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Morphology of nares associated with stereo-olfaction in baleen whales

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The sensory mechanisms used by baleen whales (Mysticeti) for locating ephemeral, dense prey patches in vast marine habitats are poorly understood. Baleen whales have a functional olfactory system with paired rather than single blowholes (nares), potentially enabling stereo-olfaction. Dimethyl sulfide (DMS) is an odorous gas emitted by phytoplankton in response to grazing by zooplankton. Some seabirds use DMS to locate prey, but this ability has not been demonstrated in whales. For 14 extant species of baleen whale, nares morphometrics (imagery from unoccupied aerial systems, UAS) was related to published trophic level indices using Bayesian phylogenetic mixed modelling. A significant negative relationship was found between nares width and whale trophic level ($\beta = -0.08$, lower 95% CI = -0.13, upper 95% CI = -0.03), corresponding with a 39% increase in nares width from highest to lowest trophic level. Thus, species with nasal morphology best suited to stereo-olfaction are more zooplanktivorous. These findings provide evidence that some baleen whale species may be able to localize odorants e.g. DMS. Our results help direct future behavioural trials of olfaction in baleen whales, by highlighting the most appropriate species to study. This is a research priority, given the potential for DMS-mediated plastic ingestion by whales.

1. Introduction

Baleen whales (or Mysticeti) represent some of the most extreme trophic ecologies among vertebrates. Not only do they engage in highly energetically

demanding methods of feeding [1,2], but they must also locate ephemeral, energetically dense food patches within the expanse of their oceanic habitats. How they locate such prey patches, however, remains poorly understood. While known to use a combination of acoustic and visual sensory modalities, the role of chemoreception, including olfaction, has not been clearly resolved [3].

Several lines of evidence support the use of olfaction (smelling in air) by baleen whales [4–7]. They exhibit features only found in those mammals with a functioning sense of smell, including a cribriform plate supporting olfactory bulbs [4,5] and the olfactory marker protein is expressed in baleen whales [6,8]. Theoretical evidence suggests that gradients of dimethyl sulfide gas (DMS) could orient zooplanktivores such as baleen whales to areas of higher prey biomass than by randomly searching by other means [7].

For those baleen whale species that forage at lower trophic levels, olfaction might be used to locate planktonic food patches that produce DMS [9], an odorous secondary metabolite released by phytoplankton in response to grazing by zooplankton [10,11]. For example, seabirds are known to use DMS as a cue for zooplankton availability and hence feeding opportunities at distances in excess of 20 km downwind of the source [12]. Studies exploring the response of baleen whales to DMS have provided inconclusive evidence suggesting that this may also be an important cue for these species, albeit at a smaller spatial scale of several hundreds of metres [9]. However, while DMS may indicate the presence of high-density food patches, whether baleen whales use olfaction to gain more directional cues has not been tested.

All cetaceans have paired bony nasal passages underlying a blowhole (nares hereafter), which comprises soft tissue [13–15]. Nares are paired in baleen whales [15] while they have evolved into a single conduit in toothed whales (Odontoceti) [4]. Baleen whales have also retained functional olfactory bulbs, unlike odontocetes which apparently lack olfaction [4,16]. Paired nares are associated with stereo-olfaction, a trait found in a range of species, including humans [17–19] and can play an important role in directionally localizing odorants, as demonstrated in experimental studies on a range of taxa from mammals to insects [20,21].

In baleen whales, which must rely on coming to the sea surface to gain orthonasal olfactory (smelling in air) information, the presence of widely spaced nares may provide additional directional information for odorous cues. However, the importance of such cues is likely to vary across baleen whale species, given their trophic diversity. For example, balaenid species such as right (*Eubalaena australis, E. glacialis, E. japonica*) and bowhead whales (*Balaena mysticetus*), predominately feed on zooplankton (e.g. calanoid copepods and euphausiids) that, in turn, are directly associated with DMS-emitting phytoplankton [22–24].

While right and bowhead whales can feed at depth, they also take advantage of prey concentrations at the sea surface and employ surface-skimming [24,25]. Sei whales (*Balaenoptera borealis*) are able to switch between subsurface lunging and surface skimming, depending on availability and type of prey species [2], as they can target both small fishes or zooplankton at a range of depths [26,27]. Here we use vertical, overhead images and video stills collected non-invasively from unoccupied aerial systems (UAS; drone) to measure baleen whale nares. We test the hypothesis

that those baleen whale species occupying lower trophic levels have wider nares, associated with the capacity for stereo olfaction.

