Canadian Journal of Zoology

Morphological differences in skulls and feeding apparatuses between Antarctic and common minke whales, and the implication for their feeding ecology

Journal:	<i>Canadian Journal of Zoology</i>
Manuscript ID	cjz-2020-0237.R2
Manuscript Type:	Article
Date Submitted by the Author:	30-Jun-2021
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Is your manuscript invited for consideration in a Special Issue?:	Not applicable (regular submission)
Keyword:	<i>Balaenoptera bonaerensis</i> , <i>Balaenoptera acutorostrata</i> , Antarctic minke whale, common minke whale, skull morphology, feeding morphology, engulfment capacity

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Morphological differences in skulls and feeding apparatuses between Antarctic and common minke whales, and the implication for their feeding ecology

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Abstract

The differences in rorqual feeding ecology have been linked to the presence of different morphological markers. The Antarctic minke whale (*Balaenoptera bonaerensis* Burmeister, 1867) and common minke whale (*Balaenoptera acutorostrata* Lacépède, 1804) are closely related species, but their morphological differences have not been fully investigated. In this study, we compared 21 skull and 11 feeding apparatuses (baleen and mouth-related parts) measurement points between these two species using hundreds of individuals covering a wide range of body lengths in both sexes. Their engulfment capacities were estimated using these measurements. Our results show that Antarctic minke whales have (1) proportionally larger skulls to the body length, (2) more dorsoventrally and laterally curved rostra, (3) proportionally larger feeding apparatuses to the condylobasal length, and (4) significantly larger engulfment capacity than common minke whales. These differences could indicate that Antarctic minke whales have developed a feeding strategy suitable for feeding on krill, which forms large schools. In contrast, common minke whales have adapted to prey on small pelagic

67 fishes that are agile and form small schools.

68 **Key words**

69 *Balaenoptera bonaerensis*, *Balaenoptera acutorostrata*, Antarctic minke whale, common minke

70 whale, skull morphology, feeding morphology, engulfment capacity

71 **Introduction**

72 Feeding is one of the most fundamental aspects for any animal species as it is directly tied to
73 their survival. Each cetacean species has its own feeding ecology (i.e., the way in which the species
74 exists in the environment from the perspective of feeding). These species are assumed to adapt a
75 suitable feeding strategy in response to abiotic and biotic factors (Simões-Lopes et al. 1998;
76 Anderwald et al. 2011, 2012). Feeding strategies are important to understand the species' feeding
77 ecology. Although the term "feeding strategy" has been used in various contexts to date (Markowitz
78 et al. 2004; Slater et al. 2010; Giménez et al. 2017; Hocking et al. 2017; McMillan et al. 2019), we
79 define it here as "a plan that includes prey selection, food consumption, the pattern of movement, and
80 behavior that results in optimal foraging (i.e., maximizing energy intake), which is ultimately linked
81 to the species' survival and reproduction". "Tactics", which include behaviors, are used to accomplish
82 feeding strategies (Heithaus et al. 2018). Questions related to feeding tactics include: (1) what and
83 how much individuals feed on (feeding habits), (2) how individuals feed on the prey (feeding method
84 and feeding behavior), and (3) when and where individuals feed (temporal and spatial scales of
85 feeding). Understanding the feeding morphology (i.e., the shape and size of the body parts and
86 apparatuses related to feeding) is fundamental to answer these questions because the morphology
87 constrains the species' feeding strategies and tactics.

88 Balaenopteridae (rorqual) is the largest family of parvorder Mysticeti, which comprises the

largest number of species; it ranges from the smallest species, the common minke whale (*Balaenoptera acutorostrata* Lacépède, 1804), to the largest species, the blue whale (*Balaenoptera musculus* Linnaeus, 1758). Rorquals employ a unique filtering method called lunge filter feeding, in which they first engulf prey-laden water on an enormous scale. Then, they filter the water using baleen racks (baleen series) unique to Mysticeti. This filtering method allows them to feed efficiently on large numbers of small-sized prey (i.e., zooplankton and small pelagic fishes), which are required to sustain their large bodies. Scientists have been trying to reveal the details of the rorqual feeding using various research methods and devices. For example, the feeding habits of rorquals can be studied by analyses of stomach contents (e.g., Sigurjónsson et al. 2000; Flinn et al. 2002), stable isotopes (e.g., Mitani et al. 2006), and estimation of prey consumption using energetic models (e.g., Spitz et al. 2018). Archival tags and drones are also used to obtain data related to the behaviors of whales (Goldbogen et al. 2017a, 2017b; Torres et al. 2020). Morphological analysis has also provided insights into the feeding strategy in combination with data obtained using archival tags. Goldbogen et al. (2012) indicated that lunge frequency (i.e., number of lunges per dive from tag data) is inversely related to engulfment capacity in some rorqual species. They suggested that larger engulfment capacity limited lunge frequency, which could be related to the prey selection by rorquals.

The Antarctic minke whale (*Balaenoptera bonaerensis* Burmeister, 1867) and the common minke whale were considered as a single species until recently (Murase et al. 2020). Authoritative

107 scientific bodies such as the International Whaling Commission's Scientific Committee (IWC/SC)
108 (IWC 2001) and the Society for Marine Mammalogy (Committee on Taxonomy 2021) now recognize
109 them as separate species. Antarctic and common minke whales are distributed in the Southern
110 Hemisphere and the Northern Hemisphere, respectively. The North Atlantic minke whale
111 (*Balaenoptera acutorostrata acutorostrata* Lacépède, 1804) and the North Pacific minke whale
112 (*Balaenoptera acutorostrata scammoni* Deméré, 1986) are recognized as subspecies of the common
113 minke whale (Committee on Taxonomy 2021). The dwarf minke whale (*Balaenoptera acutorostrata*
114 subspecies) is suggested as a subspecies of the common minke whale by Rice (1998), but its taxonomic
115 status is still open to question. Furthermore, several stocks of Antarctic and common minke whales
116 are recognized or suggested (Goto and Pastene 1997; Pastene and Goto 2016). Interspecific hybrids
117 were reported between the Antarctic minke whale and the North Atlantic minke whale although the
118 frequency of occurrence is uncertain (Glover et al. 2010, 2013). The existence of several subspecies,
119 stocks, and hybrids indicates the complexity of the minke whale clade. The morphological differences
120 between Antarctic and common minke whales are worth studying because genetic differences are
121 ultimately reflected in the morphology of whales.

