed that the reliance on zooplankton as diet is positively associated with gap size relative to teeth width. Having large gap size would promote expelling water, which is necessary for eating small prey without drinking excessive water. On the other hand, a small tooth gap was observed in *Phoca* seals, where robust teeth are essential for chewing larger prey. This result is consistent with the previous study showing that teeth gap width is associated with feeding modes in seals (Churchill & Clementz 2015).

In conclusion, we provided new insights into the link between feeding morphology and diets by examining postcanine teeth of phocid seals. Baikal seals have the most specialized, multi-cusped, postcanine teeth among northern species, which mirrors their high reliance on pelagic amphipods as diet. Furthermore, we showed that, in the whole Phocidae family, specialized multi-cusped postcanine teeth are associated with predation on small zooplankton such as amphipods and krill. This overall trend implies that the functional role of multi-cusped postcanine teeth as a sieve is not a prerogative of crabeater seals, but also present in many phocid seals feeding on zooplankton. We acknowledge that our analyses are limited to two dimensions; therefore, three-dimensional analysis of postcanine teeth could provide deeper insight into their function in future studies.

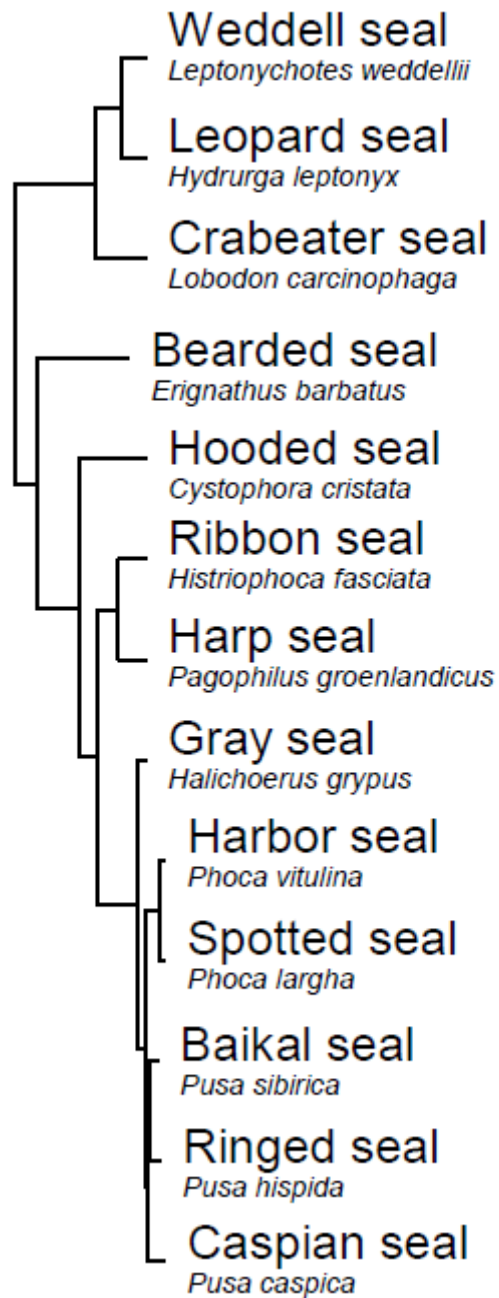


Fig. 1 Phylogenetic tree of phocid seals used in this research. The phylogenetic tree is created according to the published phylogenetic relationships (Fulton & Strobeck 2010).

