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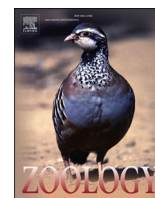
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Range-wide variation in grey seal (*Halichoerus grypus*) skull morphology

Anders Galatius^{a,*}, Michelle Strecker Svendsen^b, Dolores Messer^c, Mia Valtonen^{d,e},
Michael McGowen^f, Richard Sabin^g, Vedrana Andersen Dahl^c, Anders Bjorholm Dahl^c,
Morten Tange Olsen^{b,h,*}

^a Marine Mammal Research, Department of Ecoscience, Aarhus University, Denmark

^b Section for Molecular Ecology and Evolution, Globe Institute, University of Copenhagen, Denmark

^c Section for Visual Computing, Department of Applied Mathematics and Computer Science, Technical University of Denmark, Denmark

^d Institute of Biotechnology, University of Helsinki, Finland

^e Wildlife Ecology Group, Natural Resources Institute, Finland

^f Department of Vertebrate Zoology, Smithsonian National Museum of Natural History, Washington, DC, USA

^g Division of Vertebrates, Department of Life Sciences, Natural History Museum, London, UK

^h Natural History Museum of Denmark, University of Copenhagen, Denmark

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ABSTRACT

The large interspecific variation in marine mammal skull and dental morphology reflects ecological specialisations to foraging and communication. At the intraspecific level, the drivers of skull shape variation are less well understood, having implications for identifying putative local foraging adaptations and delineating populations and subspecies for taxonomy, systematics, management and conservation. Here, we assess the range-wide intraspecific variation in 71 grey seal skulls by 3D surface scanning, collection of cranial landmarks and geometric morphometric analysis. We find that skull shape differs slightly between populations in the Northwest Atlantic, Northeast Atlantic and Baltic Sea. However, there was a large shape overlap between populations and variation was substantially larger among animals within populations than between. We hypothesize that this pattern of intraspecific variation in grey seal skull shape results from balancing selection or phenotypic plasticity allowing for a remarkably generalist foraging behaviour. Moreover, the large overlap in skull shape between populations implies that the separate subspecies status of Atlantic and Baltic Sea grey seals is questionable from a morphological point of view.

1. Introduction

Marine mammals are characterised by large interspecific variation in skull and dental morphology driven by diverse ecological specialisations to foraging and communicating in aquatic environments (Churchill and Mark, 2015; Kienle and Berta, 2016; Randau et al., 2019; Franco-Moreno et al. 2021). The characteristics and drivers of such morphological variation are increasingly understood at the interspecific level (Galatius et al. 2020; Galatius et al. 2019; Hocking et al. 2017); however, much less is known about variation in skull and dental morphology at the intraspecific level (but see Galatius and Gol'din, 2011; Galatius et al., 2012). This has implications for understanding the intraspecific range of foraging behaviours and more generally, what putative morphological differences may entail in terms of delineating populations and subspecies for taxonomy, systematics, management and

conservation.

The grey seal (*Halichoerus grypus*) is a relatively large-bodied seal, belonging to the subfamily of northern true seals (Phocinae). The species has a cold temperate to sub-Arctic distribution across the North Atlantic, with haul-out substrates ranging from sandy beaches and reefs to rocky shores and sea-ice. In contrast to other phocid seal species, grey seals are characterised by a high degree of intraspecific variability in skull shape, not fitting into any model of skull development or morphospace categories defined for other phocid seal species (Kienle and Berta, 2016; Randau et al., 2019). Part of this intraspecific variation can be attributed to sex and age, with adult grey seal males being approximately 50% larger than females and characterised by an elongated and straight snout (Savriama et al. 2018; Beck et al. 2003). In addition to variation attributed to age and sex, Chapskii (in Heptner et al. 1976) reported differences in skull shape between Northeast Atlantic and Baltic Sea grey

* Corresponding authors.

E-mail addresses: agj@ecos.au.dk (A. Galatius), morten.olsen@sund.ku.dk (M.T. Olsen).

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seals, suggesting that geography may be a major source of intraspecific variation. Unfortunately, detailed information on Chapskii's sample size and analytical approach is hard to obtain, so it is uncertain to what extent grey seals exhibit variation in skull shape across their range.