122 The feeding behavior and feeding morphologies of Antarctic and common minke whales have
123 been studied previously. Friedlaender et al. (2014) and Kahane-Rapport and Goldbogen (2018)
124 suggested that both species employed the same feeding strategy (i.e., smaller engulfment capacity and

higher lunge frequency compared with those of other rorqual species). However, interpretation of these results had some limitation either because a study only relied on data recorded by archival tags (Friedlaender et al. 2014) or the other study used morphological data that treated Antarctic and common minke whales as the same species, “*Balaenoptera acutorostrata*” (Kahane-Rapport and Goldbogen 2018).

Morphological studies on skulls (Omura 1975; Arnold et al. 1987; Zerbini and Simões-Lopes 2000) and baleen (Williamson 1959; Kasuya and Ichihara 1965; Ohsumi et al. 1970) of the two species have been conducted in the past. However, the interspecific differences remain obscure because of the following shortcomings. First, developmental changes and sex differences were not considered. These studies did not fully consider the differences in body length or skull length, although Zerbini and Simões-Lopes (2000) divided individuals into three categories based on cranial maturity. Second, the aforementioned studies also used inadequate morphometric methods and/or statistical analyses. These six studies relied on qualitative visual inspection along with a simple comparison of measurement values or the average values of the proportion to the skull length. Finally, the species comparisons depended on only a few individuals. The maximum sample size among these studies was 18 individuals of Antarctic minke whales (Zerbini and Simões-Lopes 2000), and interpretation of the results was limited because of the small sample size. Furthermore, the morphologies of other feeding apparatuses, such as palate length and width, and the length from the snout to the angle of gape, were

rarely compared in these studies. However, these measurements are important to understand baleen morphology and engulfment capacity.

In this study, we provide new information on the feeding morphologies of Antarctic and common minke whales using morphometric data on skulls and feeding apparatuses. We conducted statistical analyses of these data to clarify the interspecific differences and then estimated the engulfment capacities of these two species. We used hundreds of samples of each species, including a wide range of body lengths of both sexes. We discuss the potential links between the feeding morphologies and ecologies of these two species.

Materials and methods

General

Antarctic and common minke whales were sampled by the Japanese Whale Research Program under Special Permit in the Antarctic (JARPA), the New Scientific Whale Research Program in the Antarctic Ocean (NEWREP-A), the second phase of the Japanese Whale Research Program under Special Permit in the Western North Pacific (JARPN II), and the New Scientific Whale Research Program in the western North Pacific (NEWREP-NP). The sampling methods can be found elsewhere (IWC 2015, 2017). All surveys were conducted under permits issued by

the Government of Japan in accordance with the provisions of Article VIII of the International Convention for the Regulation of Whaling (ICRW). All sampling was conducted in Antarctic waters south of 60°S and between 130°E and 120°W, or in the western North Pacific off Japan (the areas off Abashiri, Kushiro, Hachinohe, and Ayukawa). These surveys were conducted only within Japan's territorial waters, exclusive economic zones (EEZs), and the high seas. The sighting locations of the individuals used in this study are shown in Figure 1. Measurement data of Antarctic minke whales were collected in the austral summers of 1990/91 and 2017/18, and those of common minke whales were collected from 2008 to 2019. A male Antarctic minke whale that had a single testis weighing ≥ 400 g was regarded as sexually mature (Ohsumi et al. 1970). A male common minke whale with a single testis weighing ≥ 290 g and a female whale of both species with at least one corpus luteum or albicans in its ovaries were considered sexually mature, as described by Maeda et al. (2017). The body mass of an individual whale was measured to the nearest 0.01 tons in the survey fields. Measurement data were recorded to cover a wide range of body lengths in both sexes. However, the number of samples varied between the skull, feeding apparatuses, and engulphment capacity estimation because measurements were conducted on an opportunistic basis along with other biological research in the field.

Skull measurement

179 A total of 98 Antarctic minke whales (52 males and 46 females) and 248 common minke whales
180 (129 males and 119 females) were measured at the survey fields. The male sample set covered the
181 Body length (BL; note the first letter of each measurement point is capitalized for clarity) range from
182 4.74 to 9.00 m (mean $\pm$ SE: 7.01 $\pm$ 0.20 m) for Antarctic minke whales and from 3.70 to 8.05 m
183 (6.14 $\pm$ 0.11 m) for common minke whales. The female sample set covered the BL range from 4.60 to
184 9.68 m (7.77 $\pm$ 0.23m) for Antarctic minke whales and from 3.69 to 8.85 m (6.23 $\pm$ 0.13m) for
185 common minke whales. Muscles and connective tissue were removed from the skulls using a knife
186 and scalpel. A total of 21 measurement points likely to be related to feeding were measured using
187 vernier calipers or anthropometers. Ten measurement points described by Nakamura and Kato (2014)
188 were selected and measured, and 11 measurements, including the measurements of transverse sections
189 at the rostrum base and the middle of the rostrum length, were unique to this study. For the eight
190 measurements of transverse sections of the rostrum, the rostrum was cut perpendicular to the rostrum
191 and the median of the skull using either a bone saw or chain saw. All measurements were taken to the
192 nearest 0.1 cm (Table 1 and Fig. 2).

