

RESEARCH ARTICLE



Exploring factors shaping the craniomandibular shape of extant walrus

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Funding information

Belgian American Educational Foundation (BAEF) post-doctoral fellowship; Overseas Musha Training Support Program for Graduate Students; the Support Program for Participation in Overseas Conferences of the Habatake! Program; National Science Foundation (NSF DBI-2128146); the Jackson School of Travel Grant from the Society of Vertebrate Paleontology; the Hans de Bruijn Foundation

Abstract

As both iconic Arctic megafauna and long-exploited marine resources, walruses (*Odobenus rosmarus*) have left an abundant osteological record across the Holarctic. However, distinguishing sex, ontogenetic stage, and subspecies assignment from disarticulated skeletal elements remains challenging. Quantifying cranial and mandibular shape variation while disentangling the effects of individual intrinsic factors (sexual dimorphism, ontogeny, geographic distribution) but also their combined influence offers new insights into these key axes of morphological differentiation. Here, two-dimensional geometric morphometric analyses are applied to 166 skulls and 143 mandibles representing the Atlantic (*O. r. rosmarus*) and Pacific (*O. r. divergens*) subspecies. Analyses revealed that sexual dimorphism is the dominant morphological signal: males develop more compact and reinforced skulls and mandibles, reflecting strong constraints to grow tusks and handle combat stresses, whereas females retain more gracile morphologies. Juveniles closely resemble adult females, with males diverging later through delayed hypermorphic growth. Subspecific comparisons confirmed significant differences, with Pacific walruses exhibiting more robust morphologies and greater developmental canalization, while Atlantic walruses show higher variability, likely linked to heterogeneous ecological conditions. Population-level analyses highlighted additional structuring, with Pacific groups tightly constrained and Atlantic groups occupying a broader morphospace. Unlike previous studies that examined sexual dimorphism, ontogeny, or subspecific differences separately, our study evaluates all three factors within a unified framework, revealing a hierarchical organization of craniomandibular variation shaped by sexual selection, developmental timing, and ecological divergence. These results provide new insights into walrus evolutionary history and their differential vulnerability to past human exploitation and ongoing Arctic environmental change.

KEYWORDS

geometric morphometrics, *Odobenus rosmarus*, ontogeny, sexual dimorphism, subspecies

1 | INTRODUCTION

The extant walrus (*Odobenus rosmarus*) is the sole surviving species of Family Odobenidae, which belongs to the Suborder Pinnipedia, which also include fur seals, sea lions, and true seals (Berta, 2009). These aquatic mammals live around the Arctic Circle and are characterized by two large and elongated upper canine teeth, otherwise known as “tusks.” Like many pinnipeds, walruses possess marked sexual dimorphism, linked to polygynous behavior (e.g., Bartholomew, 1970; Garlich-Miller & Stewart, 1998; Lindenfors et al., 2002; Mesnick & Ralls, 2018). Polygyny is an integral part of walrus life (Fay, 1982). An ontogenetic signal of polygyny in walruses can also be seen in the different growth rates between male and female *O. rosmarus*. In walruses, males and females reach sexual maturity at different ages (Born, 2003; Fay, 1982, 1985). Although females may start ovulating between 4 and 7 years of age, they do not reach full physical and sexual maturity until about 10 years old, with peak fertility occurring between 10 and 11 years (Fay, 1982, 1985). Males become fertile between 5 and 6 up to 12 years, but do not mate until fully developed, and a second stage of growth enables them to be large and powerful enough to compete with other bulls for the right to mate, around the age of 15 years (Born, 2003; Fay, 1982, 1985). Throughout the growth of the individual and even continuing throughout its life, the anterior margin of the rostrum swells to support the continued growth of the tusks, primarily used in a display role but possibly during fights (Fay, 1982; Miller, 1975).

Another distinctive feature of the extant walrus is the fact that they have two distinct populations, recognized as subspecies, including geographical and genetic differences, one with a northern Pacific distribution (*Odobenus rosmarus divergens*) and one with a northern Atlantic distribution (*Odobenus rosmarus rosmarus*) (Berta & Churchill, 2012; Cronin et al., 1994). A third subspecies (*Odobenus rosmarus laptevi*) corresponding to a population located in the Laptev Sea (Russia) has been proposed (Chapksii, 1940) but recently genetic analyses have shown that this population is the westernmost Pacific subpopulation (Lindqvist et al., 2009; Mills et al., 2024). Allen (1880) presented morphological differences in the skull and mandible between the two subspecies. Among these differences, Allen noted that the Pacific walrus possesses longer and thicker tusks, the forehead outline is straighter in the skull, a broader snout, the anterior part of the skull being more elongated compared to the occipital part or a more developed anterior part of the mandible, than its Atlantic counterpart. It remains unclear when the two populations split, although one study suggests it was during the Middle Pleistocene (Cronin

et al., 1994; Hoelzel, 2002) while others have suggested that the Atlantic population had a more recent evolutionary history (Mills et al., 2024). Other researchers believe that the Pacific subspecies is actually the result of a recolonization of the Pacific by a North Atlantic stock of specimens during the late Pleistocene and the Sangamonian Stage, after having disappeared there around 2 million years ago (Fay, 1982, 1985; Harington & Beard, 1992; McLeod et al., 2014; Repenning, 1976). Beyond the subspecies level, the recent evolutionary history of the extant walrus is well documented, with nine extant populations recognized (seven for *O. r. rosmarus* and two for *O. r. divergens*) and two extirpated ones (e.g., McLeod et al., 2014; Higdon & Stewart, 2018; Ruiz-Puerta et al., 2023; NAMMCO).

Tusks have been used to quantify intraspecific variation in the walrus (Allen, 1880; Fay, 1982; Mohr, 1942). However, other skeletal elements, more particularly the mandible or skull without tusks, could be used as a proxy to differentiate sexual dimorphism, ontogenetic stages or subspecies differences (e.g., Allen, 1880; Boisville et al., 2022; Dierickx et al., 2025; Fay, 1985; Taylor et al., 2020; Wiig et al., 2007).

Geometric morphometrics is widely used to quantify shape variation in relation to ontogeny (e.g., Chatar et al., 2024; Dierickx et al., 2025; Segura et al., 2013; Segura & Prevosti, 2012), sexual dimorphism (e.g., Boisville et al., 2022; Christiansen & Harris, 2012; Hood, 2000; Loy et al., 2004; Oliveira et al., 2005), and subspecies-level differences (e.g., Machado & Teta, 2020). Here, we apply two-dimensional geometric morphometrics to disentangle the relative contributions of ontogeny, sexual dimorphism, and subspecific/geographical variation to craniomandibular shape in the extant walrus (*O. rosmarus*). Whereas prior studies have typically focused on one of these factors at a time, or examined the cranium and mandible separately, our study is the first to jointly evaluate ontogeny, sexual dimorphism, and subspecific variation within an integrated framework, providing a more comprehensive understanding of craniomandibular shape variation in the walrus (*O. rosmarus*). Subspecies-level comparisons can shed light on the processes driving divergence between the two living walrus populations, as can finer-scale demographic analyses that highlight eco-morphological differences related to their distinct environmental and ecological contexts. While mandibular sexual dimorphism has already been documented (Boisville et al., 2022), the skull offers complementary insights into sex-related differences. Moreover, ontogeny and sexual dimorphism have been documented in the cranium and mandible of the Atlantic walrus (*O. r. rosmarus*) (Dierickx et al., 2025), but not in the Pacific walrus (*O. r.*

divergens). Together, examining cranial and mandibular variation across both subspecies but also among populations is key to reconstructing the evolutionary pressures that shaped the walrus lineage.

This study will investigate cranial and mandibular morphology in the walrus (*O. rosmarus*) using morphometric analyses to evaluate the effects and interactions of ontogeny, sexual dimorphism, and geographic variation, as well as their discriminative power in extant populations. These results will then be integrated into a broader evolutionary framework to provide new insights into morphological diversification within the species.

2 | MATERIALS AND METHODS

2.1 | Institutional abbreviations

ANSP, Geology and Zoology sections, Academy of Natural Sciences of Drexel University, Philadelphia, USA;

CBMPV, Chiba Natural History Museum and Institute, Chiba, Japan;

CMNFV, Fossil vertebrates collection, Canadian Museum of Nature, Ottawa, Canada;

CMNMA, Mammals collection, Canadian Museum of Nature, Ottawa, Canada;

IINH RM, Icelandic Institute of Natural History, Garðabær, Iceland;

IRNSB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium;

NHMUK, The Natural History Museum, London, England, UK;

NMNS-M, Mammals collections, National Museum of Nature and Science, Tokyo, Japan;

NMR, Natuurhistorisch Museum Rotterdam, Rotterdam, the Netherlands;

NNM (RMNH.MAM), formerly Geological Museum, Amsterdam University, Amsterdam, The Netherlands; now stored at National Museum of Natural History, Naturalis Biodiversity Center, Leiden, the Netherlands;

NNM (ZMA), formerly Zoological Museum collections of Amsterdam University, Amsterdam, The Netherlands; now stored at National Museum of Natural History, Naturalis Biodiversity Center, Leiden, the Netherlands;

SINRC, South Iceland Nature Research Center, Sandgerði, Iceland;

UMZC, University Museum of Zoology, University of Cambridge, Cambridge, England, UK;

USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, DC, USA;

UZMK, Universitetets Zoologiske Museum, Copenhagen, Denmark;

ZIN, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

2.2 | Biological sample

The dataset includes 166 *O. rosmarus* skulls and 143 mandibles. The sample comprises specimens from various geographical regions, from the Bering Strait to west coast Greenland, through Kara Sea and the Foxe Basin, representing the two currently recognized subspecies in the Pacific and Atlantic (*O. r. divergens* and *O. r. rosmarus*, respectively), and including subfossil specimens derived from zooarchaeological or historical contexts (Canadian Maritimes; Iceland) (Figure 1, Tables S1, S2). Specimens of *O. rosmarus* were assigned to their corresponding subspecies according to their locality of discovery if the subspecies attribution was not clear in the specimen metadata. Overall, 69 skulls and 60 mandibles were assigned to Pacific walrus (*O. r. divergens*), and 71 skulls and 63 mandibles were assigned to Atlantic walrus populations (*O. r. rosmarus*). If recorded, the origin of the specimens follows the various populations described by Born et al. (2001), Higdon and Stewart (2018) and Ruiz-Puerta et al. (2023), as represented in Figure 1 (Tables S1, S2).

Sex was identified in 106 of the 166 skulls examined (70 males (*m*) and 36 females (*f*)), and in 103 mandibles (65 males and 38 females). The proxies used to determine the ontogenetic stage are: the relative suture of bones, as explained in Sivertsen (1954) and presented in Kastelein and Gerrits (1990) and Dierickx et al. (2025), the absolute values of the width of the mastoid and mandible, as expressed in McLeod et al. (2014), and the relative sizes and eruption of cheek teeth, when possible, as expressed in Cobb (1933) and Doult (1942). Age classes were first assigned following Fay (1982, 1985) and Born (2003), designated either as newborns (between 0 and 2 years for both sexes), juveniles (from 2 to 4 yo until 7 yo for females, 1–2 until 5–6 for males), subadults (from 4 to 7 yo until 10–11 yo for females, 5–6 until 12–15 years for males), and adults (>10–11 yo for females, >12–15 for males). However, because of the wide ontogenetic span of the subadult stage and the small sample size for both newborns and subadults, individuals were grouped into two categories: juveniles (comprising newborns, juveniles) per Fay (1982, 1985) and Born (2003); and adults (comprising subadults and adults) (Tables S1, S2). This resulted in 33 skulls and 28 mandibles being classified as juveniles.