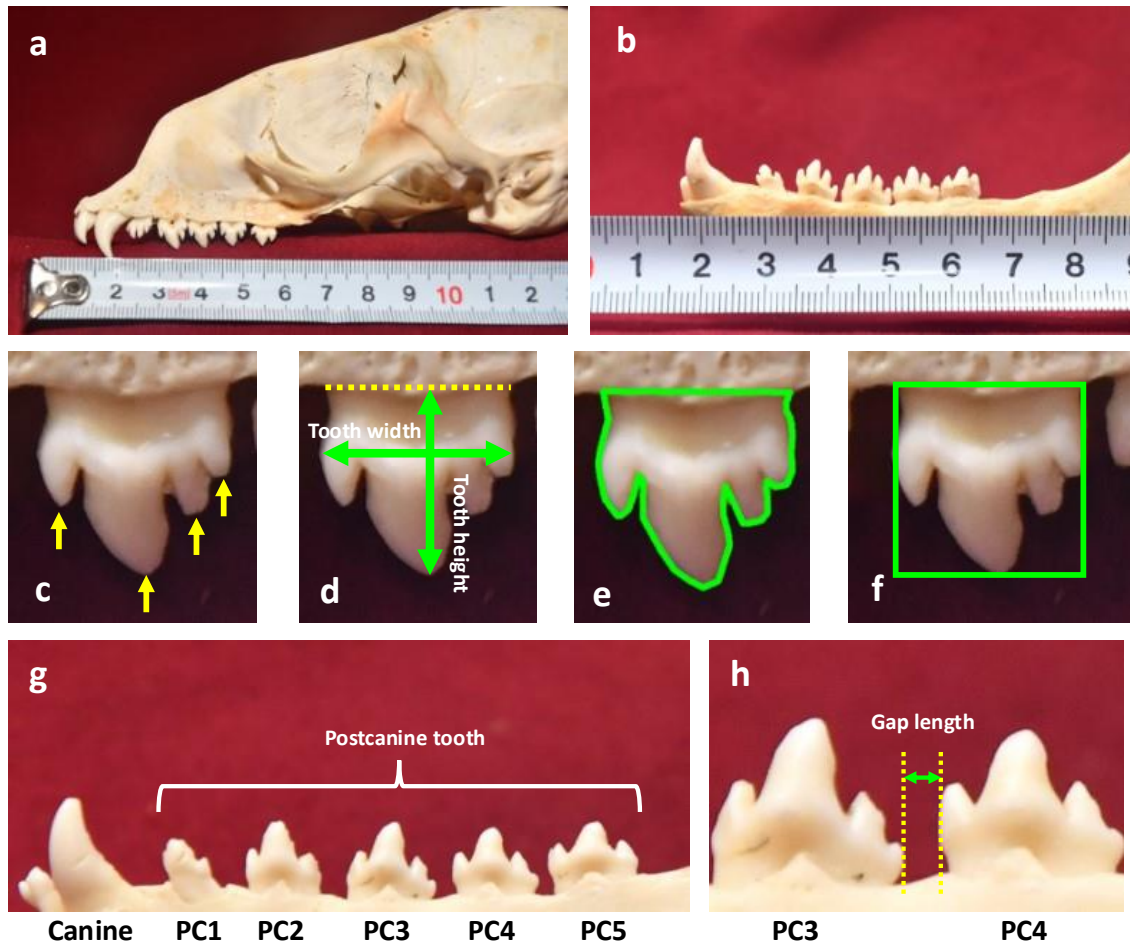


Fig. 2 An example of Baikal seal (*P. sibirica*) skull specimens. (a) Maxilla and (b) mandible tooth row of a Baikal seal. (c)~(f) Enlarged view of maxilla teeth. (c) Yellow arrows represent the number of cusps. (d) Yellow dashed line represents teeth-jaw junction, horizontal green arrow depicts tooth width, and vertical green arrow depicts tooth height. (e) Green line shows tooth perimeter. (f) Green line shows perimeter of the smallest bounding rectangle of teeth. (g) Picture of mandible teeth row, showing canine and five postcanine teeth. (h) Green arrow shows gap length between postcanine 3 and postcanine 4.