193

194 **Feeding apparatus measurement**

195 A total of 644 Antarctic minke whales (310 males and 334 females) and 704 common minke
196 whales (381 males and 323 females) were measured. The male sample set covered the BL range from

4.74 to 9.17 m (mean $\pm$ SE: 7.85 ± 0.06 m) for Antarctic minke whales and from 3.70 to 8.04 m (5.93 ± 0.06 m) for common minke whales. The female sample set covered the BL range from 4.60 to 9.80 m (8.24 ± 0.06 m) for Antarctic minke whales and from 3.69 to 8.85 m (5.77 ± 0.06 m) for common minke whales. Measurements of the Snout to angle of gape (SAG), Palate length and Palate width (PL and PW, respectively) were taken to the nearest 1 cm using a tape measure (Fig. 2). Baleen rack length (BRL) is the distance between the most anterior and the most posterior elements of the baleen rack measured in a straight line parallel to the axis of the baleen rack (taken to the nearest 1 cm using a tape measure). Baleen racks were measured after being cut off from the whale body and placed horizontally. A pair of baleen plates was sampled from the maximum region of the left and right baleen racks, and three lengths (outer and inner length and width) were measured in a straight line for each baleen plate (Fig. 2). These measurements were taken to the nearest 0.1 cm using vernier calipers or anthropometers. The measurements are listed in Table 1 and are shown in Figure 2.

Engulfment capacity estimation

A total of 318 Antarctic minke whales (143 males and 175 females) and 909 common minke whales (483 males and 426 females) were used to estimate the engulfment capacity. The male sample set covered the BL range from 4.74 to 9.00 m (mean $\pm$ SE: 7.50 ± 0.10 m) for Antarctic minke whales and from 3.70 to 8.04 m (6.07 ± 0.05 m) for common minke whales. The female sample set covered

the BL range from 4.60 to 9.68 m (8.00 ± 0.10 m) for Antarctic minke whales and from 3.69 to 8.85 m (6.02 ± 0.06 m) for common minke whales. The engulfment capacity (W_E) (kg) was estimated following the methods of Goldbogen et al. (2010) and Kahane-Rapport and Goldbogen (2018), as described below.

$$(1) \ W^E = \left\{ \frac{\pi}{3} (L^{VGB} - L^{jaw}) 1.17 L^{jaw} \frac{1}{2} W^{head} + \frac{\pi}{3} L^{jaw} 1.17 L^{jaw} \frac{1}{2} W^{head} \right\} \times 10^3$$

where L_{VGB} is the Length of the ventral grooves (LVG) (m), L_{jaw} is SAG (m), and W_{head} is the Greatest width of the skull (GWS) (m). SAG was used as L_{jaw} instead of the projected length of the mandible used by Goldbogen et al. (2010) and Kahane-Rapport and Goldbogen (2018) because of the lack of measurement data for this point in our data set. Equation (1) estimates the engulfed sea water weight by adding the posterior (former part in curly braces) and anterior (latter part in curly braces) part volumes of the buccal cavity (Goldbogen et al. 2010). LVG was the length from the tip of the snout to the end of the ventral grooves measured parallel to the body axis (Fig. 2).

Statistical Analysis

The allometries of the Condylbasal length (CBL) and GWS to BL were compared between the two species. Interspecific differences in skull measurements were analyzed as the dependent variable of CBL for comparison purposes because each skull part is traditionally analyzed in proportion to CBL.

The measurements of feeding apparatuses were also analyzed as the dependent variable of CBL to investigate the relationship between morphologies of skull and feeding apparatuses. The following allometric equation was used for comparison:

$$(2) Y = \beta X^{\alpha}$$

where X is either BL (m) or CBL (cm), Y is the length of each measurement (m or cm), and α and β are the allometric coefficient and constant to be estimated, respectively. An individual allometric equation was converted to the natural logarithmic form, and its allometric coefficient (slope) and constant (intercept) were compared between species. The Standardized Major Axis (SMA) Tests and Routines (“smatr”) package (Warton et al. 2012) was applied to estimate the allometric equations and test interspecific differences in slopes and intercepts. In this analysis, the differences in the slopes of the regression lines were analyzed between the species (test of parallelism). Intercepts of the logarithmic equations with the common slope to two species were subsequently compared between species only when the slopes were not significantly different between species ($p > 0.05$) (i.e., interspecific comparison of the adjusted means). The difference between the intercepts of two parallel regression lines shows a proportional difference (difference in the measurement length at the same BL or CBL). Given that there was no significant difference ($p > 0.05$) in the slope and there was a significant difference ($p < 0.05$) in the intercept, the measurement was regarded as proportionally

different between the two species. This is theoretically the same as the differences between the allometries produced by ANCOVA (Oliveira and Almada 1995; Schmidt et al. 2015). It is important to note that CBL measurements taken to the nearest 0.1 cm were used for the analyses of skulls and the maximum baleen plates. To analyze SAG, palate, and baleen rack, CBL measurements taken to the nearest 1 cm were used because CBL of individuals used in these analyses were not taken to the nearest 0.1 cm.

Equation (2) was applied to compare the engulfment capacity between species. In this analysis, X is BL (m), and Y is W_E (kg). The individual allometric equation was converted to the base 10 logarithmic form to compare our results with those of Kahane-Rapport and Goldbogen (2018). The slope and intercept of the logarithmic equation were compared between species using the same method and software as those used in the morphological analyses of skull and feeding apparatuses. All statistical analyses were conducted separately for males and females using R version 4.0.5 (R Core Team 2021).

Results

Skull morphology

There was no interspecific difference in slopes of the logarithmic equations of CBL to BL in

female whales and GWS to BL in male and female whales. In male whales, the slopes of CBL to BL showed significant interspecific difference ($p < 0.05$). The comparison of intercepts revealed that male Antarctic minke whales have wider skulls than male common minke whales and female Antarctic minke whales have longer and wider skulls than female common minke whales ($p < 0.01$, Table 2 and Fig. S1). Although the slopes of males differed significantly in the analysis of CBL, the estimated slopes of males showed considerably similar values to those of females, and the regression line of Antarctic minke males suggested larger CBL in allometry (Table 2 and Fig. S1). In sexually mature individuals, the proportion of CBL to BL ranged from 19.24 to 22.52% (mean $\pm$ SE: $21.07 \pm 0.12\%$) in male common minke whales and 19.96 to 23.19% ($21.46 \pm 0.14\%$) in female common minke whales, and 22.77 to 25.03% ($24.05 \pm 0.16\%$) in male Antarctic minke whales and 22.59 to 26.25% ($24.53 \pm 0.19\%$) in female Antarctic minke whales.