Because not all specimens could be included in every analytical framework, sample sizes varied according to the objective of each analysis. Every specimen could be attributed to an ontogenetic stage so that the whole

Odobenus rosmarus populations Meghalayan (4,200 - 0 years B.P.)

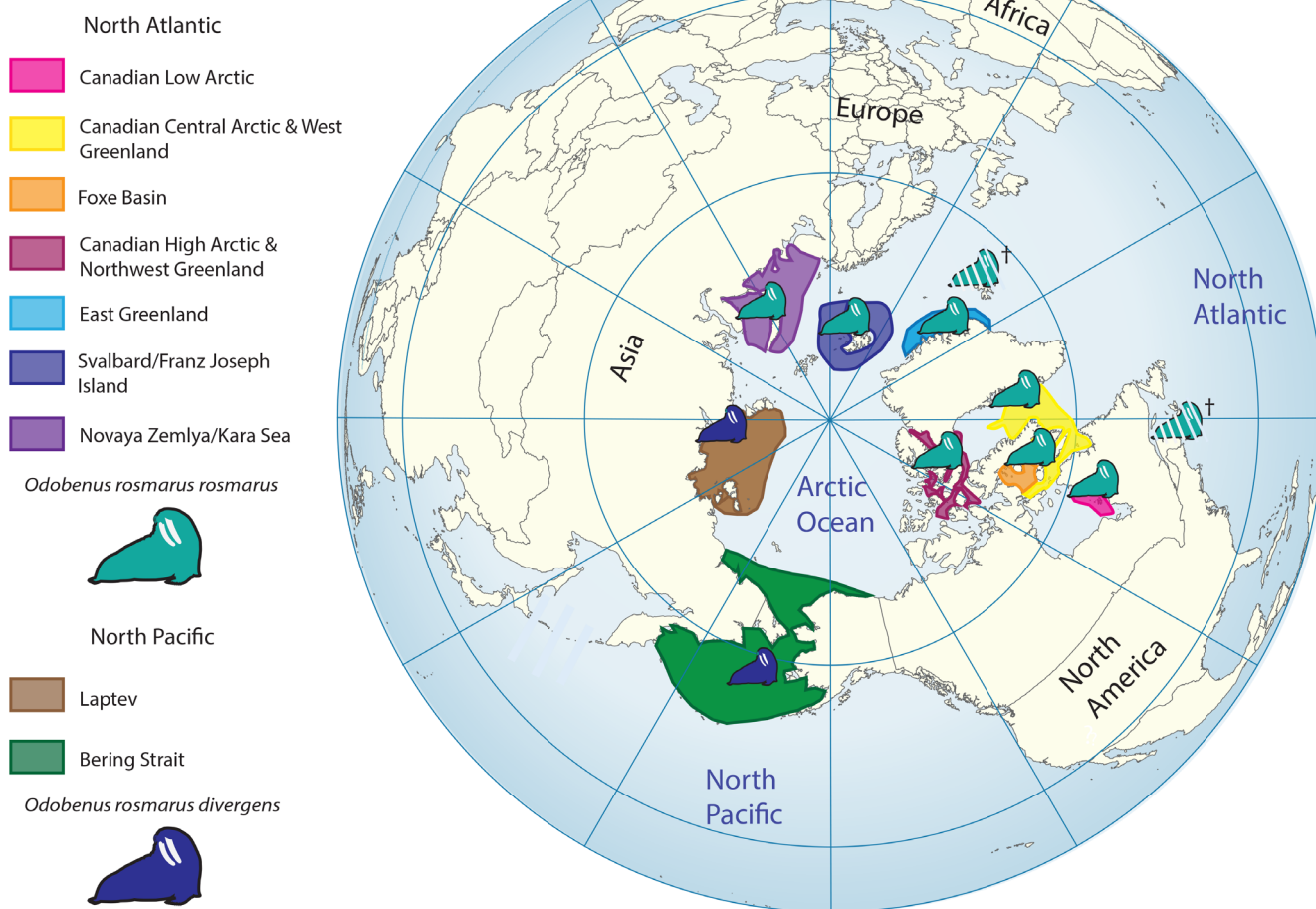


FIGURE 1 Polar projection map representing the currently recognized populations of *Odobenus rosmarus*, for the Atlantic subspecies (*O. r. rosmarus*, green) and the Pacific subspecies (*O. r. divergens*, blue) (Meghalayan, 4200–0 years Before Present), according to Born et al. (2001), Stewart and Higdon (2017), Higdon and Stewart (2018) and Ruiz-Puerta et al. (2023). The hatched silhouettes correspond to the two populations (Iceland, Greater Gulf of St. Lawrence) which became extinct respectively in the 14th and 18th centuries, due to human activity. Map and silhouettes drawn by N. Chatar and M. Boisville.

dataset (166 skulls and 143 mandibles) was used for analyses dealing with ontogeny. In contrast, analyses focusing on sexual dimorphism were restricted to specimens classified as adults and with identified sex; these analyses therefore included 133 skulls and 115 mandibles. Finally, subspecies-level analyses were also limited to adult individuals and excluded specimens for which subspecific attribution or discovery locality was unknown, as such information is required for reliable assignment. This resulted in a final sample of 112 skulls and 99 mandibles.

2.3 | Anatomical terminology

The anatomical nomenclature utilized in this study is the same as presented in Boisville et al. (2022) and Dierickx et al. (2025).

2.4 | Geometric morphometrics

To assess the shape variation in both skulls and mandibles within our sample, we employed two-dimensional geometric morphometrics. We used the same landmarking scheme as in Boisville et al. (2022) for the lateral view of the mandible. Then, we added an additional view for the mandible (occlusal view) and landmarked three different views for the skull by capturing the lateral, dorsal, and anterior views (Supplemental Dataset S1). Different views were included to encompass a larger morphological sample due to the degree of preservation of walrus material. The photography process follows the same protocol as described in Boisville et al. (2022), with the addition of certain photographs taken by the respective museum curators. For the skull, seven fixed landmarks were chosen and 82 semi-landmarks for the lateral view, 10 fixed

landmarks and 69 semi-landmarks regarding the dorsal view, and four fixed landmarks and 32 semi-landmarks concerning the anterior view. For the mandible, five fixed landmarks and 60 semi-landmarks were selected to enhance the occlusal shape. The morphological characteristics, represented by the fixed landmarks, are featured in Figure S1 and presented in Table S3. For each view, a specified number of curves were positioned between the fixed landmarks, along which the sliding semi-landmarks were positioned (Table S3). Landmark coordinates were digitized using tpsDig (Rohlf, 2006), and associated utility procedures were performed with tpsUtil32 (Rohlf, 2018). Landmark and semi-landmark coordinates are provided as a .tps file (Supplementary Data S1). Missing landmarks and semi-landmarks were estimated using the function *fixLMtps* implemented in the Morpho package, which applies weighted averages derived from complete specimens to incomplete datasets (Schlager, 2017). A generalized Procrustes analysis was performed in the R Studio environment v.4.5.0 (R Development Core Team, 2025), using the *gpagen* function (Geomorph package) with bending energy for sliding (Adams et al., 2020; Schlager, 2017). This procedure removed non-shape variation related to position, orientation, and scale, yielding aligned Procrustes coordinates for subsequent analyses.

Analyses were conducted to formally test group differences before exploring the underlying structure of shape variation. Prior to discriminant-based tests, standard multivariate assumptions (multivariate normality, homogeneity of covariance matrices, and group size relative to dimensionality) were evaluated to guide the choice of appropriate statistical methods. Depending on whether these assumptions were met, linear or regularized discriminant analyses (LDA/RDA), together with Procrustes ANOVA and between-group analyses (BGAs), were used to quantify and validate shape differences among predefined biological groups. Principal component analyses (PCA) were subsequently employed as a descriptive and interpretative tool to visualize morphospace structure and to identify the main morphological features underlying the statistically supported patterns.

2.5 | Assessment of group differences

Prior to testing for significant differences among groups (i.e., sex, ontogenetic stage, and subspecies), standard assumptions were evaluated: (i) each group follows a multivariate normal distribution; (ii) covariance matrices are homogeneous; and (iii) the smallest group contains more specimens than the number of variables. In this dataset, the number of variables greatly exceeded the number of specimens. Multivariate normality was assessed using

Mardia Skewness and Mardia Kurtosis tests implemented in the MVN package. If both tests were satisfied at the 0.05 significance level, a LDA was applied to landmark coordinates using the *lda* function (MASS package) (Venables & Ripley, 2002), with Box's M-test (Box, 1949) employed to verify homogeneity of covariance matrices (Table 1, Supplemental Dataset S2). If one or both normality tests failed, an RDA was performed. RDA, a generalization of LDA, applies covariance matrix shrinkage to account for deviations from multivariate normality and/or small sample sizes (Friedman, 1989) (Supplemental Dataset S2).

2.6 | Procrustes ANOVA and allometric analyses

Subsequently, Procrustes ANOVAs were performed on landmark coordinates with 1000 permutations using the *procD.lm* function (Geomorph package) (Adams et al., 2020), to quantify differences in craniomandibular shape between sexes, ontogenetic stages, subspecies, and populations (Table 1). The null hypothesis states that the studied factor has no effect on cranial or mandibular morphology. To avoid ontogenetic bias, analyses of sex- and subspecies-related shape variation were restricted to adult individuals (Supplemental Dataset S2). For the ontogenetic stage, we further performed a permutational Multivariate Analysis of Variance (PERMANOVA) with sex, size, and sex $\times$ size as factors, using the *plotAllometry* function (Geomorph package; Adams & Otárola-Castillo, 2013), to evaluate how allometric variation in shape was associated with these factors (e.g., Chatar et al., 2024; Segura, 2013; Segura et al., 2021). Significance of regressions was tested using permutation tests with 1000 resamples (Bookstein, 1991; Mitteroecker et al., 2004) (Table 1). An additional PERMANOVA was performed using subspecies as a factor to assess potential ontogenetic differences between the two subspecies (Table 1, Supplemental Dataset S2).

2.7 | Between-group analysis

BGAs (Culhane et al., 2002) were conducted using the *ade4* package (Dray & Dufour, 2007) on the first 10 PCs (explaining $\geq 74\%$ of the total variance for each analysis) following Cardini (2024) and Hardouin et al. (2024), to evaluate whether groups were statistically independent and could be discriminated based on the variable of interest. Three complementary statistics were computed: (1) *rand-test* *p*-value; (2) explained variance ratio; and (3) $\Delta\bar{O}_{ij}$ index between the BGA factor and cross-validation factor map, calculated via the *loocv* function (Thioulouse et al., 2021) (Table 1, Supplemental Dataset S2).

TABLE 1 Summary of statistical analyses on cranial and mandibular morphology of walruses across sex, ontogeny, subspecies, populations, and ontogenetic trajectories.