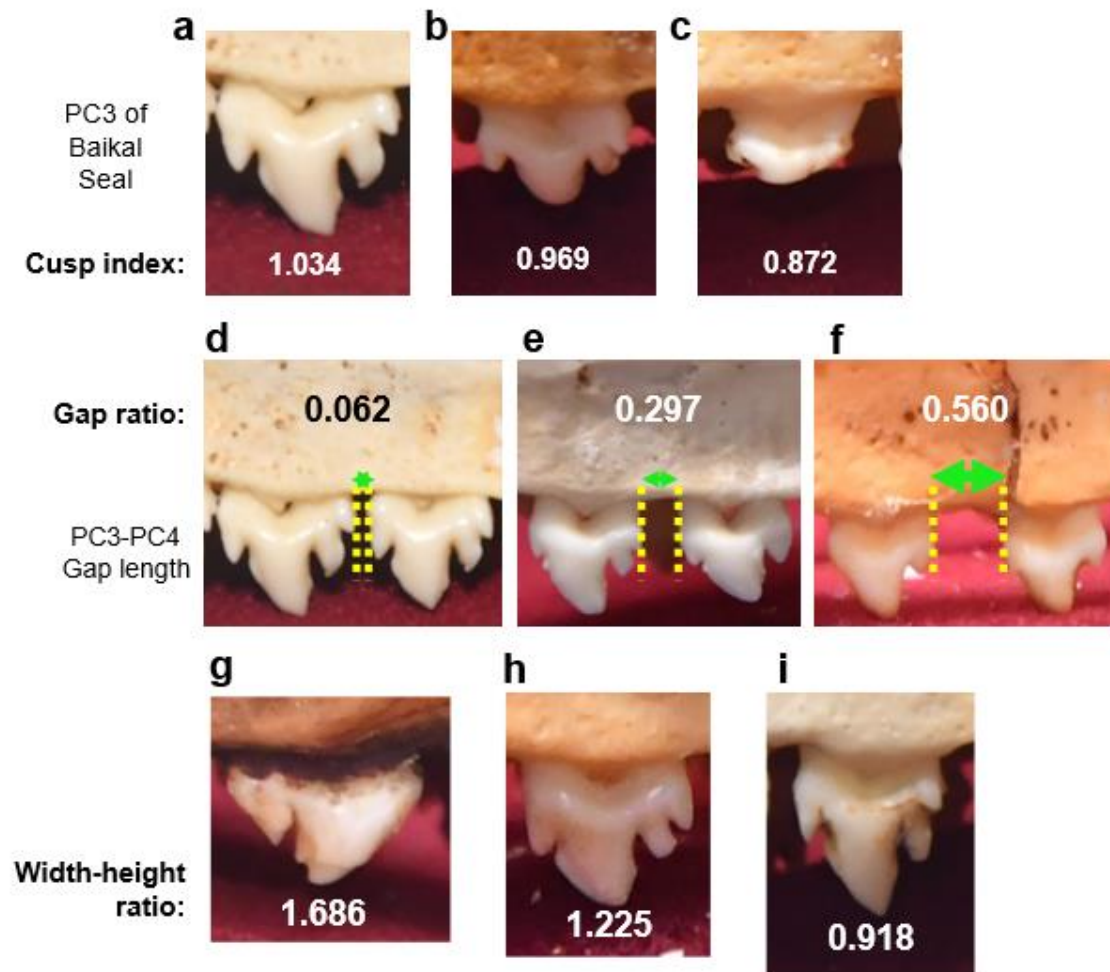


Fig. 3 Examples of cusp index, gap ratio and width-height ratio. Postcanine teeth in the maxilla with different cusp index (a~c), gap ratio (d~f), and width-height ratio (g~i) are shown. Green arrow in (d~f) represents gap length. Pictures used here are postcanine teeth in the maxilla of Baikal (a~d, h~i), ringed (e~f) and harbor seals (g).