In the analysis of the allometries of skull measurements to CBL, the slopes of the Rostrum length (RL) of both sexes and those of the Premaxilla length (PmL) (L, R) and the Rostrum edge height at the base (ReHb) of females were significantly different between species ($p < 0.05$). In males, seven measurements of Antarctic minke whales were proportionally larger than those of common minke whales ($p < 0.05$), and seven measurements were proportionally smaller than those of common minke whales ($p < 0.05$). However, four measurements of Antarctic minke whales were proportionally larger ($p < 0.05$), and five measurements were proportionally smaller in females ($p < 0.05$). Males and

females had a similar tendency on the interspecific difference in intercepts in 12 out of 20 measurements (i.e., we could make the same conclusion about which species has a proportionally larger measurement); four measurements (e.g., Rostrum height (RH) and Maxilla width at the middle (MaWm) (L), Fig. 3) were larger in Antarctic minke whales ($p < 0.01$); four measurements (e.g., Rostrum width (RW), Fig. 3) of Antarctic minke whales were smaller ($p < 0.05$); and four measurements were not significantly different between species. The interspecific differences in the proportion to CBL were especially prominent in RH and the Rostrum edge height at the middle (ReHm) (Fig. 3). The results of measurements related to lateral curvature (Rostrum width at the middle [RWm], RW, Maxilla width at the base [MaWb], and MaWm), and dorsoventral curvature (RH, ReHb, and ReHb) of the rostrum are shown in Tables 3 and 4, respectively. Antarctic minke whales tended to have rostra, which are wider in its middle, and larger RH, ReHb, and ReHb. The detailed results, including measurement points not specifically mentioned in the text, are shown in Tables S1 and S2 and Figures S2 and S3.

Feeding apparatus morphology

Some examples of allometries on feeding apparatuses (SAG and measurements of the palate, left baleen rack, and baleen plate of males) to CBL are shown in Figure 4. The slopes of SAG were significantly different between species in males ($p < 0.01$), whereas those of SAG, PL, the Inner length

of baleen plate (IL) (L, R), and the Baleen plate width (BW) (L, R) were significantly different between species in females ($p < 0.05$). Male and female Antarctic minke whales had five out of 11 measurements (PW, BRL [L, R], and Outer length of baleen plate [OL] [L, R]) which were proportionally larger than those of common minke whales ($p < 0.01$). In addition to these measurements, five measurements in male whales were significantly larger in Antarctic minke whales ($p < 0.01$). The other measurements on feeding apparatuses of Antarctic minke whales tended to be proportionally larger than those of common minke whales, even though we could not statistically compare the intercepts of these measurements because of the significant difference in slopes between species. The proportional differences in maximum baleen plates were more obvious than those in the palate and baleen rack. The growth rate of feeding apparatuses to CBL was generally higher in Antarctic minke whales as slopes showed greater value; therefore, the interspecific differences in proportion were more distinguishable in adults. The detailed results are shown in Tables S3 and S4 and Figures S4 and S5.

Engulfment capacity

Figure 5 shows the estimated sea water weight of the anterior and posterior parts of the buccal cavity and engulfment capacities of both species and sexes. There was no significant difference in the slopes of all three analyzed items, and intercepts were significantly larger in Antarctic minke whales

for both males and females ($p < 0.01$, Fig. 5 and Table S5). Especially, the interspecific difference in volume of the anterior part was more pronounced than that in volume of the posterior part, even though the estimated volume itself was smaller in the anterior part. We calculated the average engulfment-capacity-to-body-mass ratio of mature animals by dividing the engulfment capacity by the body mass. Antarctic minke whales yielded $66.69 \pm 0.73\%$ (mean $\pm$ SE) and $66.48 \pm 0.75\%$ for males and females, whereas common minke whales yielded $40.11 \pm 0.40\%$ and $42.96 \pm 0.64\%$ for males and females.

Discussion

The skulls of Antarctic minke whales were proportionally larger to BL than those of common minke whales. We compared the proportion of CBL to BL in Antarctic and common minke whales with those in the blue whale, fin whale (*Balaenoptera physalus* Linnaeus, 1758) (Mackintosh and Wheeler 1929), and Bryde's whale (*Balaenoptera edeni* Anderson, 1879) (Kato and Perrin 2009) (Table 5). This shows that the skull proportion of Antarctic minke whales is closer to that of other rorquals, even though both species of minke whales have been regarded as small rorquals.

The measurement point, RW, of Antarctic minke whales was proportionally narrower in both males and females in our study, as previously reported by Zerbini and Simões-Lopes (2000). Omura

(1975) compared the skull morphologies of Antarctic and common minke whales using four individuals (two individuals for each species) without distinguishing the sex. He reported that the rostrum width at the middle, which corresponds to RWm in our study, of Antarctic minke whales is proportionally wider than that of common minke whales. Our results also revealed that Antarctic minke whales tended to show larger RWm than common minke whales, with a significant difference in males. Wider measurements at the rostrum base (RW and MaWb) and narrower measurements at the middle of the rostrum (RWm and MaWm) indicate a sharper rostrum. Interspecific differences in these measurements related to the lateral curvature of the rostrum (Table 3, Fig. 3, Fig. S2, and S3) indicate that the rostra of Antarctic minke whales are curved more laterally than those of common minke whales. Omura (1975) described the rostra of Antarctic minke whales as flat from the lateral view. However, our analysis showed the following contradictory characteristics: Antarctic minke whales have more dorsoventrally curved rostra from the lateral view, indicated by larger RH, ReHb, and ReHm (Table 4, Fig. 3, Figs. S2, and S3). This difference between the two studies could be attributed to the condition of specimens, differences in individuals, and/or the number of samples used by Omura (1975). We investigated photographs of the specimens shown in Omura (1975) and found the distortion of the maxilla, which might arise during the preparation of the specimen. Another possible explanation for the different findings is that the evaluation of rostrum curvature by Omura (1975) was relied only on qualitative visual inspection. Arnold et al. (1987) reported that Antarctic

minke whales had longer rostra than common minke whales; however, the difference between allometries in this study was not as pronounced as they described.