The lack of morphological data from grey seals has implications for our understanding of the drivers of intraspecific variation in grey seal skull shape, and how this may relate to the grey seal's diverse foraging strategies. Moreover, it constitutes a missing piece of evidence in the current debate about the number of grey seal subspecies and populations. Specifically, differences in pelage coloration and body size (Chapskii in Heptner et al. 1976), reproductive strategies and timing (Chapskii in Heptner et al. 1976), and genetic profiles (Fietz et al. 2016; Boskovic et al. 1996; Klimova et al. 2014) all support the existence of (at least) three grey seal populations. However, currently only two subspecies are recognised; one in the Baltic Sea (*H. g. grypus*) and one in the North Atlantic (*H. g. atlantica*) (Rice, 1998; Berta and Churchill, 2012; Olsen et al. 2016; SMM, 2021). In this paper, we conducted geometric morphometric analyses using 3D surface scans of 71 grey seal skulls collected from the three main grey seal populations in the Northwest Atlantic, Northeast Atlantic and Baltic Sea, respectively. The aim is to document the range-wide geographical variation in grey seal skull shape and to examine its relation to grey seal population and subspecies delineations.

2. Materials and methods

2.1. Grey seal skulls

The 71 grey seal skulls stem from the collections of the Natural History Museum of Denmark, the University of Helsinki, the Natural History Museum in London, UK, and the Smithsonian National Museum of Natural History, Washington DC, USA. The skulls were selected to

represent the three main grey seal population centres across their Atlantic range: Northwest Atlantic (USA and Canada; $N = 20$), Northeast Atlantic (Scotland; $N = 28$), and the Baltic Sea (Denmark; $N = 23$) (Fig. 1A-B; Supplementary Table 1). To minimise allometric variation in the dataset, we aimed to sample adult specimens. However, larger juveniles were also included to obtain sufficient sample size from the four museum collections.

2.2. Collection and formatting of cranial landmarks

To assess the geographical variation in skull morphology, we first generated 3D point clouds of the 71 grey seal skull specimens by using a 3D structured light scanning setup (SeeMaLab, Eiriksson et al. 2016). For each skull, the point clouds from different orientations were aligned on the basis of geometric features using the Open3D library (Zhou et al., 2018), followed by non-rigid alignment as suggested by Gawrilowicz and Barentzen (2019). The final 3D triangular mesh model for each skull was obtained from the point clouds by Poisson surface reconstruction (Kazhdan and Hoppe, 2013) using the Adaptive Multigrid Solvers software version 12.00 by Kazhdan (Johns Hopkins University, Baltimore, MD, USA). Second, we defined 26 3D cranial landmarks that through rigorous testing of our approach on an initial set of 31 landmarks could be unequivocally located on the individual 3D models (Messer et al. 2021), and which reflect overall grey seal skull morphology and biomechanics (Fig. 1C). The landmarks were recorded using the software Stratovan Checkpoint (Stratovan Corporation, Davis, CA, USA). Additional details on methodology and selection of landmarks can be found in Messer et al. (2021) and information on each specimen in Supplementary Table 2.

All geometric morphometric analyses were conducted in R using the package geomorph (Adams et al. 2021) unless otherwise stated. Two replicate measurements for 19 skulls were used to quantify relative