	Multivariate normality	RDA/classification accuracy	Procrustes ANOVA (<i>p</i> -value)	Between-group analysis (BGA)
Sex	Not met for cranium Met for mandible → Not met	Accuracy >75% across ratios (except mandible 90/10: 66%)	<i>p</i> = 0.001*** for both structures	Significant separation (<i>p</i> = 0.001***); Cranium = 7.65%, Mandible = 7.17%; robust for Cranium ($\Delta\bar{O}ij$ = 0.79% vs. 2.41%)
Ontogeny	Not met for both structures	Accuracy >75% across ratios (both structures)	<i>p</i> = 0.001*** for both structures	Significant separation (<i>p</i> = 0.001***); Cranium = 7.09%, Mandible = 3.91%; Cranium more robust ($\Delta\bar{O}ij$ = 1.52% vs. 4.83%)
Subspecies	Not met for both structures	Accuracy >75% across ratios (both structures)	<i>p</i> = 0.001**** for both structures	Significant separation (<i>p</i> = 0.001***); Cranium = 6.77%, Mandible = 5%; Cranium more robust ($\Delta\bar{O}ij$ = 1.85% vs. 4.15%)
Populations	/	/	<i>p</i> = 0.001**** for both structures (all thresholds: <i>n</i> ≥3, 5, 9)	/
Ontogenetic trajectories	/	/	Sex: Cranium: <i>p</i> = 0.058; Mandible: <i>p</i> = 0.354 Subspecies: Cranium: <i>p</i> = 0.044; Mandible: <i>p</i> = 0.041	/

Note: The table reports multivariate normality assessments, regularized discriminant analyses (RDA), Procrustes ANOVAs, and between-group analyses (BGA). Only adult individuals were included in the sex, subspecies, and populations analyses.

2.8 | PCA and morphospace exploration

PCAs were conducted using the *gm.prcomp* function (Geomorph package) to visualize major axes of shape variation across sexes, ontogenetic stages, subspecies, and populations, and facilitate interpretation of group-level differences. PCAs were performed separately for each view and dataset, and additionally on combined datasets in which multiple views were merged into a single array using the *bindArr* function (Morpho package; Schlager, 2017). For the skull, lateral, dorsal, and anterior views were combined; for the mandible, lateral and occlusal views were combined. Log-transformed centroid size was visually represented in PCA plots by scaling point size, allowing qualitative assessment of allometric patterns (Supplemental Dataset S2).

3 | RESULTS

The statistical results have been summarized for clarity in Table 1. Detailed descriptions of shape variation for each anatomical view are presented in the Supplemental Material. Classification accuracies and discrimination metrics are interpreted as measures of morphological

separability among groups rather than as indicators of definitive individual-level identification.

3.1 | Sex-related variation

3.1.1 | Multivariate assumptions and discriminant analyses

Cranial shape did not meet multivariate normality assumptions, whereas mandibular shape did; however, to ensure methodological consistency across structures, RDA was applied in both cases. Classification accuracy, interpreted here as an index of morphological separability among groups, exceeded 75% across all training/test ratios for both structures, except for the mandible at the 90/10 split (66%). Procrustes ANOVA revealed significant shape differences between sexes for both the cranium and the mandible (*p* = 0.001).

BGAs supported statistically significant separation between sexes for both structures (rand-test *p* = 0.001), with comparable proportions of explained variance (~7.41%). Cranial shape showed a more consistent pattern of separation, with lower overlap between male and female morphospaces ($\Delta\bar{O}ij$ = 0.79%) than the mandible.

Those analyses highlighted the strong sexual dimorphism in both the cranium and the mandible, with a somewhat stronger signal in the cranium.

3.1.2 | PCA and sexual dimorphism

Our PCAs reveal that sexual dimorphism is primarily expressed along PC1, with males generally exhibiting more robust cranial and mandibular morphologies and females more gracile configurations. Morphological differences are more pronounced in the cranium than in the mandible (Figures 2–4).

Across all cranial views, the first two principal components capture a consistent morphological gradient

related to cranial elongation, overall robusticity, and the development of structures associated with the maxilla, nuchal crest, and mastoid process (PC1), as well as variation in maxillary and alveolar morphology (PC2). Together, these axes explain between 43% and 60% of cranial shape variance depending on the view (Figure 2). Sexual dimorphism is expressed primarily along PC1, with males tending toward higher or more extreme values, while females cluster toward lower or intermediate values, although partial overlap persists depending on the view.

When interpreted morphologically, this separation reflects general trends in cranial configuration between sexes. Males generally exhibit a more compact and robust cranium, characterized by a relatively shortened and

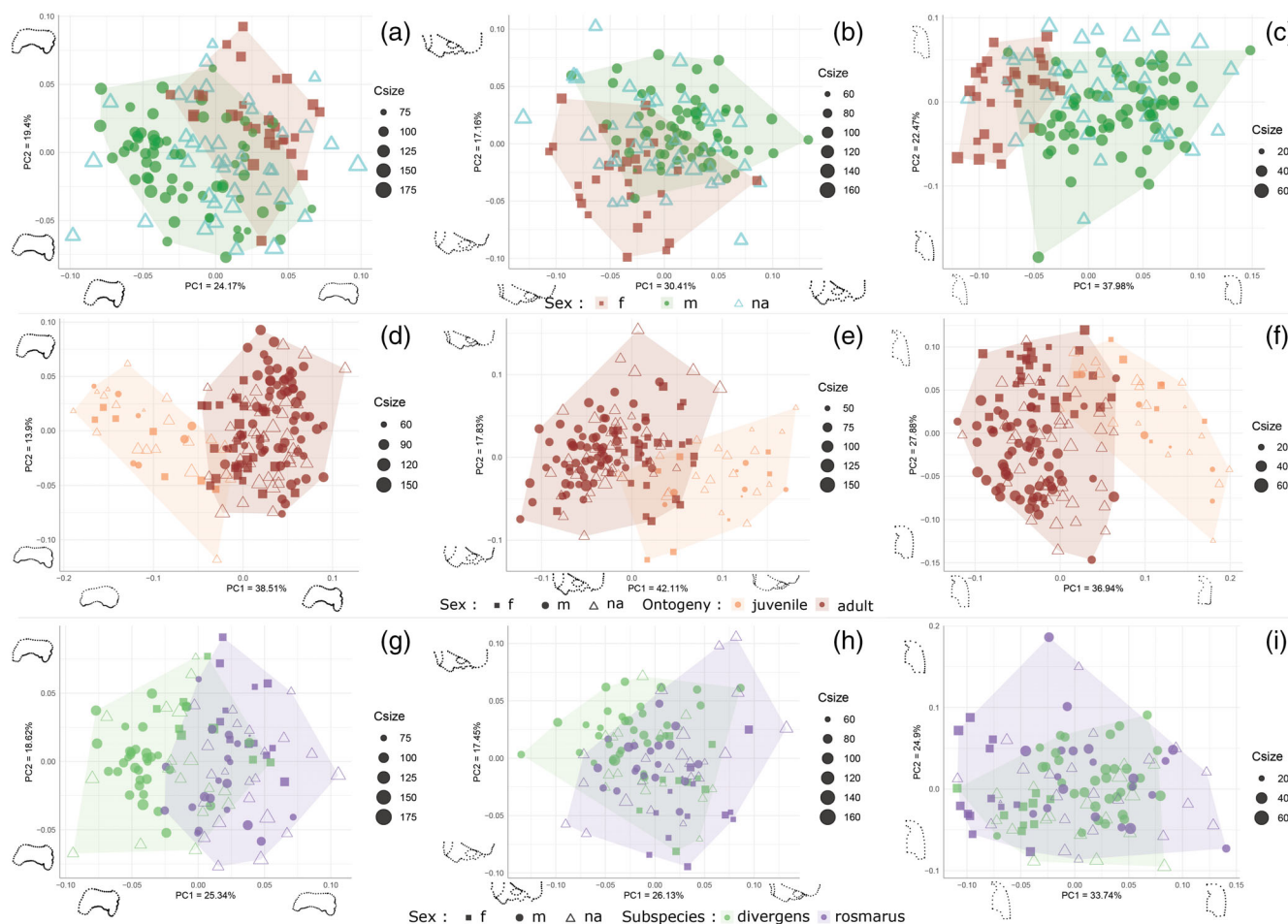


FIGURE 2 Graph of the PCA for the axes PC1 (on the x-axis) and PC2 (on the y-axis) for the cranial morphology. From top to bottom: Sex ($n = 133$), ontogeny ($n = 166$), subspecies ($n = 112$). From left to right: Lateral (a, d, g), dorsal (b, e, h), anterior (c, f, i). Sex: Green dot: Males of *O. rosmarus*; red square: Females; empty blue triangle: Sex not determined. Ontogeny: Dot: Males of *O. rosmarus*; square: Females; empty triangle: Sex not determined; red color: Adult individuals; salmon color: Juvenile individuals. Subspecies: Dot: Males of *O. rosmarus*; square: Females; empty triangle: Sex not determined; green color: *O. r. divergens*; purple color: *O. r. rosmarus*. Only adult individuals were included in the sex and subspecies analyses. The point size of the specimens is determined by the log-transformed centroid size. Extreme morphotypes of each axis have been placed at the ends of these axes. Each assignment corresponds to the corresponding specimens in Table S1.