Antarctic minke whales tended to have significantly larger feeding apparatuses (Fig.4, Tables S3, S4, Figs. S4, and S5). Based on analyses that consider sex differences and developmental changes, our findings support the results of Williamson (1959) and Kasuya and Ichihara (1965) that Antarctic minke whales have larger baleen plates. Larger baleen racks and baleen plates of Antarctic minke whales suggest larger filtration area of this species. Kahane-Rapport et al. (2020) calculated engulfment capacity and filtration time using a species-mixed dataset and found that filtration time of larger rorquals increases because larger rorquals have to filter a disproportionately large amount of water to their filtration area. They calculated filtration time using filtration area estimated as a function of BL. In their study, the same proportionality coefficient was adopted for all species. However, interspecific differences in allometries and proportion of baleen measurements to CBL indicated in this study may result in a different proportionality coefficient for the estimation of filtration area and eventually different allometries of filtration time at the species level. It is worth investigating them at the species level, instead of the family level, if an appropriate dataset is available. In this study, a sample size of fewer than 40 baleen plates of common minke whales was smaller than that of the other analyzed measurements and that of Antarctic minke whales. More samples could be helpful to improve accuracy.

Antarctic minke whales have proportionally longer baleen racks and baleen plates than common minke whales. They have dorsoventrally and laterally curved rostra to possess longer baleen racks. The presence of dorsoventrally curved rostra of Antarctic minke whales is also reflected in longer baleen plates. In addition, the proportionally wider PW of Antarctic minke whales would be related to laterally curved rostra. Although many studies have focused on the morphologies of the skull and feeding apparatuses separately, their relationship has not been discussed in detail. Our study indicated that the head region morphology of both species, especially CBL and morphology of rostrum, is strongly related to the morphologies of feeding apparatuses.

Goldbogen et al. (2012) studied the feeding strategies of three rorqual species (blue, fin, and humpback whales [*Megaptera novaeangliae* Borowski, 1781]) using morphological data and data from archival tags, and suggested that engulfment capacity and lunge frequency are important components in their feeding strategies. They indicated that there is a trade-off between lunge frequency and engulfment capacity: lunge frequency decreased in larger rorquals with greater engulfment capacity. Friedlaender et al. (2014) reported the lunge frequency of Antarctic minke whales using archival tags. They considered that Antarctic minke whales would have smaller engulfment capacities, as they showed high lunge frequency. Kahane-Rapport and Goldbogen (2018) compared the engulfment capacity of six rorqual species (blue, fin, sei [*Balaenoptera borealis* Lesson, 1828]), humpback, Bryde's, and minke whales) based on morphometric data. They suggested that minke

whales had smaller engulfment capacities. These two studies considered that the two minke whale species employ the same strategies. However, these inferences require caution because the former study focused only on Antarctic minke whales, whereas the latter study did not distinguish between the two species of minke whales.

Our study revealed that Antarctic minke whales had significantly greater engulfment capacity than common minke whales and showed larger interspecific differences in the volume of the anterior part than that of the posterior part. This indicates that SAG is an especially important parameter that results in the remarkable differences in engulfment capacity. The slopes and intercepts in our study differ from those estimated by Kahane-Rapport and Goldbogen (2018), with smaller slopes and larger intercepts found here for both species. The most likely cause is that Kahane-Rapport and Goldbogen (2018) estimated these values using a dataset that did not distinguish two species. The differences in acquisition method of morphological data and selection of a morphological parameter could also have some influence. We used the actual measured values as parameters, while they used some of the estimated values. Furthermore, we estimated engulfment capacity using SAG instead of the projected length of the mandible. Regardless of these methodological differences, it is noteworthy that the two minke whale species show species-specific engulfment capacity. The engulfment capacity of mature whales was estimated as ~66% of body mass in Antarctic minke whales and ~40–43% of body mass in common minke whales. This result for Antarctic minke whales roughly agrees with the estimated

value reported by Friedlaender et al. (2014). However, there might be some caveat, as they seem to estimate this capacity based on the body length of common minke whales, which may have led to overestimation. Putting together with the results of our morphological study and those of Friedlaender et al. (2014) showing an inverse relationship between engulfment capacity and lunge frequency, it is indicated that Antarctic minke whales might have fewer lunges in a single feeding dive in comparison with common minke whales because the former have greater engulfment capacity than the latter.

Engulfment capacity is an important factor in energy efficiency. A proportionally larger head region, which indicates greater engulfment capacity, generates a higher energetic cost of lunge feeding because drag would be sustained over longer distances (Potvin et al. 2010). Rorquals have different engulfment capacities to ensure energy intake greater than the feeding cost (Goldbogen et al. 2012; Kahane-Rapport and Goldbogen 2018). Larger rorquals (blue and fin whales) prefer to feed on krill (Nemoto 1959, 1970) and target very dense krill schools using massive gulps for high feeding efficiency (Goldbogen et al. 2011, 2012; Kahane-Rapport and Goldbogen 2018) to acquire sufficient energy from prey. Hence, these species have proportionally larger head regions to BL because the proportion of head area directly affects engulfment capacity. In contrast, a proportionally smaller head region is more effective for feeding on larger and more agile prey (Goldbogen et al. 2010).