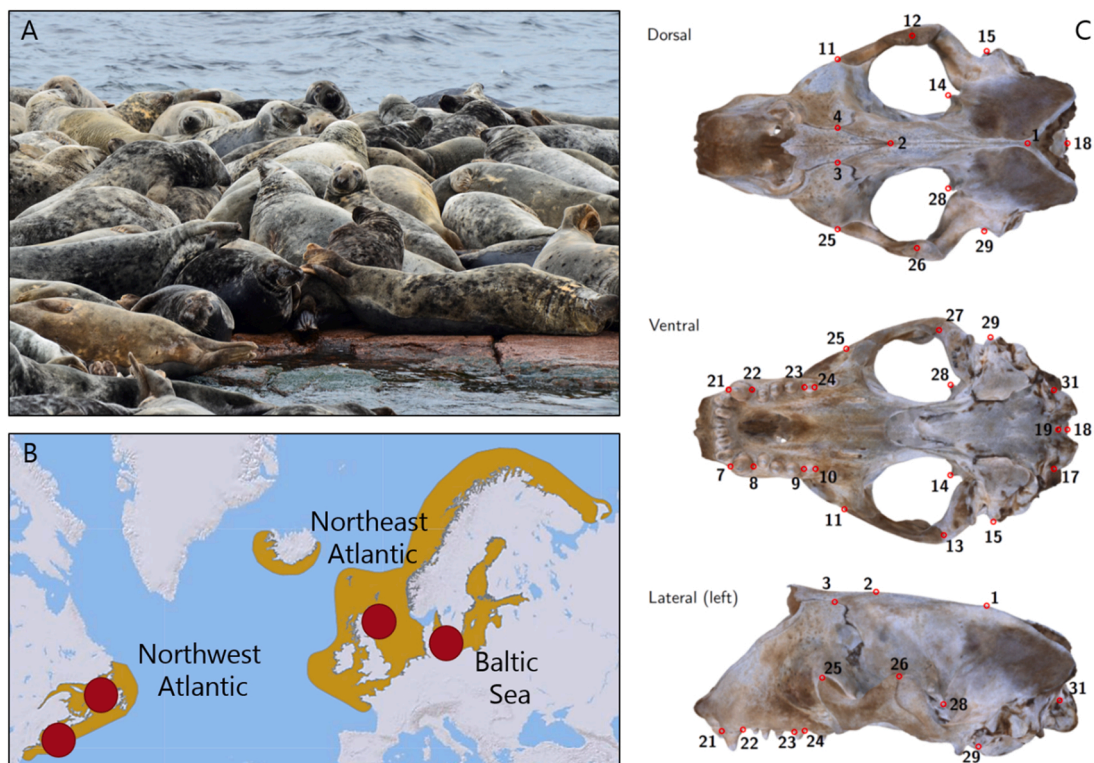


Fig. 1. Study species, sampling localities and the cranial landmarks for geometric morphometric analysis of range-wide variation in grey seal skull morphology. A: Baltic grey seals (*H. g. grypus*) hauling out on Ertholmene, Denmark (photo: Morten Tange Olsen). B: Sampling localities marked by red circles and the grey seal's main distributional range in orange C: Dorsal, ventral and lateral 3D surface scans of grey seal specimen C7-98 (MorphoSource ID 10.17602/M2/M364293) with illustration of the 26 cranial landmarks used for geometric morphometric analyses as described in Messer et al. (2021).

Map modified from www.iucnredlist.org

measurement error by way of a Procrustes ANOVA (procD.lm) with 1000 iterations on Procrustes superimposed configurations (see below), quantifying variation from measurement error and individual shape variation. The raw landmark coordinates of the 71 skulls were run through the generalized least-squares Procrustes superimposition (Rohlf and Slice, 1990), using the gpagen function. For all other analyses, we used the symmetric component of shape from the bilat.symmetry function, as we were not interested in variation in asymmetry. This function uses a Procrustes procedure amended according to the suggestions of Klingenberg et al., (2002) to deal with the redundancy of data points caused by the object symmetry of the vertebrate skull.

2.3. Effects of age and gender on skull shape variation

To investigate the effects of sex and adult/juvenile status, we first conducted analyses without the Baltic Sea specimens, for which information on maturity and sex was mostly not available. Analyses were run on 45 skulls from the Northwest and Northeast Atlantic, for which such information was available. A Procrustes ANOVA with 1000 iterations on region, with sex and the logarithm of centroid size (CS; the square root of the summed squared distances of each landmark to the averaged coordinates of the configuration) as covariates, was used to investigate and quantify shape variation related to these variables. Models that included the interactions of sex and CS as well as sex and region were also investigated to elucidate potential links between sex and size (differential allometry between sexes) and sex and region (different patterns of sexual dimorphism between the regions). To create size-independent variables for further analyses, the plotAllometry function was used to define the common allometric component (CAC), and residual shape components (RSCs). The residual shape components are principal components of a Principal Components Analysis on the residuals of the CAC, the latter defining the general shape vector associated with differences in size. The RSCs were then plotted to investigate if maturity and sex had notable effects on the distribution in shape space, that is, had detectable effects after correction for size.