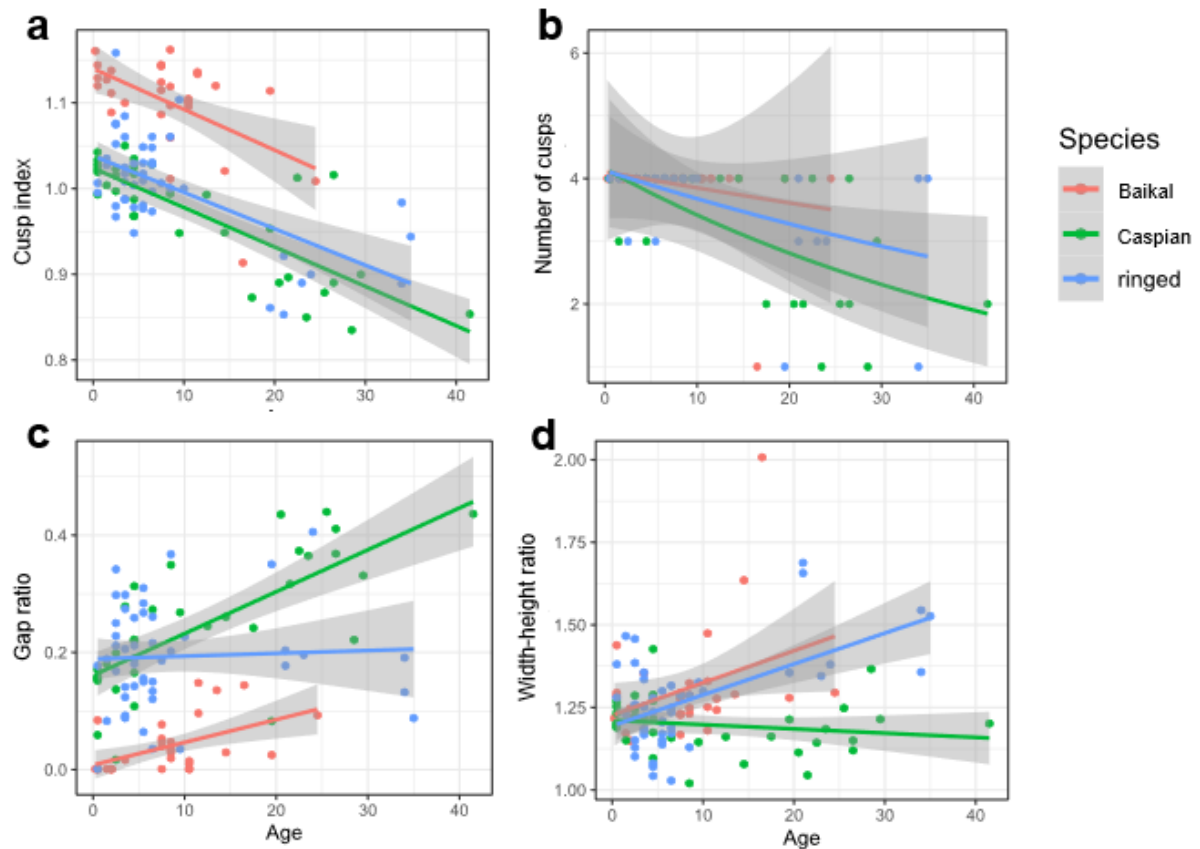


Fig. 4 Relationship between age and postcanine teeth morphologies in three *Pusa* species (Baikal, Caspian, and ringed seals). Effect of age on (a) cusp index, (b) number of cusps, (c) gap ratio, (d) width-height ratio of mandible are shown for Baikal (red), Caspian (green), and ringed seals (blue). Gray bands show 95% credible interval. Graph of maxilla is available in Supplemental Information.

Table. 1 Result of model selection for number of cusps and tooth morphological indices of maxilla. Statistical information of the best model selected are written in the table below. SE stands for Standard Error, AIC stands for Akaike Information Criteria. See Table. S1 for the result of mandible.

cusp index					gap ratio				
Coefficients:	Estimate	SE	t value	P value	Coefficients:	Estimate	SE	t value	P value
(Intercept)	1.070	0.009	114.362	< 0.001	(Intercept)	0.057	0.020	2.898	0.005
Age	-0.004	0.001	-6.812	< 0.001	Age	0.010	0.001	8.222	< 0.001
Caspian seal	-0.111	0.011	-9.927	< 0.001	Caspian seal	0.204	0.024	8.682	< 0.001
ringed seal	-0.106	0.011	-9.820	< 0.001	ringed seal	0.221	0.023	9.689	< 0.001
Residual SE = 0.043, df = 99.					Residual SE = 0.092, df = 99.				
Adjusted R-squared = 0.640					Adjusted R-squared = 0.640				
F = 61.5 on 3 and 99 DF, p < 0.001					F = 61.69 on 3 and 99 DF, p < 0.001				
number of cusps					width-height ratio				
Coefficients:	Estimate	SE	z value	P value	Coefficients:	Estimate	SE	t value	P value
(Intercept)	1.532	0.111	13.752	< 0.001	(Intercept)	1.085	0.029	36.926	< 0.001
Age	-0.020	0.008	-2.341	0.019	Age	0.005	0.002	2.833	0.006
Caspian seal	-0.299	0.139	-2.155	0.031	Caspian seal	0.005	0.035	0.130	0.897
ringed seal	-0.322	0.132	-2.447	0.014	ringed seal	0.096	0.034	2.816	0.006
Null deviance = 25.932, df = 102.					Residual SE = 0.137, df = 99.				
Residual deviance = 12.946, df = 99					Adjusted R-squared = 0.098				
Family = Poisson distribution, log link function, AIC = 332.19					F = 4.7 on 3 and 99 DF, p = 0.004				