Antarctic minke whales feed exclusively on the Antarctic krill (*Euphausia superba* Dana, 1850) (Ichii and Kato 1991; Tamura and Konishi 2009). In contrast, common minke whales are opportunistic

429 feeders known to feed on a variety of prey species. They feed on schooling small pelagic fishes such
430 as the Japanese anchovy (*Engraulis japonicus* Temminck and Schlegel, 1846), Pacific saury
431 (*Cololabis saira* Brevoort, 1856), and krill in the western North Pacific (Tamura and Fujise 2002;
432 Murase et al. 2007; Konishi et al. 2009). Notably, krill fed on by common minke whales in the western
433 North Pacific is smaller than Antarctic krill in terms of body size. Although common minke whales
434 feed on a variety of prey species, Murase et al. (2007) reported that common minke whales tend to
435 select Japanese anchovy and avoid krill. Small pelagic fishes occupy an intermediate trophic level,
436 and Antarctic krill play a similar role in the ecosystem of the Southern Ocean in the absence of these
437 fishes (Essington and Munch 2014). The school size of Antarctic krill is generally larger than that of
438 small pelagic fishes, although their roughness (surface-area-to-volume ratios of school) are similar
439 (Brierley and Cox 2010). Our study showed that the skulls of Antarctic minke whales were remarkably
440 larger to BL than those of common minke whales. Antarctic minke whales have proportionally larger
441 feeding apparatuses (i.e., baleen, palate, and SAG) and distinguishable skull morphology from
442 common minke whales, which is related to the morphology of the feeding apparatuses. All these
443 morphologies give Antarctic minke whales greater engulfment capacity, and thus, they could have
444 lower lunge frequency than common minke whales. The greater engulfment capacity of Antarctic
445 minke whales could be suitable for feeding on Antarctic krill, which forms larger schools in
446 comparison with small pelagic fishes. Our study indicated that morphological differences could be

related to the differences in prey species, even between close species.

The fact that two closely related species have different morphologies is also noteworthy from an evolutionary biology perspective. Antarctic and common minke whales are closely related species and are estimated to have diverged in the Southern Hemisphere 4.7 million years ago (Pastene et al. 2007). Adaptive radiation to the Northern Hemisphere could be related to the acquisition of new prey niches by common minke whales (e.g., small pelagic fishes as prey). Common minke whales would have experienced morphological differentiation through natural selection, which eventually resulted in speciation. The availability of prey could be a driver of speciation.

We confirmed that there were significant differences in the morphologies of skulls and feeding apparatuses between Antarctic and common minke whales with a large number of samples covering a wide range of body lengths of both sexes. Moreover, our study clarified the difference in the engulfment capacities between Antarctic and common minke whales, which had been considered to be similar. These differences could be reflected in their feeding ecology and, hence, change their feeding strategies.

The expansion rate of the ventral grooves and tongue volume of these two species, which could also be related to engulfment capacity, are yet to be examined. These apparatuses may alter the engulfment capacity estimated in this study. The taxonomy of the minke whale clade is complex. Although this study focused on morphological differences between Antarctic and common minke

whales at the species level, it could be beneficial to study the morphology of minke whales at lower taxonomic levels (i.e., subspecies and stocks) in the future. There is no observation of feeding behavior of common minke whales using archival tags to date; such observations of Antarctic minke whales are also limited in number. Further research on the feeding strategies of these two species should be conducted in combination with morphological and behavioral studies, although feeding strategies of rorquals have tended to be investigated separately (e.g., either behavior or morphology). Because feeding strategies consist of multiple dimensions, integrative approaches are necessary to understand the whole picture. Evaluation of the feeding performance landscape in multiple dimensions, such as kinematics, morphology, and prey in a model (e.g., Olsson et al. 2020), is one of the possible approaches to address this question.

Acknowledgments

We are grateful to all personnel involved in the field surveys who participated and contributed to the sampling for this study. This study was supported by the Institute of Cetacean Research, Japan Fisheries Research and Education Agency, and the Fisheries Agency of Japan. We thank Dr. Hideyoshi Yoshida (Fisheries Resources Institute, Japan Fisheries Research and Education Agency) for helping with sampling and Dr. Takashi Hakamada and Dr. Genta Yasunaga (Institute of Cetacean

Research) for their advice on statistical analyses. The work of Futaba Nishimura was partially supported by the Moritani Scholarship Foundation and the Nakato Scholarship Foundation. We also thank anonymous reviewers for insightful comments to improve the manuscript.

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Figure captions

Fig. 1. Sighting locations of Antarctic minke whales (*Balaenoptera bonaerensis* Burmeister, 1867) and common minke whales (*Balaenoptera acutorostrata* Lacépède, 1804) used in this study (i) and ii), respectively). The circles and triangles indicate Antarctic and common minke whales, and black and white symbols indicate males and females, respectively. a) Overview of survey area off Japan, b) off Abashiri, c) off Kushiro, d) off Hachinohe, and e) off Ayukawa. Star symbols are Abashiri, Kushiro, Hachinohe, and Ayukawa port, respectively. The map of the Antarctic Ocean (i)) was made using ArcGIS version 10.7 (ESRI, Redlands, CA, USA) with data from the SCAR Antarctic Digital Database (Gerrish at al. 2021). Geographic coordinate system is WGS 1984 while projection coordinate system is in the South Pole Polar Stereographic projection with central meridian at 180° and latitude of origin at 71°S. The map off Japan (ii)) was made in QGIS version 3.16 with a base map from Natural Earth (Patterson and Kelso 2021). Geographic coordinate system is WGS 1984 while projection coordinate system is global default projection.

Fig. 2. Measurement points in this study. a) and b) Dorsal view of the skull, c) left-side view of the skull, d) transverse section at the rostrum base, e) transverse section at the middle of the rostrum length, f) measurements of the Snout to angle of gape and the Length of the ventral grooves (broken

line shows the body axis), g) ventral view of the palate, h) left baleen rack, and i) left maximum baleen plate. Measurements of paired bone or apparatuses are shown left or right side only, even though both sides were measured. The numbers in the figure corresponds to Table 1.