2.4. Regional differences in skull shape

Once the preliminary analyses of the Northwest and Northeast Atlantic data confirmed that any regional variation in skull shape was unrelated to variation caused by gender and age, we proceeded to analyse the full dataset including Baltic Sea specimens. A Procrustes ANOVA with 1000 iterations on geographical region, with the logarithm of centroid size as covariate, was used to investigate regional differences in skull shape, while accounting for size variation. We also assessed the variation of skull shapes within each region by computing the Procrustes distance of each specimen to the respective regional mean shapes. The pairwise function of the RRPP package (Collyer and Adams, 2021) was used for post hoc tests of regional shape differences. We used the shape.predictor function to define allometry-corrected regional shapes by predicting regional-specific shapes at the grand mean regression score. These were plotted using the plotRefToTarget function. To create size-independent variables for further analyses, the plotAllometry function was used to define the common allometric component (CAC), and residual shape components (RSCs). Linear models of the whole suite of RSCs were used to define vectors describing the shape difference between the three investigated regions and between males and females. The angles between the sexual dimorphism vector and the regional vectors were calculated to investigate if there was co-variation between sexual differences and regional differences that could confound analyses of the latter.

Multivariate linear models of RSCs on region were used to test whether shape differences across the three geographic areas formed a continuum: a vector describing shape differences between Northwest and Northeast Atlantic was compared to a vector describing shape differences between the Northeast Atlantic and the Baltic Sea. If the shape

differences form a continuum, the angle between the two vectors should be close to 0°. Such a continuum of vectors from Northwest Atlantic to the Baltic Sea would indicate that detected differences across the geographic range were related to isolation-by-distance, rather than isolated populations (Galatius et al., 2012). The boot function of the boot library (Canty and Ripley, 2021) with 1000 iterations was used to calculate a 95% confidence interval of the angle between the vectors. Finally, to obtain an estimate of the shape overlap between the regions, while accounting for the relatively low sample sizes, a linear discriminant analysis of regional differences with jackknife cross-validation were run on a number of RSCs selected by the 'broken stick' method (Legendre and Legendre, 2012).

3. Results

3.1. Measurement error

The Procrustes ANOVA on the two replicates of 19 skulls revealed a relatively small variation from measurement error (Rsq= 0.03) compared to individual shape variation (Rsq=0.97, F=39.28, $p < 0.001$).

3.2. Effects of age and gender

Comparisons of models using the 'anova' function revealed that a Procrustes ANOVA including the interactions of skull centroid size (CS) and sex, as well as region and sex, offered a better explanation of the data. Among the samples from the Northwest and Northeast Atlantic, there was a large and significant influence of CS on shape variation (Rsq=0.42, F=33.34, $p < 0.001$). Effects of sex (Rsq=0.03, F=2.28, $p = 0.007$) and region (Rsq=0.04, F=3.14, $p < 0.001$) were much smaller, but still significant. The interactions of CS and sex (Rsq=0.02, F=2.15, $p = 0.016$) and sex and region (Rsq=0.03, F=2.29, $p = 0.008$) also had small effects, but were statistically significant. Distribution of the samples along log(CS) and the common allometric component is provided in Supplementary Fig. 1. In the plots of RSCs, the juvenile specimens scored intermediate values and there were no detectable patterns related to sex. RSCs 1 and 3 provided some segregation of the Northwest and Northeast Atlantic specimens, albeit with considerable overlaps (Supplementary Fig. 2). These results indicate that effects of size (age) and sex were separated from regional differences in the RSCs. This was corroborated by comparing the vectors describing regional differences between all three regions and sexual differences. The vector describing shape differences between the Northwest and Northeast Atlantic had an angle of 90.1° (95% CI: 68.5–108.0) with the vector describing sexual differences. When adding data from the Baltic Sea, we found that the Northwest Atlantic to Baltic Sea vector had an angle of 89.5° (95% CI: 76.9–103.2), while the Northeast Atlantic to Baltic Sea vector had an angle of 89.1° (95% CI: 70.0–109.1) with the vector describing sexual differences. Thus, sexual differences in skull shape were highly independent from regional differences.