2. Methods

(a) Data collection

Morphometric measurements were made for free-ranging whales mostly using UAS or aircraft-based imagery, including stills from video footage (electronic supplementary material, figure S1, table S1). The selection criteria for images were that they were vertical, in focus and clearly showed the nares. Altitude was typically between 10–60 m, however accurate altimetry data were not available for all flights and therefore relative measurements (i.e. pixel counts) were used. Because images were compiled from a range of different studies, the UAS, camera, camera sensor, lens focal length, altitude and thus pixel resolution will have varied among sampling events (electronic supplementary material, table S1). Similarly, lens distortion will vary in its effect on whale measurements due to differences among UAVs. To mitigate possible effects from image distortion, only images where the subject of interest (head) was in the centre of the frame (≥30% from all frame edges) were used (electronic supplementary material, table S2).

Absolute measurements were not generated in this study, rather those previously published (total body length) estimates were used (electronic supplementary material, tables S1 and S2). To compile a dataset of 14 extant species of baleen whales, additional images for those rarely documented species were sourced from publications and reports [28–32]. Two of these photographs were taken from a ship [30] or underwater [28], but all clearly showed the nares. For each individual whale, the clearest available overhead image (i.e. photograph or video still) was used to measure the maximum width (pixels) of the open or closed nares and the maximum width of the head (pixels) at the nares using the straight-line tool in ImageJ Analyze and Measure (https://imagej.nih.gov/ij/index.html).

The maximum-nares-width measurements could vary depending on what point during the respiration cycle the measurement was made, from fully closed through to fully open [33]. We considered this by assigning two simplified nares states which were assigned to each set of measurements: open (ranging from fully to partially open: bubbles, vapour or respiratory tract visible) and closed (no bubbles, vapour or respiratory tract visible). The aim was to obtain a set of measurements for both states for each whale, which was not always possible.

To assign a trophic level to each whale species, we used available estimates based on diet from the SeaLifeBase database [34]. There were no available estimates in the database for pygmy right (*Caperea marginata*), Rice's (*B. ricei*) and Omura's (*B. omurai*) whales. Instead, we determined the preferred prey for these whale species from published sources [27–29,35] and applied trophic level estimates of the preferred prey plus 1 [34]. For phylogeny, we used the dated mammal phylogeny from Upham *et al.* [36] which was truncated to include only those species present in our dataset. Because Rice's whale is missing from Upham *et al.* [36], we added it as a sister species, Eden's whale (*B. edeni*), based on its current phylogenetic positioning [32].

(b) Analysis

To test our hypothesis that nares-to-head-width ratio would be greatest for predominately zooplanktivorous species, we fitted Bayesian phylogenetic mixed models (BPMM) using the *MCMCglmm* package [37] in R version 4.2.2 [38]. To account for allometric effects associated with body size we used the ratio of maximum nares width to maximum head width

at the nares, where the head width was measured with the mouth closed and in the relaxed position (electronic supplementary material, figure S1). This approach allowed for the body sizes (not absolute size) associated with each individual to be accounted for in the analysis. Because body length and the width of the head change as a whale grows [39], it was necessary to test if the maximum-nares-width-to-head-width ratio is a valid metric to use with regards to ontogeny. Therefore, a linear regression was carried out comparing the nares-width-to-head-width ratio to the body length for each individual with species as a factor, for a subset of five taxonomically disparate species (electronic supplementary material, figure S2, table S2). Furthermore, nares dimensions and trophic level may vary between different sexes, ontogenetic stages and individuals living in different habitats. Because neither data nor a thorough understanding of the possible effects of sex or age were available, a caveat in our approach is the assumption that they are insignificant.

The structure of the main model was *nares-to-head-width ratio~trophic level + nares state (closed versus open)*, with closed nares used as the baseline. To account for potential pseudoreplication due to the evolutionary relationship between species, we used the animal term in MCMCglmm [37]. This term uses a distance matrix of the phylogenetic distance between species to control for the expected similarity in trait values due to common descent. We calculated the term h^2 as the relative variance attributable to the animal [40]. This term can be interpreted in a similar fashion to the phylogenetic lambda value, with a h^2 value close to 1 indicating a Brownian model of trait evolution, and a value close to 0 indicating independence between trait values [40].