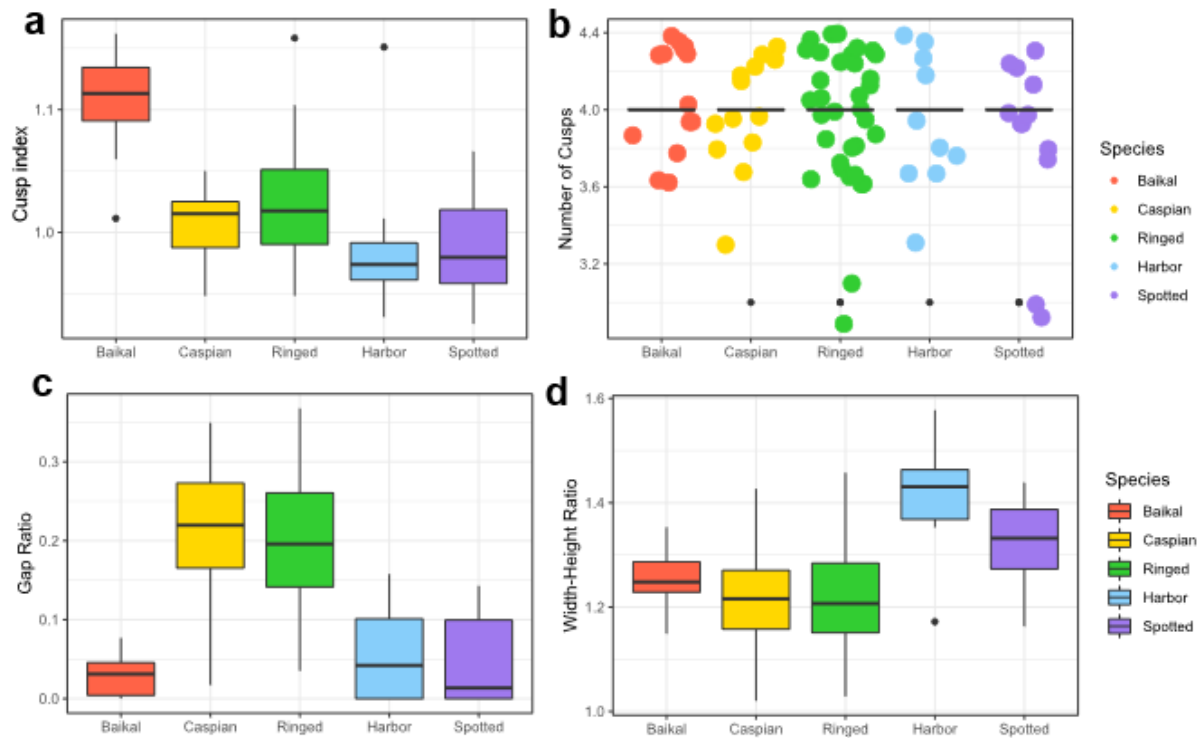


Fig. 5 Box plot of (a) cusp index, (b) number of cusps, (c) gap ratio, (d) width-height ratio of mandible of *Pusa* and *Phoca* species. The box represents Inter-Quartile Range (IQR), while whisker illustrate data range by showing highest or lowest value of data. Outliers (data that are lower than $1st\ quartile - 1.5 \times IQR$ or higher than $3rd\ quartile + 1.5 \times IQR$) are shown in black dots. Since (b) number of cusps were similar in most specimens, data were presented by jitter plot which represents data points in the form of single dots. Black bold lines in (b) represent species' average. Box plot of maxilla data is available in Supplemental Information.