3.3. Regional differences in skull shape

The Procrustes ANOVA including the full sample of 71 grey seal skulls revealed a large and significant influence of skull size on shape variation (Rsq=0.51, F=74.75, $p < 0.001$), with the effect of region being substantially smaller, albeit also statistically significant (Rsq=0.04, F=2.84, $p < 0.001$). The post hoc tests revealed significant differences among the three regions (Northwest Atlantic-Northeast Atlantic: Z = 3.90, $p < 0.001$, Northwest Atlantic-Baltic Sea; Z = 2.46, $p = 0.008$, Northeast Atlantic-Baltic Sea: Z = 3.23, $p = 0.002$). The angle between the Northwest Atlantic-Northeast Atlantic vector and the Northeast Atlantic-Baltic Sea vector was 90.5° (95% CI: 70.0–110.9), thus the shape differences did not constitute a geographical continuum.

Investigation of the RSCs revealed that RSC 4 showed some

segregation between the Northwest and Northeast Atlantic, while Baltic Sea specimens tended to have higher scores along RSC 7, although there were large overlaps among the samples along all axes. The ‘broken stick’ method resulted in the inclusion of the first 14 RSCs in the linear discriminant analysis. These RSCs constituted 84.3% of the variance in the data set with the last included RSC (RSC14) responsible for 2.4% variance. The linear discriminant analysis provided reclassification success rates of 52% for Baltic Sea skulls, 74% for Northeast Atlantic skulls and 75% for Northwest Atlantic skulls. In addition, 100 random reshufflings of the skulls among the regions led to median classification success rates of 30% for Baltic skulls (range: 0–70%), 43% for Northeast Atlantic skulls (range: 21–68%) and 25% for Northwest Atlantic skulls (range: 0–55%). Distributions related to CS (size) and the common allometric component (shape related to size) are provided in [Supplementary Fig. 3](#). Distributions along the first eight RSCs are provided in [Fig. 2](#). Subsequent components did not show any patterns with regard to region or sex and each accounted for < 5% of the residual variance.

On a regional scale, the Procrustes distances between mean residual shapes of the common allometric component (CAC) were 0.022 between Northwest and Northeast Atlantic, 0.021 between Northwest Atlantic and Baltic Sea and 0.019 between Northeast Atlantic and Baltic Sea skulls. In comparison, we found that the median distance from a specimen to its own regional mean shape ranged from 0.037 to 0.040 and hence was considerably larger than the distance between regional means. Moreover, the median distance from a specimen to its regional mean shape overlapped considerably with distances of the same specimens to the means of other regions ([Fig. 3](#)). Finally, bearing in mind the very large regional overlap in skull shapes, we found that the comparatively trivial differences between regions could be described as skulls from the Northwest Atlantic being slightly shorter with ear canals displaced caudally, Northeast Atlantic skulls being slightly taller at the level of the posterior molars and compressed ventrally in the braincase area, and Baltic Sea seal skulls being slightly wider at the zygomatic bones and slightly narrower at the brain case ([Fig. 4](#)).