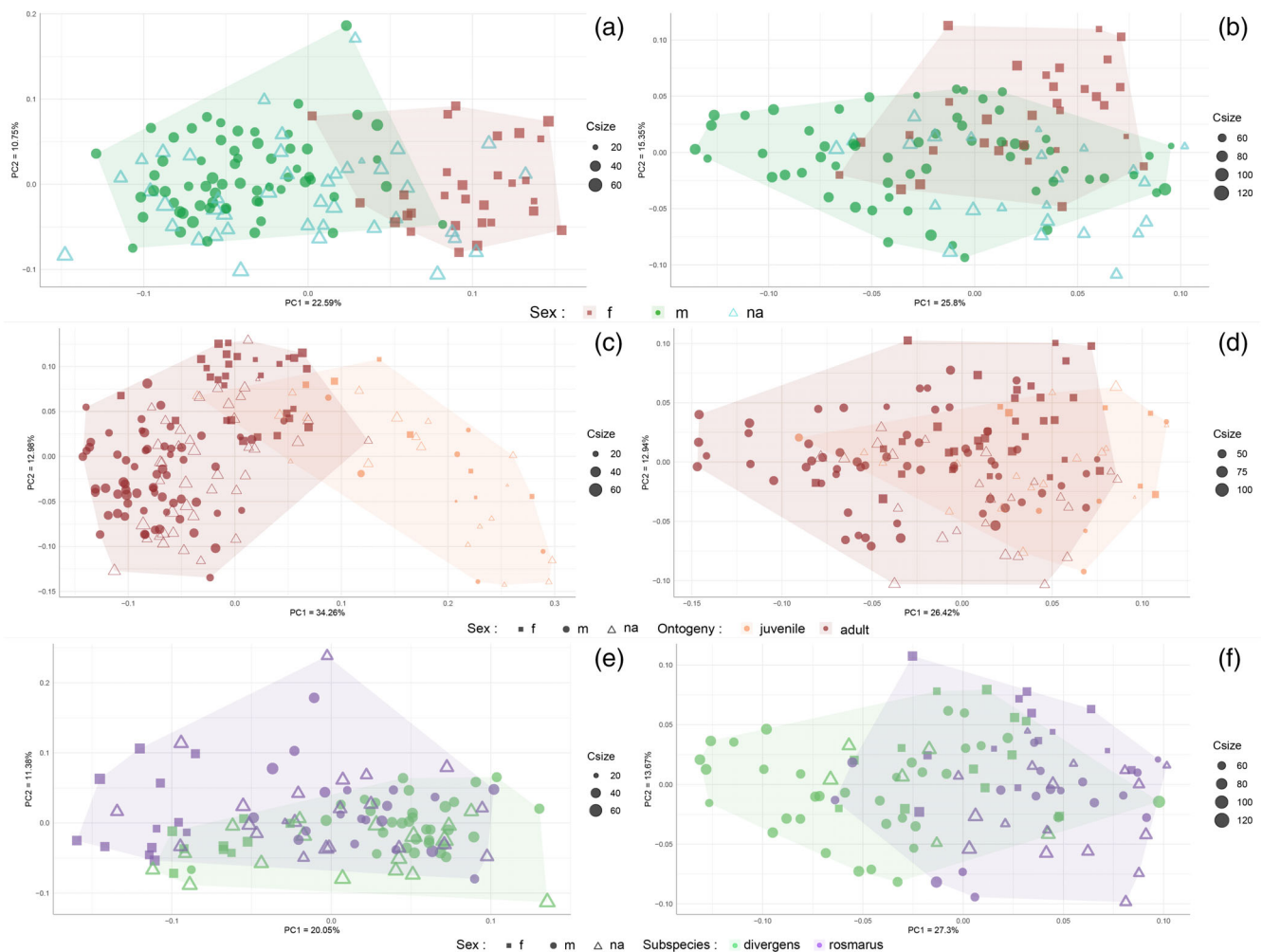


FIGURE 3 Graph of the PCA for the axes PC1 (on the x-axis) and PC2 (on the y-axis) integrating all views into a single morphospace plot for the cranium (a, c, e) and for the mandible (b, d, f). From top to bottom: Sex ($n = 133$ (skull), $n = 115$ (mandible)), ontogeny ($n = 166$ (skull), $n = 143$ (mandible)), subspecies ($n = 112$ (skull), $n = 99$ (mandible)). Sex: Green dot: Males of *O. rosarius*; red square: Females; empty blue triangle: Sex not determined. Ontogeny: Dot: Males of *O. rosarius*; square: Females; empty triangle: Sex not determined; red color: Adult individuals; salmon color: Juvenile individuals. Subspecies: Dot: Males of *O. rosarius*; square: Females; empty triangle: Sex not determined; green color: *O. r. divergens*; purple color: *O. r. rosarius*. Only adult individuals were included in the sex and subspecies analyses. The point size of the specimens is determined by the log-transformed centroid size. Each assignment corresponds to the corresponding specimens in Tables S1 and S2.

more concave cranial vault, a strongly developed and posteriorly projecting nuchal crest, and a ventrally elongated and laterally expanded mastoid process (Figure 2a). In dorsal view, males further show thicker zygomatic arches and a proportionally larger anterior portion of the cranium (Figure 2b). Facial morphology in males is dominated by a pronounced maxillary inflation associated with large upper canines, resulting in a shortened alveolar process, a flatter premaxillary space, a reduced prenasal process, and bony nares positioned approximately at mid-facial height (Figure 2c). In contrast, females display a more elongated and gracile cranial morphology, with a straighter cranial vault, reduced development of the nuchal crest and mastoid process, thinner zygomatic arches, and a

relatively larger posterior portion of the cranium (Figure 2a,b). Females also show a less inflated maxilla, a ventrally elongated alveolar process, a more concave premaxillary space, a longer prenasal process, and bony nares positioned higher on the face (Figure 2c).

When all cranial views are combined into a single morphospace, the first two components explain 33.34% of the total variance. Females are restricted to positive PC1 values and mostly neutral or negative PC2 values, whereas males span a broader range along both axes (Figure 3a).

For the mandible, PC1 consistently reflects variation in anterior robusticity and proportional relationships between the horizontal and vertical rami, whereas PC2

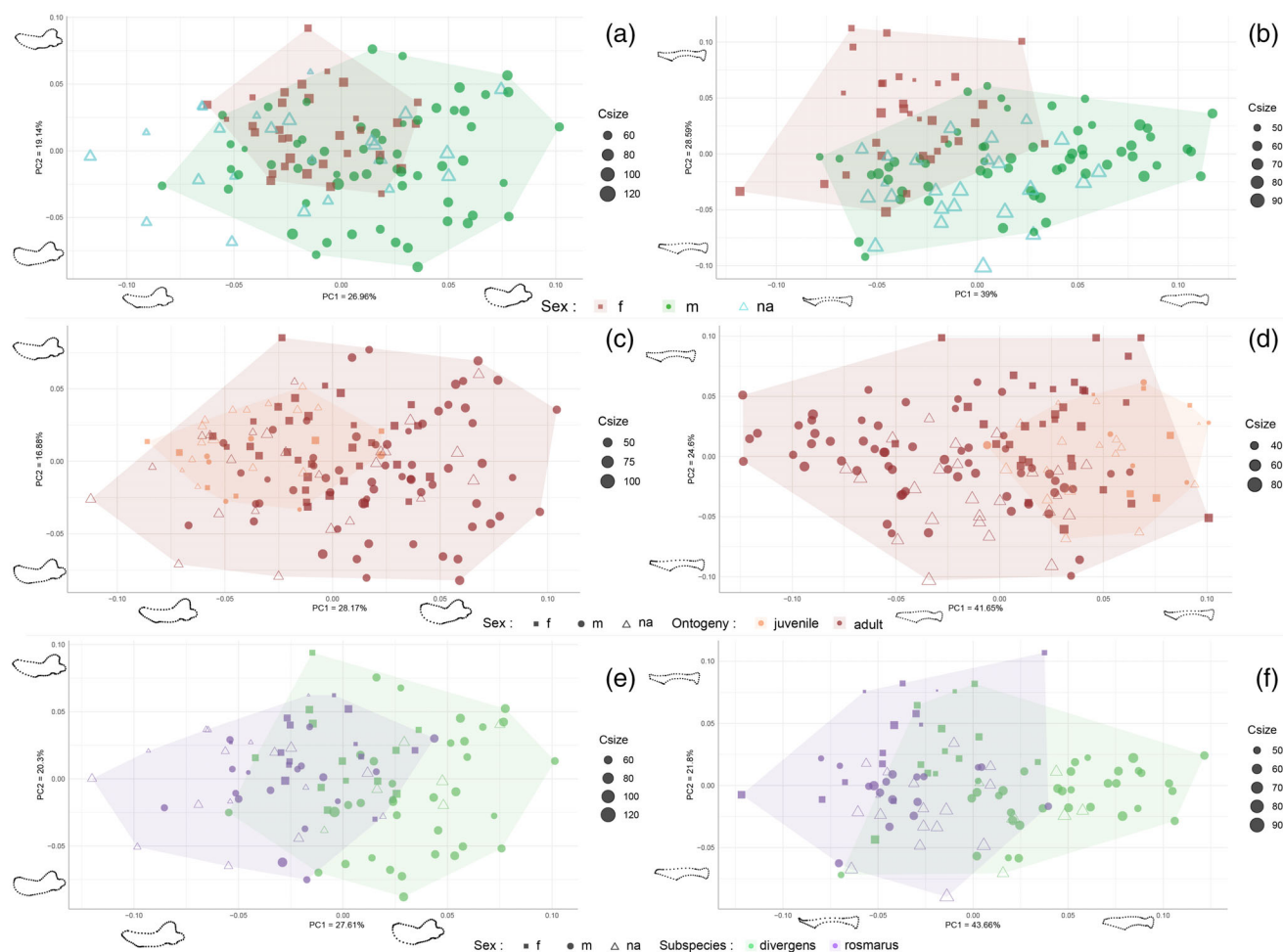


FIGURE 4 Graph of the PCA for the axes PC1 (on the x-axis) and PC2 (on the y-axis) for the mandibular morphology. From top to bottom: Sex ($n = 115$), ontogeny ($n = 143$), subspecies ($n = 99$). From left to right: Lateral (a, c, e), occlusal (b, d, f). Sex: Green dot: Males of *O. rosamarus*; red square: Females; empty blue triangle: Sex not determined. Ontogeny: Dot: Males of *O. rosamarus*; square: Females; empty triangle: Sex not determined; red color: Adult individuals; salmon color: Juvenile individuals. Subspecies: Dot: Males of *O. rosamarus*; square: Females; empty triangle: Sex not determined; green color: *O. r. divergens*; purple color: *O. r. rosamarus*. Only adult individuals were included in the sex and subspecies analyses. The point size of the specimens is determined by the log-transformed centroid size. Extreme morphotypes of each axis have been placed at the ends of these axes. Each assignment corresponds to the corresponding specimens in Table S2.

captures variation in ventral margin shape and condylar morphology. The first two PCs explain between 46% and 68% of mandibular shape variance depending on the view (Figure 4). Sex-related separation is weaker in the mandibular morphospace than in the cranium, particularly in lateral view, where substantial overlap is observed; although occlusal view provides improved discrimination.

Sexual dimorphism in mandibular morphology is expressed as a tendency toward more robust male and more gracile female configurations. Males are characterized by increased anterior robusticity, with a strongly convex anterior margin, a shortened horizontal ramus relative to the vertical ramus producing a dorsally elevated anterior portion, a rectilinear ventral margin, and a posteriorly developed mandibular condyle (Figure 4a). In

occlusal view, males further exhibit an anteriorly elongated and convex mandibular terminus, a thick horizontal ramus, and a rounded mandibular condyle (Figure 4b). Females, in contrast, display a more elongated and gracile mandibular morphology, characterized in lateral view by a flatter anterior margin, a proportionally elongated horizontal ramus with a posteriorly extended angular process, a slightly concave ventral margin, and a more ventrally oriented mandibular condyle (Figure 4a). In occlusal view, female mandibles are distinguished by a pinched and laterally concave mandibular terminus, a slender horizontal ramus, and an oval mandibular condyle with medial extension (Figure 4b).

In the combined mandibular morphospace, the first two PCs explain 41.15% of total variance, with males broadly distributed across PC1 and clustering toward

neutral or negative PC2 values, whereas females preferentially occupy positive PC1 and PC2 values (Figure 3b).

3.2 | Ontogenetic disparity

3.2.1 | Multivariate assumptions and discriminant analyses

Neither cranial nor mandibular shape met multivariate normality assumptions. Classification accuracy exceeded 75% for all training/test ratios. Procrustes ANOVA revealed significant shape differences between juveniles and adults for both structures ($p = 0.001$).

BGAs confirmed significant ontogenetic separation (rand-test $p = 0.001$), with the cranium explaining approximately twice the proportion of variance compared to the mandible (7.09% vs. 3.91%). Cranial morphology also exhibited reduced overlap between age groups ($\Delta\bar{O}_{ij} = 1.52\%$) relative to the mandible.

Just as for the sexual dimorphism, the cranium appears to carry more discriminant power between ontogenetic stages than the mandible.

3.2.2 | PCA and ontogenetic trajectories

PCAs reveal clear ontogenetic variation, with juveniles resembling adult females but smaller and more gracile, adult females intermediate, and adult males the most robust and extreme; ontogenetic differences are more pronounced in the cranium than in the mandible (Figures 2–4).

Across all cranial views, PC1 represents the main ontogenetic gradient, reflecting overall cranial elongation, robusticity, development of the nuchal crest and mastoid process, and maxillary expansion, whereas PC2 captures secondary variation in maxillary and prenasal morphology. Together, the first two PCs explain between 52% and 65% of cranial shape variance depending on the view (Figure 2).

Juvenile crania are characterized by a short, convex cranial vault, limited development of the nuchal crest and occipital condyle, and weakly inflated maxillae, consistent with underdeveloped tusks. In lateral view, juveniles occupy negative PC1 values, with slightly convex cranial vaults, ventrally positioned mastoid processes, and undifferentiated premaxillae and alveolar processes (Figure 2d). Dorsal views show juveniles with proportionally larger posterior crania, thin zygomatic arches, and undeveloped lateral mastoid expansions (Figure 2e). In anterior view, juveniles exhibit less lateral maxillary inflation, more developed ventral alveolar processes, a

concave premaxillary space, and nasals positioned high on the face (Figure 2f). Overall, juvenile cranial morphology resembles that of adult females but is smaller, less robust, and lacks pronounced cranial and maxillary structures.