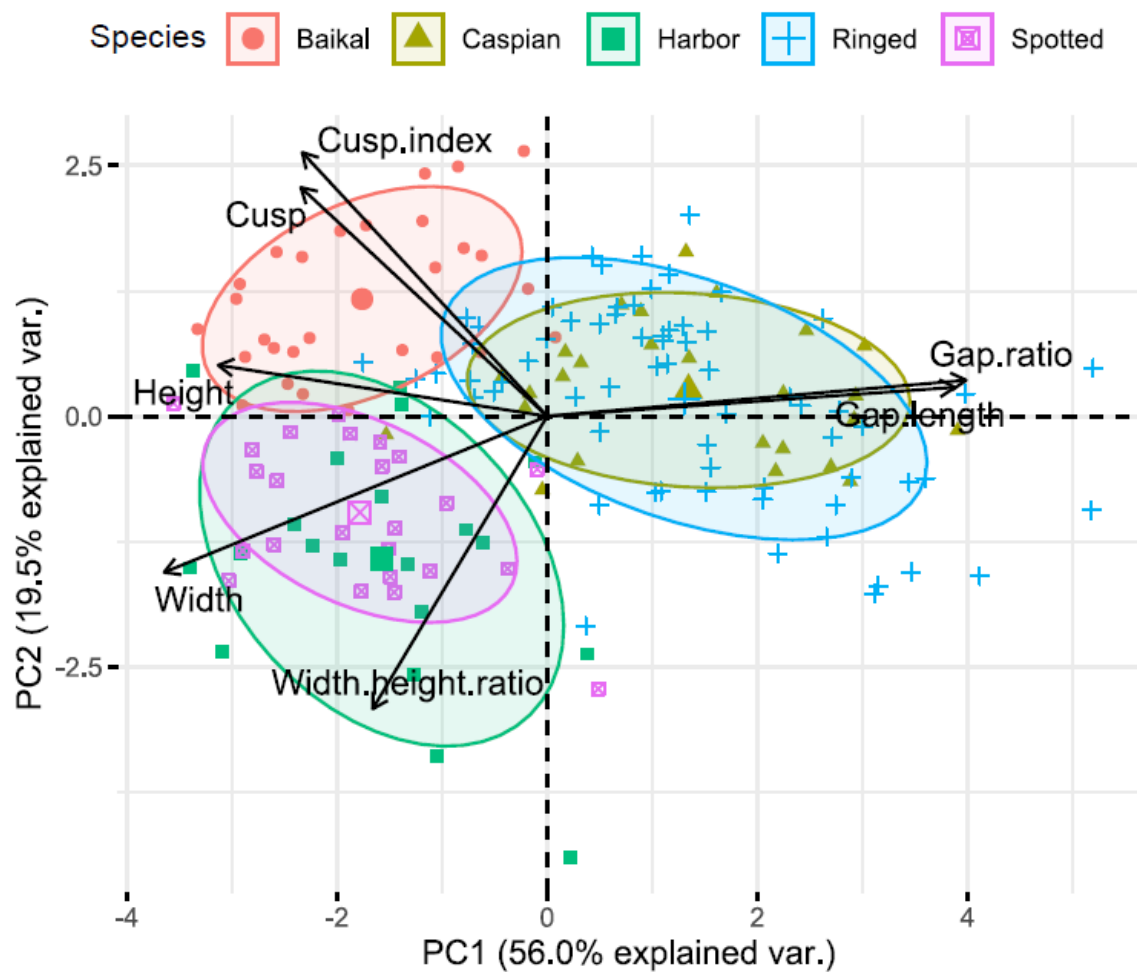


Fig. 6 Result of Principal Component Analysis (PCA) on postcanine teeth morphology in *Pusa* and *Phoca* species. Horizontal axis represents Principal component 1 and vertical axis represents Principal component 2. 68% credible ellipses are shown by ellipse with each species color. Principal component loadings of each variable are represented by arrows.

Table. 2 Result of model selection for zooplankton proportion and frequency of occurrence

(FO) of zooplankton in diets. Only top five models based on AIC are shown, with the best

model denoted by bold.