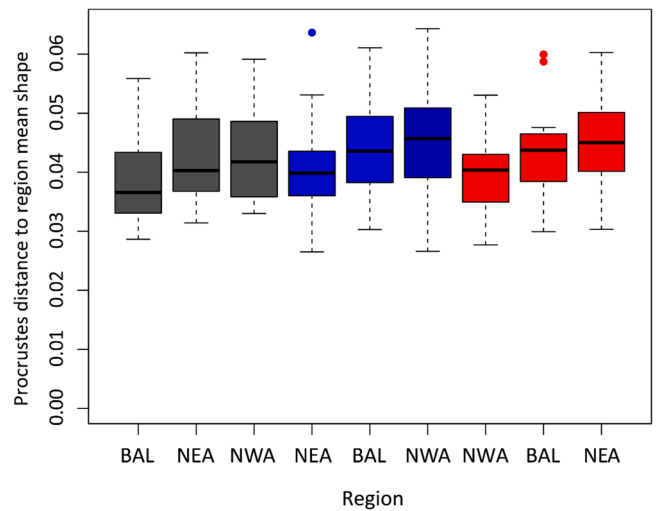


Fig. 3. The variation and median Procrustes distance between specimens within and between each of the three regions and the regional mean shapes. Distances from Baltic specimens are with dark grey boxes and symbols, Northeast Atlantic specimens are with blue, Northwest Atlantic specimens are in red. The bold horizontal line shows the median and the bottom and top of the box show the 25th and 75th percentiles, respectively. The vertical dashed lines (whiskers) show one of two things; either the maximum value or 1.5 times the interquartile range (roughly 2 standard deviations) of the data, whichever is the smaller. Points are outliers, defined as more than 1.5 times the interquartile range above the third quartile (below the first quartile).

4. Discussion

4.1. Age, sex and geographical variation in skull shape

The skull of an adult grey seal is massive and characterised by substantial age-related elongation caused by predominant growth of the facial portion, a feature most evident in adult males ([Savriama et al. 2018](#); [Beck et al. 2003](#); [Heptner et al. 1976](#)). We found that grey seal skull shape was affected by sex and age, but this did not interfere with

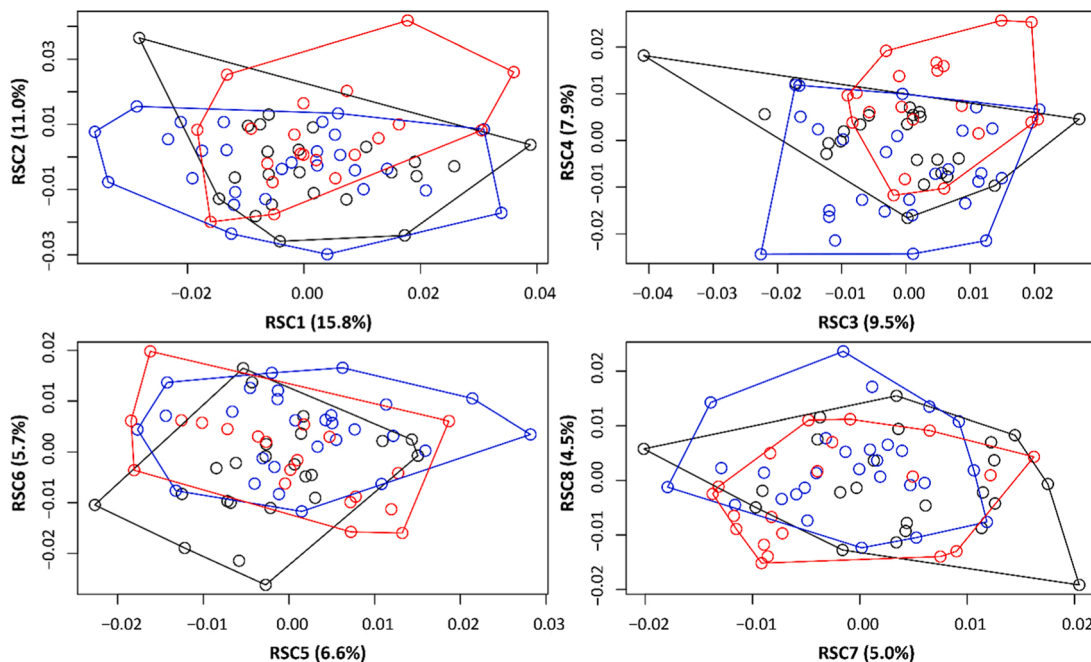


Fig. 2. Morphospace representation of grey seal cranial shapes using the first eight Residual Shape Components (RSCs), representing 65% of the residual variation after correcting for allometry. Symbol and convex hull polygon colour codes: Red=Northwest Atlantic; blue=Northeast Atlantic; black= Baltic Sea.