Fig. 3. Allometries of skull measurements to the Condylbasal length (CBL) in male whales. The black circles and white triangles indicate Antarctic minke whales (*Balaenoptera bonaerensis* Burmeister, 1867) and common minke whales (*Balaenoptera acutorostrata* Lacépède, 1804), respectively. Solid and broken lines are the estimated growth lines of Antarctic and common minke whales, respectively. These lines with species-specific slopes and intercepts were estimated using the Standardized Major Axis (SMA) Tests and Routines (“smatr”) package. “Antarctic” or “Common” at the lower right indicates the proportionally larger species. **: $p < 0.01$, *: $p < 0.05$ in the comparison of intercepts.

Fig. 4. Allometries of feeding apparatuses to the Condylbasal length (CBL) in male whales. The black circles and white triangles indicate Antarctic minke whales (*Balaenoptera bonaerensis* Burmeister, 1867) and common minke whales (*Balaenoptera acutorostrata* Lacépède, 1804),

respectively. Solid and broken lines are the estimated growth lines of Antarctic and common minke whales, respectively. These lines with species-specific slopes and intercepts were estimated using the Standardized Major Axis (SMA) Tests and Routines (“smatr”) package. “Antarctic” or “Common” at the lower right indicates the proportionally larger species. **: $p < 0.01$, *: $p < 0.05$, and -: without the comparison of intercepts because of the differences in slopes between two species.

Fig. 5. Allometries of engulfment capacity to the Body length (BL) in male (upper) and female (lower) whales. The black circles and white triangles indicate Antarctic minke whales (*Balaenoptera bonaerensis* Burmeister, 1867) and common minke whales (*Balaenoptera acutorostrata* Lacépède, 1804), respectively. Solid and broken lines are the estimated growth lines of Antarctic and common minke whales, respectively. These lines with species-specific slopes and intercepts were estimated using the Standardized Major Axis (SMA) Tests and Routines (“smatr”) package. “Antarctic” or “Common” at the lower right indicates the proportionally larger species. **: $p < 0.01$, *: $p < 0.05$ in the comparison of intercepts.

Table 1. List of measurements.

No.	Term	Abbreviation	Measurement point
1	Condylobasal length	CBL	Condylobasal length
2	Rostrum width	RW	Rostrum width at the rostrum base
3	Rostrum width at the middle	RWm	Rostrum width at the middle of the rostrum length
4	Rostrum length	RL	Rostrum length
5, 6	Premaxilla length (L, R)	PmL (L, R)	Premaxilla length (L, R)
7, 8	Maxilla length (L, R)	MaL (L, R)	Maxilla length (L, R)
9	Rostrum height	RH	Rostrum height at the highest point
10	Rostrum width at the highest point	RWh	Rostrum width at the highest point of the rostrum
11	Premaxilla to the highest point	PmH	Tip of the premaxilla to the height point of the rostrum
12	Rostrum thickness at the base	RTb	Rostrum thickness at the rostrum base
13	Rostrum edge height at the base	ReHb	Inferior margin of vomer to the maxilla edge at the proximal region at the rostrum base
14, 15	Maxilla width at the base (L, R)	MaWb (L, R)	Maxilla width at the ventral aspect at the rostrum base (L, R)
16	Rostrum thickness at the middle	RTm	Rostrum thickness at the middle of the rostrum length
17	Rostrum edge height at the middle	ReHm	Inferior margin of vomer to the maxilla edge at the proximal region at the middle of the rostrum length
18, 19	Maxilla width at the middle (L, R)	MaWm (L, R)	Maxilla width at the ventral aspect at the middle of the rostrum length (L, R)
20	Greatest width of the skull	GWS	Greatest width of the skull
21	Skull height	SH	Skull height
22	Snout to angle of gape	SAG	Tip of the snout to the angle of gape measured parallel to the body axis
23	Palate length	PL	Palate length
24	Palate width	PW	Palate width
25, 26	Baleen rack length (L, R)	BRL (L, R)	Distance between the most anterior and the most posterior elements of the baleen rack measured in a straight line parallel to the axis of the baleen rack (L, R)
27, 28	Outer length of baleen plate (L, R)	OL (L, R)	Outer length of maximum baleen plate (L, R)
29, 30	Inner length of baleen plate (L, R)	IL (L, R)	Inner length of maximum baleen plate (L, R)
31, 32	Baleen plate width (L, R)	BW (L, R)	Maximum baleen plate width (L, R)
33	Length of the ventral grooves	LVG	Tip of the snout to the end of the ventral grooves measured parallel to the body axis

Table 2. Slopes and intercepts of allometric equations converted to logarithmic forms and interspecific differences in the Condylbasal length (CBL) and the Greatest width of the skull (GWS) to the Body length (BL). r^2 : adjusted R-square, n : number of specimens, **: $p < 0.01$, *: $p < 0.05$, n.s.: non-significant, -: without the comparison of intercepts because of the differences in slopes between two species.

	Measurement	Antarctic minke whale (<i>Balaenoptera bonaerensis</i> Burmeister, 1867)				Common minke whale (<i>Balaenoptera acutorostrata</i> Lacépède, 1804)				Interspecific difference	
		Slope	Intercept ^a	r^2	n	Slope	Intercept ^a	r^2	n	Slope	Intercept ^b
male	CBL	1.001	-1.340	0.98	27	0.938	-1.466	0.96	129	*	-
	GWS	1.080	-2.112	0.96	27	1.019	-2.230	0.97	129	n.s.	**
female	CBL	0.987	-1.301	0.97	33	0.942	-1.435	0.98	119	n.s.	**
	GWS	1.066	-2.125	0.97	33	1.043	-2.256	0.98	118	n.s.	**

^a: The intercept of the logarithmic equation with the common slope to two species.