Model		df	logLik	AIC	ΔAIC
Proportion	1 Proportion ~ cusp index + width-height ratio	4	-8.84	25.7	0
	2 Proportion ~ cusp index + width-height ratio + gap ratio	5	-8.14	26.3	0.61
	3 Proportion ~ cusp index + width-height ratio + <i>Cusp</i>	5	-8.54	27.1	1.40
	4 Proportion ~ cusp index + width-height ratio + <i>Cusp</i> + gap ratio	6	-7.57	27.1	1.45
	5 Proportion ~ cusp index + gap ratio	4	-10.6	29.2	3.52
FO	1 FO ~ cusp index + gap ratio + width-height ratio	5	-2.40	14.8	0
	2 FO ~ cusp index + gap ratio	4	-3.72	15.4	0.65
	3 FO ~ cusp index + gap ratio + width-height ratio + <i>Cusp</i>	6	-2.37	16.7	1.95
	4 FO ~ cusp index + gap ratio + <i>Cusp</i>	5	-3.66	17.3	2.53
	5 FO ~ cusp index + width-height ratio	4	-7.14	22.3	7.48

Table. 3 Statistical information of the best model for each diet indices. Upper and lower tables show the best selected models for zooplankton proportion of seals' diet derived from stable isotope mixing model and Frequency of Occurrence (FO) of zooplankton derived from stomach content analysis, respectively. Standardized Partial Regression Coefficient is same as estimated coefficient. VIF stands for Variance Inflation Factor, index for detecting multicollinearity. Asterisks represent significant differences at $P < 0.05$ (*) or $P < 0.01$ (**).

Best Model: Proportion ~ cusp index + width-height ratio

Variables	Standardized Partial Regression Coefficient	VIF	Std. Error	t value	Pr(> t)	
cusp index	0.781	1.01	0.177	4.42	0.002	**
width-height ratio	-0.407	1.01	0.177	-2.30	0.047	*

Best Model: FO ~ cusp index + gap ratio

Variables	Standardized Partial Regression Coefficient	VIF	Std. Error	t value	Pr(> t)	
cusp index	1.17	1.61	0.201	5.80	0.001	**
gap ratio	0.637	1.61	0.201	3.16	0.019	*

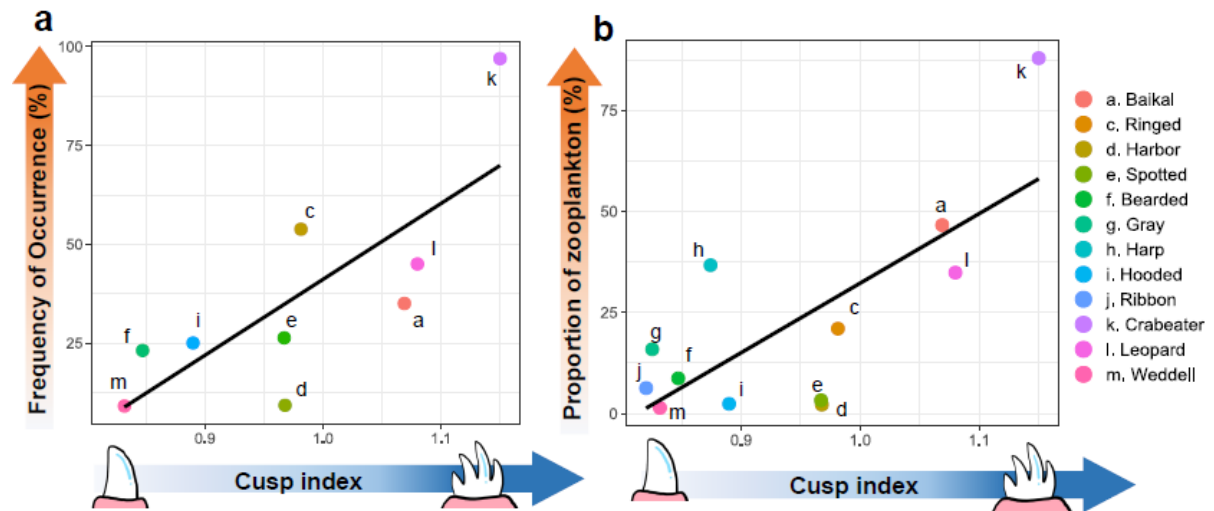


Fig. 7 Relationship between cusp index and (a) Frequency of Occurrence (%) from stomach content analysis ($P = 0.014$, Adjusted $R^2 = 0.541$), and (b) Proportion of zooplankton (%) calculated from stable isotope mixing model ($P = 0.005$, Adjusted $R^2 = 0.513$) in phocid seals.

414 **DATA AVAILABILITY**

415 Results for multiple comparisons, graph of maxilla data, box plot of maxilla data, and diet data
416 used in this research are available in Supplemental Information.

417

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