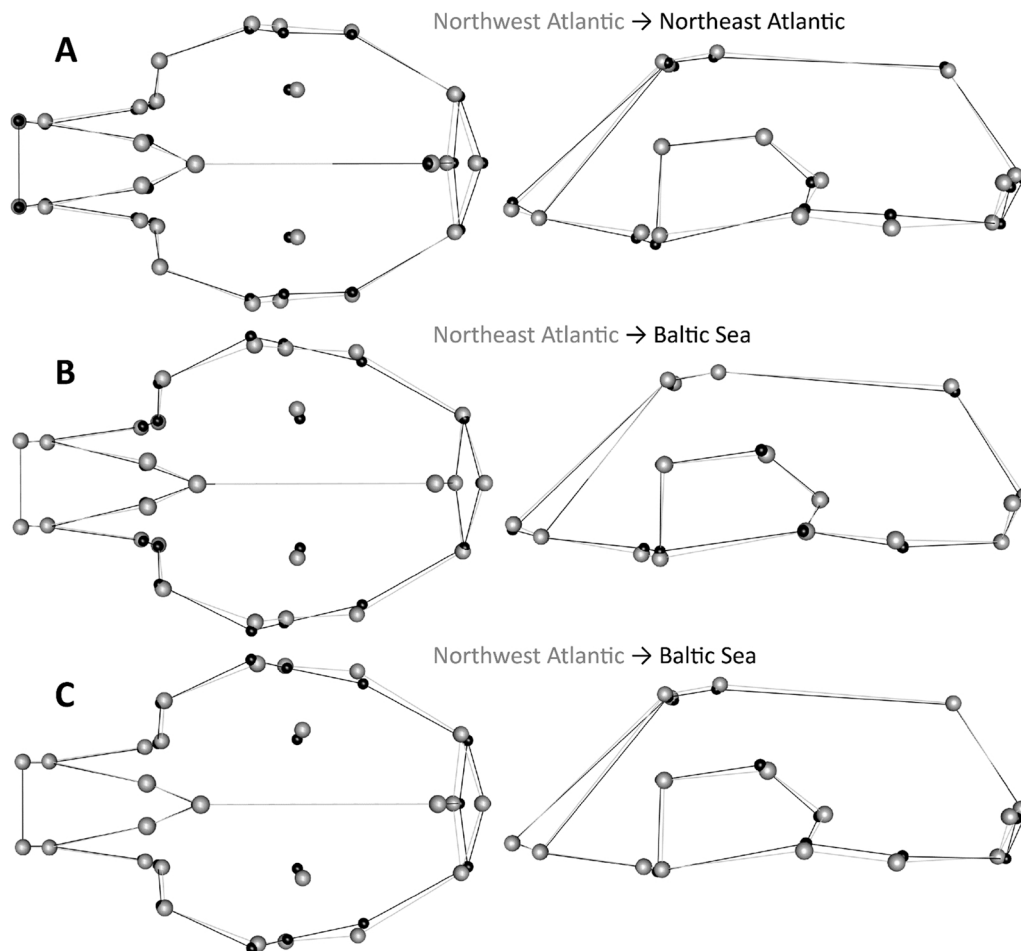


Fig. 4. Skull shape differences between grey seals from the three regions, A: difference between Northwest and Northeast Atlantic, B: difference between Northeast Atlantic and Baltic Sea, C: difference between Northwest Atlantic and Baltic Sea. Grey outline and markers represent the shape of the area written first (in grey) above the relevant panel, black outline and markers, the shape of the area written last above the relevant panel. Shape differences are exaggerated by a factor 2.

the analyses of regional differences in skull shape, which were small, yet statistically significant, for all pairwise comparisons between Northwest Atlantic, Northeast Atlantic and Baltic Sea specimens, respectively. Intriguingly, the level of intraspecific variation was substantially larger within regions than between. In other words, while regional differences do exist, they appear rather trivial compared to the overall inter-individual variation in skull shape.