^b: Interspecific difference in the intercepts of the logarithmic equations with the common slope to two species.

Table 3. Interspecific differences in allometric intercepts of the measurements related to lateral curvature of the rostrum. **: $p < 0.01$, *: $p < 0.05$, n.s.: non-significant. Positive or negative sign shows the result of the difference between the intercepts of two species (+; common minke whales have a larger intercept, -; Antarctic minke whales have a larger intercept). No. in this table corresponds to Table 1 and Fig. 2. No. 2, 14, and 15 are measurements at the rostrum base, and No. 3, 18, and 19 are measurements at the middle of the rostrum length. RW; Rostrum width, MaWb; Maxilla width at the base, RWm; Rostrum width at the middle, MaWm; Maxilla width at the middle. All measurements were analyzed as the dependent variable of the Condylbasal length (CBL).

		Antarctic minke whale (<i>Balaenoptera bonaerensis</i> Burmeister, 1867)					Common minke whale (<i>Balaenoptera acutorostrata</i> Lacépède, 1804)				Interspecific difference in intercept	
	No.	Measurement	Slope	Intercept ^a	r ²	n	Slope	Intercept ^a	r ²	n	p-value ^b	Sign
Male												
Base	2	RW	1.034	-1.630	0.96	27	1.105	-1.597	0.97	128	**	+
	14	MaWb (L)	1.132	-2.339	0.95	50	1.054	-2.341	0.92	32	n.s.	
	15	MaWb (R)	1.116	-2.301	0.95	50	1.074	-2.315	0.94	32	n.s.	
Middle	3	RWm	1.062	-2.042	0.96	23	1.090	-2.065	0.94	128	*	-
	18	MaWm (L)	1.289	-3.696	0.95	37	1.248	-3.768	0.93	29	**	-
	19	MaWm (R)	1.204	-3.319	0.95	40	1.203	-3.408	0.93	32	**	-
Female												
Base	2	RW	1.031	-1.593	0.96	33	1.094	-1.559	0.97	119	**	+
	14	MaWb (L)	1.151	-2.473	0.96	42	1.109	-2.470	0.97	28	n.s.	
	15	MaWb (R)	1.152	-2.500	0.96	43	1.122	-2.498	0.98	28	n.s.	
Middle	3	RWm	1.135	-2.433	0.93	32	1.167	-2.447	0.95	116	n.s.	
	18	MaWm (L)	1.390	-4.134	0.92	38	1.350	-4.187	0.98	31	**	-
	19	MaWm (R)	1.333	-3.941	0.92	38	1.322	-4.006	0.98	31	**	-

a: The intercept of the logarithmic equation with the common slope to two species.

b: Interspecific difference in the intercepts of the logarithmic equations with the common slope to two species.

Table 4. Interspecific differences in allometric intercepts of the measurements related to dorsoventral curvature of the rostrum. **: $p < 0.01$, *: $p < 0.05$, n.s.: non-significant, -; without the comparison of intercepts because of the significant difference in slopes between two species. Positive or negative sign shows the result of the difference between the intercepts of two species (+; common minke whales have a larger intercept, -; Antarctic minke whales have a larger intercept). No. in this table corresponds to Table 1 and Fig. 2. RH; Rostrum height, ReHb; Rostrum edge height at the base, ReHm; Rostrum edge height at the middle. All measurements were analyzed as the dependent variable of the Condylbasal length (CBL).

No.	Measurement	Antarctic minke whale (<i>Balaenoptera bonaerensis</i> Burmeister, 1867)				Common minke whale (<i>Balaenoptera acutorostrata</i> Lacépède, 1804)				Interspecific difference in intercept	
		Slope	Intercept ^a	r ²	<i>n</i>	Slope	Intercept ^a	r ²	<i>n</i>	<i>p</i> -value ^b	Sign
Male											
9	RH	1.295	−3.654	0.96	26	1.362	−3.820	0.96	36	**	—
13	ReHb	1.394	−4.943	0.83	49	1.718	−5.210	0.45	32	**	—
17	ReHm	1.266	−4.717	0.66	39	1.389	−5.028	0.66	31	**	—
Female											
9	RH	1.250	−3.248	0.95	33	1.268	−3.459	0.94	32	**	—
13	ReHb	1.389	−5.648	0.84	42	1.866	−5.821	0.86	28	-	-
17	ReHm	1.414	−5.302	0.69	38	1.442	−5.559	0.86	31	**	—

^a: The intercept of the logarithmic equation with the common slope to two species.

^b: Interspecific difference in the intercepts of the logarithmic equations with the common slope to two species.

Table 5. Interspecific comparison of the Condylbasal length (CBL) proportion to the Body length (BL).

Species	Proportion of CBL to BL (%)	
	Male	Female
Antarctic minke whale ^a (<i>Balaenoptera bonaerensis</i> Burmeister, 1867)	24.05 ± 0.16	24.53 ± 0.19
Common minke whale ^a (<i>Balaenoptera acutorostrata</i> Lacépède, 1804)	21.07 ± 0.12	21.46 ± 0.14
Blue whale ^b (<i>Balaenoptera musculus</i> Linnaeus, 1758)	23.82 – 24.81	24.26 – 24.93
Fin whale ^b (<i>Balaenoptera physalus</i> Linnaeus, 1758)	24.69 – 25.63	24.87 – 25.85
Bryde's whales ^c (<i>Balaenoptera edeni</i> Anderson, 1879)	24.1 – 25.8	

a: This study. Mean ± SE in mature animals.
b: Mackintosh and Wheeler (1929)
c: Kato and Perrin (2009)

i)

ii)

180x224mm (600 x 600 DPI)

177x235mm (600 x 600 DPI)

101x113mm (600 x 600 DPI)

136x105mm (600 x 600 DPI)

Male

Female

136x125mm (600 x 600 DPI)