Adult female crania occupy intermediate positions along PC1 and PC2. They are moderately elongated with gently developed nuchal crests and mastoid processes, slightly inflated maxillae, and a straighter cranial vault than juveniles (Figure 2d). In dorsal view, adult females display thin zygomatic arches and proportionally larger posterior cranial regions (Figure 2e). In anterior view, they show moderate premaxillary differentiation, a gently convex alveolar process, and bony nares positioned higher than in adult males (Figure 2f). Overall, adult female morphology represents a slight increase in cranial robusticity and maxillary development relative to juveniles, without reaching the extreme features observed in adult males.

Adult male crania occupy extreme PC1 values, reflecting a robust, compact cranial configuration. Lateral views show ventrally elongated and laterally expanded mastoid processes, a straighter cranial vault, and pronounced nuchal crest development (Figure 2d). Dorsal views reveal thick zygomatic arches and a proportionally larger anterior cranium (Figure 2e). In anterior view, males exhibit strong maxillary inflation, shortened alveolar processes, a flat premaxillary space, a reduced prenasal process, and bony nares positioned approximately at mid-facial height (Figure 2f). Overall, adult male crania are markedly more robust and specialized than those of adult females or juveniles.

When all cranial views are combined into a single morphospace, the first two PCs explain 47.24% of total variance. The distinction between juveniles and adults is clearly apparent, with juvenile specimens clustering distinctly within the positive values of PC1 (Figure 3c).

For the mandible, PC1 captures variation in anterior margin development, symphyseal elongation, and ramus proportions, whereas PC2 reflects ventral margin shape and condylar orientation. The first two PCs explain between 45% and 66% of mandibular shape variance depending on the view (Figure 4).

Juvenile mandibles resemble adult females, with relatively flat anterior margins, elongated horizontal rami, posteriorly extended angular processes, slender mandibular termini, and ventrally oriented condyles (Figure 4c,d). Adult female mandibles are slightly more robust than juveniles, with moderately thickened horizontal rami and mandibular termini, but retain an overall elongated and gracile profile (Figure 4c,d). Adult male mandibles are more robust, with convex anterior margins, thickened horizontal rami, expanded mandibular termini, and oval,

medially extended condyles (Figure 4c,d). In lateral view, juveniles occupy negative or near-zero PC1 values, adult females intermediate values, and adult males positive PC1 values (Figure 4c). In occlusal view, juveniles and adult females cluster at high PC1, whereas adult males occupy lower PC1 values (Figure 4d).

In the combined mandibular morphospace (39.36% variance explained), ontogenetic separation is less distinct than in the cranium, although juveniles remain preferentially distributed along positive PC1 values (Figure 3d). Across both cranial and mandibular morphospaces, shape variation closely tracks relative size as measured by Log Centroid Size, with the smallest specimens corresponding to juvenile morphology and the largest to adult males (Figures 2d–f, 4c,d).

3.3 | Subspecific morphological variation

3.3.1 | Multivariate assumptions and discriminant analyses

Cranial and mandibular morphology did not meet multivariate normality assumptions. Classification accuracy remained above 75% across all training/test ratios. Procrustes ANOVA revealed significant shape differences between Atlantic and Pacific subspecies for both structures ($p = 0.001$).

BGAs showed significant subspecific separation for both the cranium and mandible (rand-test $p = 0.001$), with cranial morphology showing slightly higher group separability and reduced morphospace overlap ($\Delta\bar{O}_{ij} = 1.85\%$) compared to the mandible.

Similar to patterns observed for sexual dimorphism and ontogeny, the cranium shows greater discriminatory power between ontogenetic stages compared with the mandible.

3.3.2 | PCA and subspecific patterns

PCA analyses indicate clear subspecific differences, with Pacific walruses (*O. r. divergens*) generally more robust and compact in both crania and mandibles, and Atlantic walruses (*O. r. rosmarus*) more gracile and elongated. Differences are more pronounced in the cranium than in the mandible, although sexual dimorphism is superimposed on subspecific variation, resulting in some overlap (Figures 2–4).

Across cranial views, PC1 captures the main subspecific gradient, reflecting variation in cranial elongation, overall robusticity, and maxillary development, while PC2 captures secondary variation in maxillary and

preauricular morphology. Together, the first two PCs explain between 44% and 59% of cranial shape variance depending on the view (Figure 2).

Pacific walruses (*O. r. divergens*) generally occupy one extreme of PC1, corresponding to a more robust, compact cranial morphology. Lateral views show relatively short cranial vaults, pronounced development of the nuchal crest and mastoid process, and ventrally positioned mastoid expansions (Figure 2g). Dorsal views indicate thicker zygomatic arches and a relatively larger anterior portion of the cranium, although overlap with Atlantic individuals is present (Figure 2h). In anterior view, Pacific individuals display strongly inflated maxillae, shortened alveolar processes, a flatter premaxillary space, and bony nares positioned mid-facially (Figure 2i).

Atlantic walruses (*O. r. rosmarus*) are generally more gracile and elongated. Lateral cranial views reveal straighter vaults, reduced nuchal crest and mastoid development, and a less pronounced ventral expansion of the mastoid process (Figure 2g). Dorsal cranial morphology is more elongated, with thinner zygomatic arches and a proportionally larger posterior cranium (Figure 2h). In anterior view, Atlantic individuals show less maxillary inflation, a more concave premaxillary space, and bony nares positioned slightly higher (Figure 2i).

When all cranial views are combined into a single morphospace, the first two PCs explain 31.43% of total variance. Pacific individuals cluster mainly toward positive PC1 and negative PC2 values, whereas Atlantic individuals are more broadly distributed, occupying near-zero or positive PC2 and negative to near-zero PC1 values (Figure 3e). Despite these trends, sexual dimorphism is superimposed on subspecific variation, resulting in considerable overlap.

For the mandible, PC1 consistently differentiates subspecies based on anterior robusticity, symphyseal development, and ramus proportions, whereas PC2 largely reflects sexual dimorphism. The first two PCs explain between 48% and 65% of mandibular shape variance depending on the view (Figure 4).

Pacific mandibles are more robust, with thicker horizontal rami, convex anterior margins, dorsally extended anterior portions reaching the level of the coronoid process, and a more posteriorly reinforced angular process (Figure 4e). In occlusal view, Pacific individuals exhibit broader mandibular termini and more medially extended condyles (Figure 4f).

Atlantic mandibles are comparatively more elongated and gracile. They have flatter anterior margins, proportionally longer horizontal rami, narrower symphyseal regions, and less robust mandibular termini. Condyles are rounder and show reduced medial extension. In lateral view, Atlantic mandibles generally occupy near-zero

or negative PC1 values, whereas Pacific mandibles cluster at higher PC1 values (Figure 4e). Occlusal views confirm this trend, with Pacific specimens distributed at zero or positive PC1 and Atlantic specimens at zero or negative PC1 (Figure 4f).

In the combined mandibular morphospace, the first two PCs explain 40.97% of total variance. Pacific individuals cluster toward higher PC1 and lower PC2 values, reflecting their more robust and compact morphology, while Atlantic individuals occupy broader PC1 and PC2 ranges, indicative of a more gracile and elongated mandibular configuration (Figure 3f). Although substantial overlap exists, subspecific differences are most pronounced along PC1 in both cranial and mandibular morphospaces.

3.4 | Morphological differences among populations

3.4.1 | Procrustes ANOVA and visualization (PCA)

Procrustes ANOVAs were performed on populations with sample sizes equal to or greater than 3, 5, and 9 individuals. Significant differences were detected for both cranial and mandibular morphology among the populations ($p = 0.001$).

To visualize potential differences among populations, PCA were conducted exclusively on the complete cranial and mandibular morphology by combining all views (Figure 5). For the cranium, a total of 31.7% of the

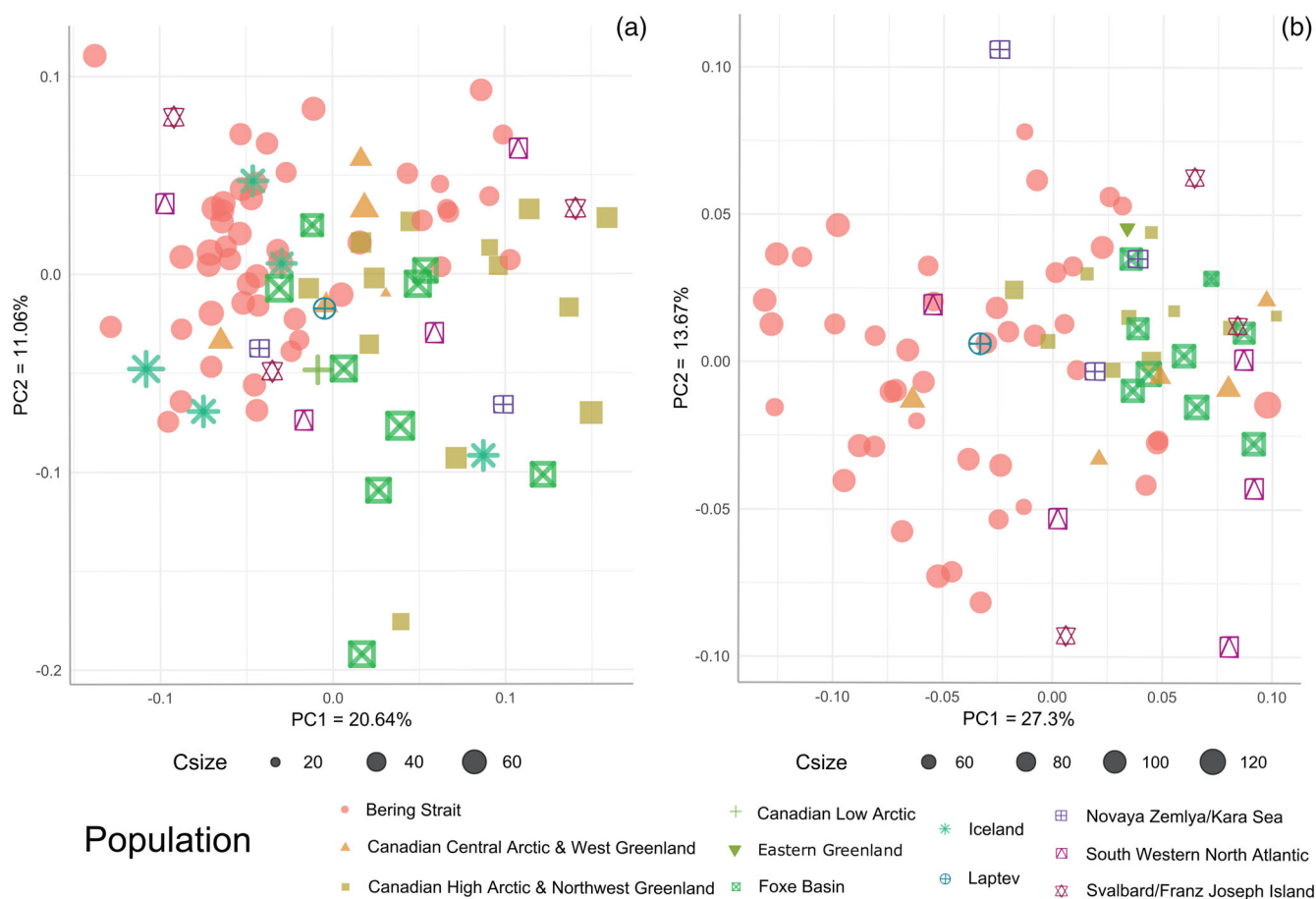


FIGURE 5 Graph of the PCA for the axes PC1 (on the x-axis) and PC2 (on the y-axis) integrating all views into a single morphospace plot for the cranium (a) and for the mandible (b) among recognized populations of extant *O. rosmarus* ($n = 112$ (skull), $n = 99$ (mandible)). Salmon dot: Bering Strait; orange triangle: Canadian Central Arctic and West Greenland; beige square: Canadian High Arctic and Northwest Greenland; green cross: Canadian Low Arctic; khaki inverted triangle: Eastern Greenland; green square with a cross: Foxe Basin; cyan asterisk: Iceland; blue circle with a target: Laptev; purple square with a cross: Novaya Zemlya/Kara Sea; pink square with a triangle: South Western North Atlantic; purple star cross: Svalbard/Franz Joseph Island. Only adult individuals were included in the analyses. The point size of the specimens is determined by the log-transformed centroid size. Each assignment corresponds to the corresponding specimens in Tables S1 and S2.

variance was explained by the first two Principal Components, while this value was 40.97% for the mandible.