The driver of the large intraspecific variation in grey seal skull shape is unknown. Like all phocid seals, the grey seal skull is characterised by multiple shifts in skull shape and modularity associated with their secondary adaptations to foraging in aquatic environments (Randau et al., 2019). However, as we have also shown here, grey seals differ in that their skull morphology shows a high degree of intraspecific variability and hence their position in morphospace relative to other seal species does not fit a particular type of foraging strategy, but rather tend to span multiple morphospace areas (i.e. filter; grip and tear; suction; and pierce feeding) (Kienle and Berta, 2016). This fits with observations that grey seals are dietary generalists, preying on fish, cephalopods, birds and mammals, which they capture using a wide range of foraging techniques varying by region, season, age and possibly sex (van Neer et al., 2015; Scharff-Olsen et al. 2018; Jessopp et al., 2013; Nowak et al. 2020). We hypothesize that the large intraspecific variation in grey seal skull shape may result from balancing selection or phenotypic plasticity, favouring an extremely generalist foraging strategy and hence the possibility to explore a wide range of prey categories and habitats.

4.2. Implications for population and subspecies delineations

The number and delineation of grey seal populations and subspecies is an unresolved question. Our range-wide analyses of variation in grey seal skull shape found specimens from the Northwest Atlantic, Northeast Atlantic and Baltic Sea to be statistically significantly differentiated, but with considerable overlaps in shape between samples. The largest distance between mean shapes was detected between Northwest and Northeast Atlantic grey seals, although this was only slightly larger than the distance between these and the Baltic grey seals. Furthermore, we found that only 52%–75% of the skulls could be correctly classified to their origin in comparisons between regions, with the highest reclassification success rates for the Northeast and Northwest Atlantic. These were higher than rates based on random reshuffling of the data, however still considerably lower than reclassification rates seen in similar analyses in other species. For instance, at the species level, geometric morphometric analyses resulted in 100% classification success of skulls from the two sister species harbour seals and spotted seals (*Phoca largha*) (Arai et al. 2021). In harbour porpoises (*Phocoena phocoena*), animals from the Northwest and Northeast Atlantic had almost no overlap in skull shape, whereas overlaps between porpoise samples from the neighbouring North Sea and Baltic Sea areas (Galatius et al., 2012) were of similar magnitude to those observed in our study for grey seal populations at the Northwest and Northeast Atlantic extremes of the species' range. There is little consensus as to whether the classification threshold for subspecies delineations should be set at 75%, 80% or 95% (Patten and Unit, 2002; Taylor et al. 2017; Donegan, 2018; Amadon, 1949), but

our estimates for grey seal subspecies clearly fall in the lower end, questioning their subspecies status from a morphological point of view.

5. Conclusion and perspectives

In conclusion, while we did find statistically significant differences in skull shape between the three currently recognised grey seal populations (Northwest Atlantic, Northeast Atlantic and Baltic Sea), these differences were trivial and there were large overlaps in shape between populations. Thus, our geometric morphometric analyses did not warrant subspecies status for any of these three populations. We further noted that the differences in skull shape within the current Atlantic subspecies are similar in magnitude to the differences between the current Atlantic and Baltic Sea subspecies. These findings are interesting in light of the greater geographical distance between Northwest and Northeast Atlantic grey seals (thousands of kilometres) compared to the close proximity (hundreds of kilometres), historical overlap and apparent recent hybridisation between Northeast Atlantic and Baltic Sea grey seals populations (Fietz et al. 2016). More strikingly, we found that variation was much larger within regions than mean differences between regions, which could be a result of adaptation to an extremely generalist foraging behaviour. Future studies should seek to increase the sample size for morphological analyses, conduct range-wide analyses of genomic data, examine grey seal evolutionary developmental biology, and review other lines of evidence (e.g. breeding phenology, social interactions, foraging strategies, movement data, body size and pelage patterns) to shed light on the fascinating skull morphology of grey seals and ultimately determine the number of grey seal subspecies.

Author contributions

AG, MSS, DM and MTO conceived and designed the study; MSS, MV, VAD, ABD and MTO provided funding; MV, MM, RS and MTO provided materials; VAD and ABD provided equipment; MSS and DM scanned skulls and collected landmarks; AG and DM performed the data analyses; AG and MTO wrote the manuscript with inputs from MSS and DM. All authors approved the final version of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.zool.2022.126023](https://doi.org/10.1016/j.zool.2022.126023).

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