All models were fit using parameter expanded priors [37]. Choice of burn-in, thinning and number of iterations was determined for each model separately to ensure effective sample sizes exceeded 1000 for all parameter estimates. We tested for convergence using the Gelman–Rubin statistic over three separate chains [41]. We also included a random term to account for within species variation. Due to the lack of UAS images for pygmy right and Omura's whales, we also ran a sensitivity analysis where we re-fitted the model without these two species. Significance was determined if the 95% credibility interval did not cross zero, which is the Bayesian analogue to a *p*-value of 0.05 [37].

3. Results

Across the 14 species in our dataset, the nares-to-head-width ratio varied from the lowest value of 0.03 measured in a humpback whale (*Megaptera novaeangliae*) to highest value of 0.31 measured in a North Atlantic right whale individual (*E. glacialis*) followed by southern right whale (*E. australis*), pygmy right whale (*C. marginata*) and Omura's whale (*B. omurai*). Trophic levels reported or estimated from Palomares & Pauly [34] ranged from 3.0 in both the North Atlantic right whale and pygmy right whale to 4.37 in Rice's whale.

In our model, we found a significant negative relationship of 0.08 between nares-to-head-width ratio and trophic level ($\beta = -0.08$, lower 95% CI = −0.13, upper 95% CI = −0.03, table 1, figure 1). This corresponds to a 39% decrease in the nares-to-head-width ratio across the range of trophic levels in our dataset (figure 1). As expected, we found that open nares had a wider ratio compared to closed nares, however the overall effect of nares state (open or closed) was small ($\beta = 0.2$, lower 95% CI = 0.01, upper 95% CI = 0.04, table 1, figure 1). We found comparable results in the sensitivity
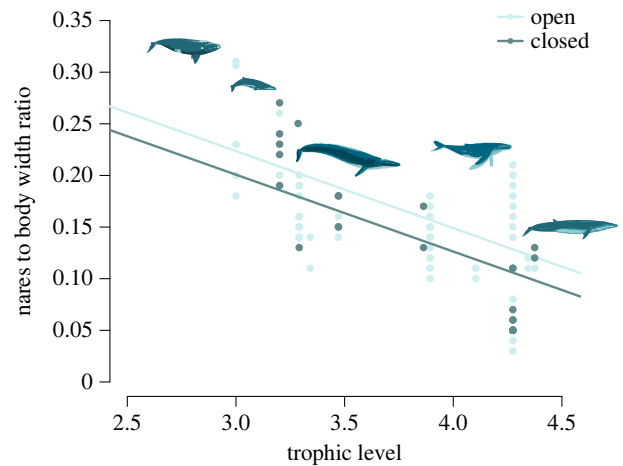

Figure 1. Ratio of nares width to body width against trophic level for 14 species of baleen whale. Observation and fitted line associated with open nares are indicated in light blue (*n* = 85) and observations and fitted line associated with closed nares in dark blue (*n* = 58). The fitted lines demonstrate a negative relationship with a slope ($\beta = -0.8$, lower 95% CI = −0.13, upper 95% CI = −0.03). Species from left to right, (TL = trophic level; silhouetted species in **bold**), **North Atlantic right whale (*Eubalaena glacialis*)** TL = 3; Southern right whale (*Eubalaena australis*); **pygmy right whale (*Caperea marginata*)** TL = 3; North Pacific right whale (*Eubalaena japonica*) TL = 3.2; Omura's whale (*Balaenoptera omurai*) TL = 3.285; gray whale (*Eschrichtius robustus*) TL = 3.29; bowhead whale (*Balaena mysticetus*) TL = 3.34; **blue whale (*Balaenoptera musculus*)** TL = 3.47; sei whale (*Balaenoptera borealis*) TL = 3.86; Antarctic minke whale (*Balaenoptera bonaerensis*) TL = 3.89; Bryde's whale (*Balaenoptera brydei*) TL = 4.1; **humpback whale (*Megaptera novaeangliae*)** TL = 4.27; fin whale (*Balaenoptera physalus*) TL = 4.34; **Rice's whale (*Balaenoptera ricei*)** TL = 4.37.

analysis with species without aerial and underwater images removed, with both a significant negative relationship of −0.06 with trophic level and a positive one associated with open nares (electronic supplementary material, table S3). A h^2 of 0.37 indicated moderate phylogenetic effects (table 1, electronic supplementary material, table S3). Linear regression indicated that the maximum nares-to-head-width ratio is not dependent on total body length, therefore its use is assumed to be appropriate for all species regardless of body size (electronic supplementary material, figure S2).