Cranial morphology reflects a distinction between the two subspecies, with Pacific individuals clustering around negative PC1 and positive PC2 values, while Atlantic individuals generally show positive PC1 and negative PC2 values (Figure 5a). At the population level, it is noteworthy that the single specimen from the Laptev Sea falls within the morphological variation of the Pacific subspecies, although some overlap with Atlantic specimens is also observed. Regarding PC2, specimens from the Foxe Basin tend to display negative values, as do those from the Canadian High Arctic & Northwest Greenland, which also extend the Atlantic subspecies' morphological variation into the positive range of PC1. The two specimens from Novaya Zemlya/Kara Sea are also positioned in the negative range of PC2, such as three specimens from Iceland (Figure 5a).

Despite some degree of overlap, both subspecies are primarily distinguished along PC1 for mandibular morphology, with Atlantic specimens generally exhibiting positive PC1 values, while Pacific specimens tend to cluster around negative values (Figure 5b). Once again, the Laptev Sea specimen falls within the range of the Pacific subspecies, displaying negative PC1 values. PC2 provides additional insights when examining the various Atlantic populations. Specimens from Novaya Zemlya/Kara Sea and the Canadian High Arctic & Northwest Greenland predominantly exhibit positive PC2 values, whereas those from the Southwestern North Atlantic and the Canadian Central Arctic and West Greenland are more often associated with negative PC2 values (Figure 5b).

3.5 | Ontogenetic trajectories across sexes and subspecies

3.5.1 | PERMANOVA and visualization

To further explore changes in relative growth, ontogenetic allometric trajectories using the first principal component of predicted values from multivariate regression of size (landmark coordinates) on size (Log centroid size) (Figure 6) were obtained using the *plotAllometry* function in the *Geomorph* package (Adams & Otárola-Castillo, 2013), which provides an efficient way to plot ontogenetic variations involving landmark coordinates (Mitteroecker et al., 2004).

Regarding the ontogenetic trajectories, no statistically significant difference between sexes was observed in cranial morphology (p -value = 0.058), although this difference is more pronounced compared to the mandibular morphology, which showed no significant difference (p -value LogCsize:sex = 0.354). The trajectory curves for cranial

morphology reveal that both sexes follow similar but staggered patterns, exhibiting negative allometry according to predicted values, with males reaching very large sizes (Figure 6a). In contrast, mandibular morphology shows distinct trajectory curves between sexes in terms of size and shape, with males occupying a larger range of mandibular size (Figure 6b). The R^2 values for the ontogenetic trajectories are relatively low overall, but higher for the cranium (0.43 (f) and 0.56 (m)) than for the mandible (0.39 (f) and 0.32 (m)). Considering the lack of significant differences in the mandible and the marginal significance for the cranium, together with the generally low R^2 values, it suggests that walrus ontogenetic growth does not follow a strictly linear pattern. These results seem adequate in light of the differentiated growth between males and females, with males undergoing a second acceleration of secondary sexual characteristics, which is consistent with the fact that marine mammals, including walruses, follow a logarithmic growth pattern (Adamczak et al., 2023; Robeck et al., 2022). Nevertheless, it can be noted that the cranium shows a better integration size-shape than the mandible, with similar allometry pattern between both sexes, which is less the case according to mandibular shape.

When examining ontogenetic allometric trajectories in relation to subspecies, significant differences are observed for both the cranium (p -value = 0.044) and the mandible (p -value = 0.041). The slopes differ between the two subspecies, indicating distinct allometric patterns between the Pacific and Atlantic populations, with the Pacific group exhibiting a steeper slope and larger individual sizes (Figure 6c,d). R^2 values indicate that the cranium demonstrates stronger morphological integration compared to the mandible across the two subspecies. Moreover, the allometric relationship is more pronounced in Pacific walruses, with higher R^2 values (0.73 for the cranium; 0.45 for the mandible), suggesting more stringent developmental constraints than those observed in Atlantic walruses (0.46 for the cranium; 0.17 for the mandible).

Based on the results, it seems that the cranium provides more information on ontogenetic shape changes between sexes but also subspecies in *O. rosmarus*, but R^2 values warrant a nuanced interpretation of these results, particularly in light of the logarithmic growth pattern exhibited by walruses.

4 | DISCUSSION

4.1 | Sexual dimorphism and functional adaptation

Geometric morphometric analyses revealed statistically supported sexual dimorphism in both cranial and

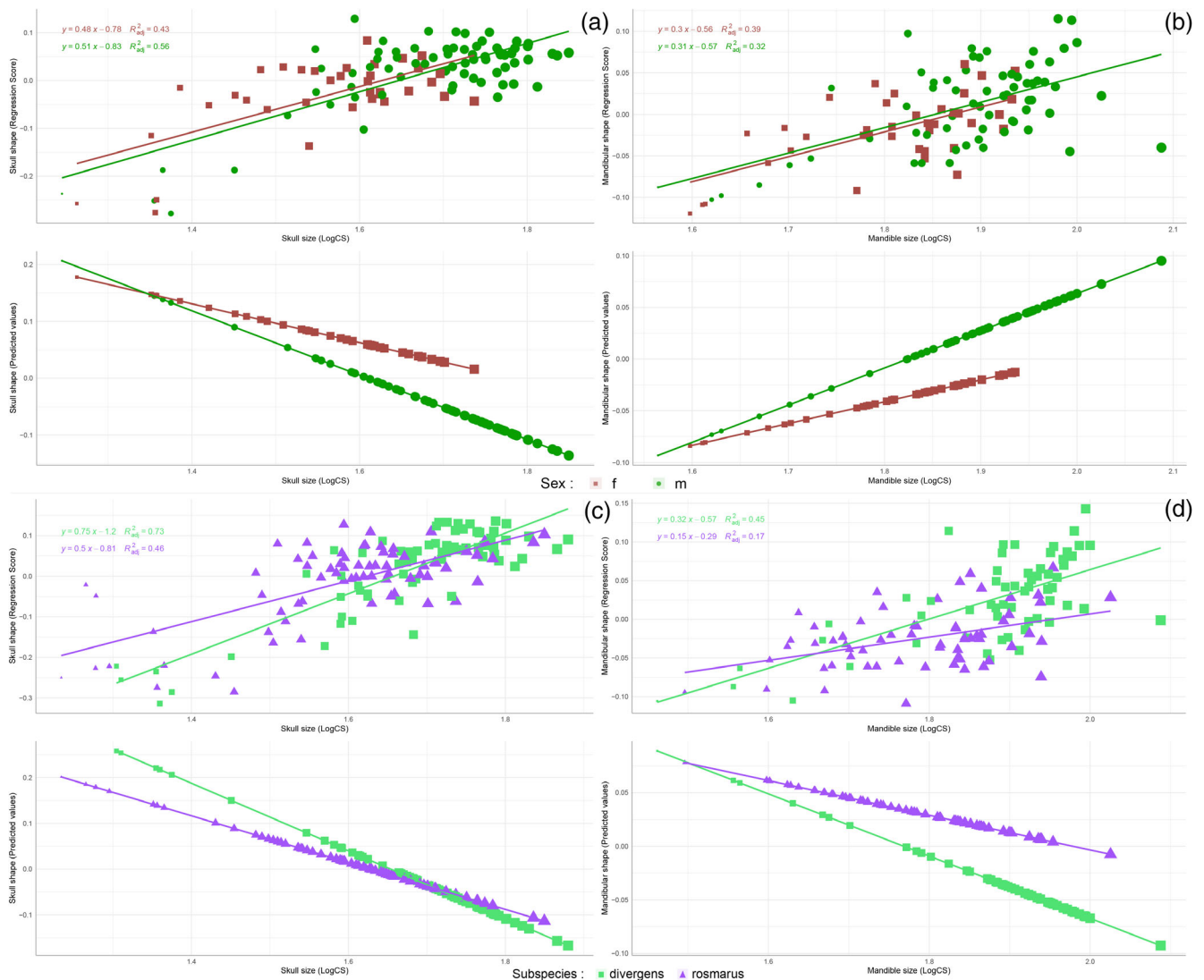


FIGURE 6 Graph of the ontogenetic allometric trajectories according sex (top) and subspecies (bottom), using the first principal component of regression score and predicted values from multivariate regression of size (landmark coordinates) on size (Log centroid size). From left to right: Cranium (a, c), mandible (b, d). Sex: Green dot: Males of *O. rosmarus*; red square: Females. Subspecies: Green square: *O. r. divergens*; purple triangle: *O. r. rosmarus*.

mandibular morphology ($p = 0.001$), with the cranium showing greater shape separability between sexes and the mandible contributing complementary information. This integrated pattern of cranio-mandibular dimorphism is consistent with earlier descriptions (Boisville et al., 2022; Dierickx et al., 2025; Fay, 1982; Miller & Kochnev, 2021; Mohr, 1942; Taylor et al., 2020; Wiig et al., 2007) and aligns with the marked sexual divergence in tusk morphology. While males may have only slightly longer tusks, their canines are substantially thicker and heavier than those of females, which are more slender, curved, and convergent (Miller & Kochnev, 2021). The reinforcement of cranial and mandibular elements in males is consistent with functional demands associated with the mechanical stresses imposed by continuously growing

tusks (Fay, 1982). During antagonistic interactions characteristic of polygynous mating systems, loads generated by tusk-to-tusk contact or strikes are transmitted through the cranium and mandible while the mouth remains closed (Miller, 1975; Miller & Kochnev, 2021; Sjøre & Stirling, 1996). Similar functional patterns have been described in other highly dimorphic pinnipeds, where robust mandibular symphyses and reinforced cranial regions enhance resistance to multidirectional stresses during aggressive encounters (Jones et al., 2013). This polygynous reproductive system may plausibly contribute to the development of a robust occipital region, hypertrophied mastoid processes, thickened zygomatic arches, and reinforced mandibular symphyses in male walruses, all of which provide anchorage for powerful cervical

musculature and enhance resistance to combat-related stresses (Kastelein et al., 1991). However, male walrus tend to restrict themselves to display, primarily through vocalizations or visual tusk threat, without physical contact, that facilitate their position within the harem (Miller & Kochnev, 2021). In addition, female walrus may also choose to mate with larger males possessing the most imposing tusks, which, as with antlers, provide an advantage in the competition for sexual selection (i.e., lek mating) (McCord et al., 2016; Riedman, 1990).

Beyond reproductive behavior, tusks serve multiple mechanical functions, including hauling onto ice or land, breaking ice, and even acting as a sled to flip substrates during feeding (Kastelein et al., 1991; Kastelein & Gerrits, 1990; McLaughlin et al., 2022). The rostrum, reinforced by robust premaxillae, maxillae, mandibles, and tusks, results in a heavy anterior portion of the skull, necessitating substantial development of the occipital region and mastoid processes to counterbalance its weight (Kastelein et al., 1991; Kastelein & Gerrits, 1990). Additional cranial specializations related to feeding ecology—such as enlarged infraorbital foramina, robust bony nares, and reinforced orbital margins—reflect the walrus's benthic foraging strategy, which relies heavily on vibrissae-guided excavation of soft substrates (Fay, 1982; Kastelein et al., 1991). Sexual dimorphism in walrus also extends to behavior and ecology. Males and females exhibit spatial segregation outside the breeding season, occupying different home ranges and exploiting distinct foraging habitats. In Pacific walrus, females spend the summer in the Chukchi Sea with their calves, whereas males are mostly found farther south, in areas such as Bristol Bay and the Gulf of Anadyr. As winter approaches, both males and females migrate toward breeding grounds around the Bering Sea, with males moving individually from herd to herd in search of mates (Higdon & Stewart, 2018). In Atlantic walrus, partial segregation is also observed, with males from western Greenland and southeastern Baffin Island tending to inhabit more offshore areas, farther from the ice edge and at greater depths, occupying a larger home range than females (Dietz et al., 2014). Behavioral sexual dimorphism also is suggested by differential tusk wear, with males showing greater anterior abrasion (Levermann et al., 2003), possibly reflecting distinct feeding strategies. Ecological sexual dimorphism has also been documented, with males also tending to select larger species of bivalves and larger individuals of bivalve species than females (Born et al., 2003). The selection of bivalve size and species may indicate a difference in foraging areas between males and females (McLaughlin et al., 2022). Females tend to forage in shallow coastal waters with softer sediments, particularly

when accompanied by their calves, likely near more sheltered beaching areas. In contrast, adult males inhabit more exposed, deeper, or richer areas, associated with longer foraging dives and corresponding differences in cranio-mandibular robustness, potentially reflecting contrasting ecological conditions (Lydersen, 2018; Noren et al., 2015; Stirling & Fay, 1978).

Taken together, the cranial and mandibular specializations characteristic of male walrus are consistent with a response to the combined pressures of polygynous mating systems and ecological demands, with sexual dimorphism emerging as the dominant axis of cranial, and to a lesser extent mandibular, morphological variation in *O. rosmarus*.

4.2 | Ontogenetic trajectories and life history constraints

Ontogenetic patterns in *O. rosmarus* reveal a close association between growth dynamics and sexual maturation. Geometric morphometric results indicate that juveniles of both sexes closely resemble adult females in cranial and mandibular morphology, suggesting limited morphological change in females throughout ontogeny (Boisville et al., 2022; Dierickx et al., 2025). PERMANOVA detected a marginally significant size–sex interaction for the cranium ($p = 0.058$), but not for the mandible, implying divergent developmental trajectories between males and females primarily affecting cranial morphology. Cranial allometry was substantially stronger than mandibular allometry, consistent with the cranium's integration of multiple functional systems and its greater susceptibility to ontogenetic reorganization, whereas the mandible remains more constrained by feeding biomechanics (Tseng et al., 2025). Ontogenetic slopes differed between sexes, with females exhibiting gradual morphological change and males showing a steeper trajectory. Juveniles overlap extensively regardless of sex, while mature males display maximal divergence, reflecting the late development of sexually selected traits. However, the marginal significance of sex-related differences in cranial slopes and the absence of significant differences for the mandible indicate that sexual dimorphism is not primarily expressed through strongly divergent linear allometric trajectories. These findings are consistent with the geometric morphometric analyses, which indicated that females undergo fewer drastic morphological changes than males, with adult females that are similar in cranial morphology to juvenile specimens (Jones & Goswami, 2010). These patterns align with observations in other highly dimorphic pinnipeds, where adult females retain juvenile-like morphology, while male

specializations emerge rapidly prior to or during adulthood (Jones & Goswami, 2010; Sanfelice & de Freitas, 2008).

Female walrus undergo a longer process of sexual maturation, with physical development completing at 10 years, reaching peak fertility between 10 and 11 years, although they can ovulate between 4 and 7 years (Fay, 1982, 1985). These findings echo the results from our ontogenetic trajectories, with females exhibiting a more gentle slope than that of males. For males, sexual maturity varies more, ranging from 5–6 years to 12 years (Born, 2003; Fay, 1982, 1985). Although they may produce spermatozoa, males cannot reproduce until fully developed. To be strong and large enough to compete with other males and defend their harem, a second acceleration of growth in sexual organs, as well as body size and tusks, occurs so that they can compete for reproduction around 15 years old (Born, 2003; Fay, 1982, 1985). The continuous growth of male tusks likely contributes to cranial reinforcement, including nuchal crest and mastoid development, as well as the development of the anterior margin of the mandible to counterbalance tusk mass (Fay, 1982; Miller, 1975).

Moreover, walrus have the longest nursing period among pinnipeds, with weaning occurring after just over a year, although calves may remain with their mothers for up to 5 years (Fay, 1982; Jones & Goswami, 2010; Kovacs & Lavigne, 1992; McLaughlin et al., 2022). Female walrus are also the only pinniped females that continue foraging while nursing their young. Consequently, walrus exhibit a much slower growth rate than similar-sized pinnipeds with typical nursing schedules (e.g., *Mirounga angustirostris*) (McLaughlin et al., 2022). The nursing period represents a critical stage for both males and females to gain a competitive edge over their cohort members, as it corresponds to the phase of most rapid growth. In walrus, the particularly pronounced differences in ontogenetic growth between males and females make them a key taxon for studying the mechanisms underlying sexually dimorphic allometric growth. Secondary growth (or bimaturism) spurt in males was also detected in other highly dimorphic pinnipeds, such as *Mirounga leonina* or *Otaria byronia*, mostly associated with an enhanced ability to defend territories (Tarnawski et al., 2014a, 2014b). Although polygynous behavior may have imposed similar selective pressures leading to comparable adult phenotypes among highly dimorphic pinnipeds, including the walrus, pup development results in differences in ontogenetic pathways (Tarnawski et al., 2014a, 2014b).

The patterns described above—juvenile-female resemblance, steep male trajectories, and secondary growth acceleration—must be interpreted within the

context of walrus life-history dynamics. The weak linear fits and low R^2 values observed in sex-related allometric analyses (cranium: 0.43–0.56; mandible: 0.32–0.39) reflect the logarithmic growth pattern characteristic of marine mammals (Adamczak et al., 2023; Fay, 1982; Robeck et al., 2022) rather than poor developmental integration. When nonlinear biological trajectories are fitted with linear models, modest R^2 values are expected. Critically, sexual dimorphism in walrus is achieved primarily through hypermorphic growth—extended growth duration and a secondary male growth spurt—rather than through fundamentally divergent allometric trajectories, explaining the marginal sex-size interaction ($p = 0.058$) and similar slopes between sexes. The combination of juvenile-female resemblance and delayed male hypermorphism underscores the central role of heterochrony and sexual selection in shaping walrus cranial morphology.

4.3 | Subspecific differentiation and geographic adaptation

Morphometric comparisons between Pacific (*O. r. divergens*) and Atlantic (*O. r. rosmarus*) walrus revealed significant cranial and mandibular differentiation ($p = 0.001$), with classification accuracies exceeding 75%, reflecting moderate to strong shape separability among subspecies rather than definitive individual-level identification. Although the cranium explained slightly more variance than the mandible, mandibular shape provided clearer subspecific separation. Pacific walrus exhibited a shorter, more robust skull with a narrower and more anteriorly oriented cranium, whereas Atlantic walrus displayed a more gracile cranio-mandibular morphology, consistent with early descriptions (Allen, 1880). These differences correspond closely to subspecific variation in tusk size, with Pacific walrus possessing longer and thicker tusks, likely driving reinforcement of the anterior skull and mandible to counterbalance increased mechanical loads. Notably, Atlantic males often overlap morphologically with Pacific females, highlighting the overall greater robustness of *O. r. divergens* relative to *O. r. rosmarus* (e.g., Dierickx et al., 2025; Dyke et al., 1999; Garlich-Miller & Stewart, 1998). Beyond absolute size differences, our results reveal clear subspecies-specific allometric trajectories, indicating that cranio-mandibular shape variation reflects not only sexual dimorphism but also distinct developmental constraints acting at the subspecific level. Unlike sex-related patterns, where modest R^2 values reflect logarithmic growth projected onto linear models, subspecific differences reflect genuine divergence in developmental programs. Pacific walrus exhibit

steeper slopes and higher R^2 values (cranium: 0.73; mandible: 0.45) compared to Atlantic walruses (cranium: 0.46; mandible: 0.17), indicating stronger developmental canalization (i.e., the tendency of developmental processes to constrain growth and shape variation along a consistent ontogenetic pathway) in the Pacific subspecies, likely driven by intensified sexual selection and more predictable ecological conditions. Atlantic walruses maintain greater developmental plasticity, potentially reflecting adaptation to more heterogeneous environments and fragmented population structure. Cranio-mandibular differences may therefore be related to subspecies-specific feeding strategies or social behaviors.

The divergence between subspecies likely reflects ecological contrasts between ocean basins. The colder, more nutrient-rich North Pacific supports larger and more abundant bivalves, potentially favoring stronger jaws and enhanced suction feeding in Pacific walruses (Reid Jr, 1961; Webb, 2023). In contrast, the Atlantic subspecies occupies more heterogeneous and less productive environments, resulting in greater morphological variability and plasticity among genetically and geographically distinct populations. Although mollusk assemblages appear broadly similar across oceans (Carlton, 1992), regional variation in mollusk fauna, prey availability linked to benthic productivity (e.g., in East Greenland), seafloor sediment type, and habitat use or bathymetry—such as deeper diving observed in some Atlantic populations (e.g., Svalbard/Franz Joseph Island)—may drive cranio-mandibular divergence among different populations (Garde et al., 2018; Lowther et al., 2015; Smith Jr et al., 1997; Yurkowski et al., 2020). The longer and thicker tusks of the Pacific subspecies may further reinforce these ecological differences by enabling distinct feeding behaviors, including substrate manipulation, such as already observed between males and females (Levermann et al., 2003), and by interacting with subspecies-specific allometric trajectories, especially cranial reinforcement, throughout ontogeny. While logarithmic growth also applies at the subspecific level, the substantially higher R^2 values for Pacific walruses indicate that subspecific allometric differences are more robust to linear modeling than sex-related patterns, reinforcing the interpretation that Pacific and Atlantic walruses follow distinct developmental pathways shaped by divergent selective regimes.

Migratory and mating behaviors likely contribute to inter-subspecific differences. Pacific walruses undertake longer and more extensive migrations, whereas Atlantic walruses are fragmented into smaller subpopulations across the Arctic (Higdon & Stewart, 2018; Miller & Kochnev, 2021). In the Pacific, pronounced spatial and seasonal segregation, combined with more frequent

male–male competition and greater female mate choice, suggests intensified size-dependent sexual selection, which may promote steeper and more canalized allometric trajectories, particularly in males (Dierickx et al., 2025; Higdon & Stewart, 2018; McCord et al., 2016; Sjare & Stirling, 1996). In contrast, weaker and more heterogeneous selective pressures in Atlantic populations may result in reduced developmental canalization and greater morphological flexibility. These findings support the hypothesis that divergent selective pressures have shaped both the morphological and behavioral traits of Atlantic and Pacific walruses, pending further observations.