4. Discussion

Our findings provide a link between nares morphology and trophic ecology, with clues about how baleen whales might locate patches of prey in a vast habitat. As hypothesized, trophic status predicts baleen whale nares spacing, when body size among individuals and phylogenetic relationship among 14 extant species is accounted for (figure 1; table 1). This provides further evidence in support of functional olfactory ability in baleen whales [5,9,42,43] and the first evidence that nasal morphology and trophic niche may be codependent over evolutionary timescales in baleen whales. Whether this effect is mediated by DMS or other olfactory stimuli has yet to be verified. Determining this is a conservation priority because biofouling on floating plastic debris emits DMS, which may predispose seabirds to plastic ingestion [44]. If some baleen whales are similarly attracted to DMS, it could lead to plastic ingestion or disruption to foraging attempts [45].

Table 1. Summary of main model results, with mode (β) and 95% credibility intervals (CI) of the posterior distributions for the fixed terms of trophic level and nares state (open, closed) and for the random terms associated with phylogenetic variance, within species variation and residual variation (units). A plot of the associated posterior distributions is also included on the right of the table, with a broken reference line for zero (no slope). (N = 143 observations across 14 species.)

model	estimate (β)	lower CI	upper CI	posterior distribution
fixed effects				
intercept	0.44	0.24	0.63	
trophic level	−0.08	−0.13	−0.03	
nares state open	0.02	0.01	0.04	
random effects				
phylogeny	0.002	0.000	0.007	
species	0.001	0.000	0.003	
units	0.002	0.001	0.002	

Behavioural studies investigating olfaction have focused on humpback whales which respond to odorants [9] and orientate into wind more often than by chance, in the presence of odorants [42]. In addition, the opening and closing of nares are bilaterally coordinated in those baleen whale species investigated to date: humpback and North Atlantic right whale [33]. This supports our interpretation of the link between nares morphology and trophic status because bilateral coordination is required for effective stereo-olfaction [21]. While serial olfaction can be sufficient to locate odorant sources, employing olfaction bilaterally (in stereo) increases efficiency [20,21]. However, humpback whales are a higher trophic species with a small body-to-nares-width ratio (figure 1). Our findings suggest that future field trials of DMS localization in whales should instead focus on lower trophic species such as blue and right whales.

Baleen whale sensory processes are likely to be complimentary and highly scale-dependent [3]. Olfaction is therefore unlikely to be a dominant sense for baleen whales. For piscivorous (e.g. Rice's whale) or mainly benthic feeding species (e.g. grey whale), DMS is unlikely to be a reliable indicator of prey occurrence given the absence of phytoplankton grazing by such prey. The recent finding that tactile hairs may have a role in the sensory ecology of North Atlantic right whales serves to highlight that our fundamental understanding of these sensory processes in whales is still evolving [46]. In addition to orthonasal olfaction, it has been theorized that baleen whales may employ retronasal olfaction, whereby odorants from ingested food or water could be passed from the oral cavity to the nasal chambers [45].

In this study, species were assigned a single trophic level index, based on a global synthesis of dietary information, with the caveat that age and sex were assumed to be inconsequential [34]. In practice, some species like blue and right whales occupy a narrow trophic niche, whereas e.g. fin, humpback and minke whales can be plastic or geographically diverse with regard to trophic width [47–49]. The evolution of a single nares accompanied with the loss of olfaction in odontocetes [4,6] is consistent with our argument that nares width may be a useful proxy for predicting trophic level in extinct or newly discovered species of baleen whales. Finally, our findings have implications for anthropogenic disturbance of baleen whales from intentional or incidental introduction of odorants in the marine environment.

Authors' contributions. C.R.: conceptualization, data curation, formal analysis, methodology, project administration, writing—original draft, writing—review and editing; M.C.I.M.: data curation, formal analysis, methodology, software, writing—original draft, writing—review and editing; K.H.: conceptualization, data curation, formal analysis, methodology, software, validation, visualization, writing—original draft, writing—review and editing; L.B.: data curation, investigation, writing—review and editing; S.C.: data curation, investigation, writing—review and editing; F.C.: data curation, investigation, writing—review and editing; J.D.: data curation, investigation, writing—review and editing; H.F.: data curation, investigation, writing—review and editing; S.F.: data curation, investigation, writing—review and editing; A.F.: data curation, investigation, writing—review and editing; W.R.K.: data curation, investigation, writing—review and editing; C.M.: data curation, investigation,

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