At finer geographic scales, significant population-level structuring was detected. PCA revealed a tight morphospace cluster for the Pacific subspecies, consistent with reduced variability, whereas Atlantic populations occupied a broader morphospace. Individuals from Foxe Basin displayed intermediate morphologies, while populations from the Canadian High Arctic/Northwest Greenland and Novaya Zemlya/Kara Sea converged morphologically despite geographic isolation, potentially reflecting consistent selective pressures in extreme environments (plausibly linked to regional differences in feeding ecology, as Inuit hunters report clam-dominated diets in Foxe Basin walruses and increased seal consumption in more northern populations; Ruiz-Puerta, pers. comm.). Historical and extirpated populations further illustrate this variability. The former southeastern Canadian Maritimes (i.e., South Western North Atlantic) population may have developed distinct ecological adaptations prior to its extinction, and the disappearance of the Icelandic population was likely driven by a combination of climatic, volcanic, and anthropogenic pressures (Keighley et al., 2019; McLeod et al., 2014) (consistent with unpublished isotopic data suggesting distinct trophic ecology in the Canadian Maritimes population; Ruiz-Puerta, pers. comm.). Levermann et al. (2003) also reported a tendency for individuals from the eastern Greenland population to preferentially use the right flipper during feeding, a behavioral asymmetry that may influence forelimb proportions but likely reflects individual-level variation rather than strong ecological differentiation among populations, pending further evidence. While the differences between Atlantic populations are primarily genetic (e.g., Andersen et al., 1998; Shafer et al., 2014), notably with the establishment of their populations during the deglaciation at the end of the Pleistocene/Holocene (e.g., Ruiz-Puerta et al., 2023), the potential existence of ecological/feeding strategy differences between populations, such as with the Canadian Maritimes (McLeod et al., 2014), North-western Greenland (Knutsen & Born, 1994), or the

Svalbard/Franz Joseph Island populations (Lowther et al., 2015), may be one of the reasons why slight morphological differences are observed, although sampling bias needs to be considered (with males generally over-represented in samples, biogeographical seasonal/sexual segregation, or small sample sizes for distinct populations (e.g., Dierickx et al., 2025; Solovyova et al., 2024; Wiig et al., 2007)). Although represented by only one individual, the male Laptev specimen, while exhibiting a comparatively more gracile morphology than other males from the Pacific region and somewhat overlapping with some Atlantic individuals, still falls within the morphological variation of the Bering Strait population, consistent with the notion that the Laptev population is considered a population of *O. r. divergens* (Lindqvist et al., 2009; Mills et al., 2024). Boeskorov et al. (2018) even suggested that the Laptev population may have migrated to the New Siberian Islands, probably during the early or middle Holocene. This population is poorly understood, and more information about it would help understand if their ecology differs from those living in the Bering Strait, especially considering their supposed intermediate size between the two subspecies (Dierickx et al., 2025; Higdon & Stewart, 2018; Lindqvist et al., 2009; Mills et al., 2024).

Climate change and anthropogenic pressures increasingly shape walrus ecology and survival, particularly in the Atlantic subspecies, which occupies several small, fragmented populations despite its relatively broad morphological variation. Ongoing sea-ice loss reduces the availability of critical haul-out sites, forcing walruses into dense terrestrial aggregations that elevate risks of trampling, disease transmission, and energetic stress, while also altering benthic productivity and prey accessibility, potentially modifying foraging efficiency and reproductive success (e.g., Albouy et al., 2020; Born et al., 2021a; Kovacs et al., 2015; MacCracken, 2012; Stewart & Higdon, 2017). Historical overexploitation for meat, tusks, and skins caused severe population declines, leaving some populations especially vulnerable to contemporary human activities such as hunting, shipping, resource exploration, pollution, and tourism (e.g., Keighley et al., 2019; McLeod et al., 2014; Ruiz-Puerta et al., 2023, 2024; Star et al., 2018). These pressures disrupt habitats, induce behavioral stress, and increase mortality, particularly where reduced sea ice forces large land-based haul-outs (e.g., Born et al., 2021b; Gjertz, 2021; Gotfredsen et al., 2018; Keighley et al., 2022; Mills et al., 2024; Stewart et al., 2014; Stewart & Higdon, 2017). Such pressures may guide differences in ecological behavior among populations. As keystone species of Arctic marine ecosystems, walruses play a critical role in benthic

community dynamics and nutrient redistribution. Their sensitivity to combined climatic and anthropogenic stressors highlights the need for population-specific management strategies that account for behavioral responses and cumulative impacts to ensure long-term conservation (e.g., Albouy et al., 2020; Dierickx et al., 2025; Higdon & Stewart, 2018; Mills et al., 2024). As Arctic ecosystems continue to transform, further integrative studies of morphological, developmental, and behavioral variation among walrus populations will be essential for improving predictions of population responses to ongoing environmental change.

4.4 | Evolutionary implications

The morphological patterns identified in this study align with phylogeographic evidence for a divergence between Pacific (*O. r. divergens*) and Atlantic (*O. r. rosmarus*) walruses. Some researchers have suggested that the Pacific subspecies may have been a recolonization of the Pacific by a stock of specimens from the North Atlantic during the late Pleistocene (Fay, 1982, 1985; Harington & Beard, 1992; McLeod et al., 2014; Repenning, 1976). Others have suggested that the Atlantic population had a more recent evolutionary history than that of the Pacific (e.g., Mills et al., 2024). The oldest specimen of *Odobenus* comes from a tusk of the Shiranuka Formation (Kohn et al., 1995; Sasa & Okazaki, 1967) and a skull from the seabed of Sakhalin in Russia, from the Pliocene-Pleistocene transition (Miyazaki et al., 1992). Other remains have been found in various formations in Japan during the Middle Pleistocene (ca. 0.6–0.5 Ma) (Ishiguri & Kimura, 1993; Kohn et al., 1995; Tomida, 1989). No known specimens have been found outside of the North Pacific before the end of the Pleistocene (ca. 0.2 Ma) (Ponomarev et al., 2023), suggesting an evolutionary history primarily in the North Pacific before dispersing to the North Atlantic via the Arctic. Countless remains attributed to *O. rosmarus* have been found at much lower latitudes than the Arctic throughout the Pleistocene (e.g., Japan, North Carolina, North Sea), indicating a recent adaptation to the cold Arctic environment (e.g., Boessenecker & Churchill, 2021; Erdbrink & van Bree, 1986, 1999a, 1999b, 1999c; Gallagher et al., 1989; Hoshimi & Akagi, 1994; Kardas, 1965; Kohn et al., 1995; Post, 2005; Sanders, 2002). To better understand the forces that guided this dispersion and adaptation, it would be interesting to observe the morphological differences among fossil representatives of *O. rosmarus*. Cranial and mandibular structures, bearing ecological information, could be key to understanding the impact of climate change on populations throughout the Quaternary.

5 | CONCLUSIONS

This study demonstrates that cranial and mandibular morphology in the walrus (*O. rosmarus*) is shaped by the combined influences of sexual selection, ontogeny, and ecological divergence. Sexual dimorphism appears to represent the primary axis of cranial and mandibular morphological variation. Juveniles initially resemble females, with males diverging later in life through delayed hyper-morphic growth, underscoring the critical role of ontogenetic timing and mating systems in shaping adult morphology.

Subspecific comparisons revealed pronounced differences between Pacific (*O. r. divergens*) and Atlantic (*O. r. rosmarus*) walruses. Population-level analyses further highlighted localized adaptations, with High Arctic groups showing specialized morphologies, while intermediate populations retained higher morphological plasticity. Given these morphological and developmental differences, vulnerability to environmental change likely varies across subspecies and populations.

AUTHOR CONTRIBUTIONS

Mathieu Boisville: Conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; visualization; validation; methodology; software; formal analysis; project administration; data curation; resources; supervision. **Narimane Chatar:** Data curation; supervision; resources; conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; visualization; formal analysis; software; project administration; methodology; validation. **Emily J. Ruiz-Puerta:** Conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; visualization; validation; methodology; software; project administration; formal analysis; resources; supervision; data curation. **James P. Rule:** Conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; visualization; validation; methodology; formal analysis; software; project administration; resources; supervision; data curation. **Naoki Kohno:** Conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; visualization; validation; methodology; software; formal analysis; project administration; resources; supervision; data curation.

ACKNOWLEDGMENTS

The authors thank the following individuals and institutions for providing access to and assistance, or photographs of, specimens under their care: Academy of Natural Sciences of Drexel University (Philadelphia,

USA): Ned Gilmore, Ted Daeschler; Canadian Museum of Nature (Ottawa, Canada): Scott Rufolo, Shyong En Pan, Aaraya Aad; Chiba Environmental Research Center (Chiba, Japan): Takahiro Kojima; Chiba Natural History Museum and Institute (Chiba, Japan): Satoshi Maruyama, Hisayoshi Kato; Icelandic Institute of Natural History (Garðabær, Iceland): Snæbjörn Pálsson; Icelandic Museum of Natural History (Seltjarnarnes, Iceland): Hilmar Malmquist; Museum of Zoology, University of Cambridge (Cambridge, UK): Robert Asher; Natuurhistorisch Museum (Rotterdam, the Netherlands): Hidde Bakker, Bram Langeveld, Klaas Post; National Museum of Nature and Science (Tokyo, Japan): Yuko Tajima; Naturalis Biodiversity Center (Leiden, the Netherlands): Anne Schulp, Jelle Reumer, Anne van de Weerd, Willem Renema, Klaas Post; Royal Belgian Institute of Natural Sciences (Brussels, Belgium): Pascal Godefroit, Sébastien Bruaux, Terry Walschaert, Olivier Pauwels, Olivier Lambert, Leonard Dewaele; Smithsonian National Museum of Natural History (Washington DC, USA): Darrin Lunde, Michael McGowen, John Ososky; The Natural History Museum (London, UK): Phaedra Kokkini; University of Cambridge (Cambridge, UK): Daniel Field; University of Copenhagen (Copenhagen, Denmark): Morten Tange Olsen, Sarah Saboya de Medeiros, Anne Birgitte Gotfredsen; Zoological Institute, Russian Academy of Sciences (St. Petersburg, Russia): Gennady F. Baryshnikov, Alexei Tikhonov. The authors also express their sincere gratitude to Olivier Lambert and Leonard Dewaele, with whom the initial ideas for this project were developed during a research stay at the Royal Belgian Institute of Natural Sciences (Brussels) in 2020. Mathieu Boisville was supported by the Overseas Musha Training Support Program for Graduate Students and the Support Program for Participation in Overseas Conferences of the Habatake! Program from the University of Tsukuba. Additional support was provided by the Jackson School of Travel Grant from the Society of Vertebrate Paleontology and by the Hans de Bruijn Foundation, which funded visits to museum collections in the Netherlands. Narimane Chatar was supported by a Belgian American Educational Foundation (BAEF) post-doctoral fellowship as well as a grant from the National Science Foundation (NSF DBI-2128146).

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How to cite this article: Boisville, M., Chatar, N., Ruiz-Puerta, E. J., Rule, J. P., & Kohno, N. (2026). Exploring factors shaping the craniomandibular shape of extant walrus. *The Anatomical Record*, 1–23. <https://doi.org/10.1002/ar.70200>