GROWTH-RELATED CHANGES IN CRANIUM OF KILLER WHALES IN THE WESTERN NORTH PACIFIC

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Abstract

One of the crucial questions for using the skull morphology for classification purposes in cetaceans is whether the skull features have growth-dependent differences. This question was addressed by examining cranial specimens collected from killer whales in different localities of the western North Pacific. The present study is the first to investigate developmental change in the skull morphology of western North Pacific killer whales. A total of 24 cranial measurement characters were examined from 22 animals collected between 1937 and 2011. Two kinds of analyses were conducted 1) the relationships between body length (BL) and cranium length (condylobasal length CBL), and 2) between CBL and each measurement character. For these analyses, an allometric equation was used. The relationship between BL and CBL showed a negative growth pattern, consistent with previous studies in delphinid species. The length of the lacrimal bone and the width of the internal nasal cavity showed isometric change. Therefore, these characters can be used as criteria for sex and/or species/subspecies classification as their proportions are free from relative change with respect to skull growth in CBL. Regarding ontogenic growth, this study showed that the anteroposterior length of the temporal fossa, the zygomatic process and the space where the temporal muscle passes became proportionally larger as their skull grows. The development and activity of temporal muscles would produce these changes. On the morphometric features involved in the generation and modification of acoustic signals, this study found the following changes: the width of the posterior regions of the rostrum and preorbital bone became wider; the ventral surface of the preorbital process became thick and sturdy, and the maxillary crest became more apparent with the skull growth. Therefore, these morphometric features might be used to characterize species/subspecies of the killer whales, which have highly divergent foraging behavior and vocalization.

Key words: killer whale, skull morphology, growth-related change, western North Pacific.

Introduction

The skull is an anatomical feature that consistently and compellingly displays species-specific characteristics and is an essential tool to study morphological differentiation (Miyazaki, 1994). Hence, the skull size and shape can be essential as classification criteria. Studies on small cetaceans showed that the shape and size of the skull could provide information on geographical distribution of the species, intraspecific subpopulations with different ecological characteristics such as feeding ecology and acoustic properties, and social behavior, e.g., Van Waerebeek (1993), Yoshida *et al.* (1995), Galatius and Gol'din (2011), Costa *et al.* (2016). Kitchener *et al.* (1990) studied the skull morphology of false killer whale *Pseudorca crassidens* from three ocean basins, Australia (n=34), Scotland (n=58), and South Africa (n=53), showing considerable divergence among localities, including sexual dimorphism in the skull morphology. They considered this helpful information for the conservation and management of the species.

Comparative analyses of skull morphology require large sample sizes; however, the availability of samples and data for such studies is limited for most cetacean species, including the killer whales *Orcinus orca*. Killer whales are distributed throughout all oceans and contiguous seas, from equatorial regions to the polar pack-ice zones. Still, they are most numerous in coastal waters and cooler areas where productivity is high (Rice, 1998). Their wildly divergent diet preferences, cultural practices, and external morphological characteristics seem incongruent with their current categorization as a single taxon (Heyning and Dahlheim, 1988; Pitman and Ensor, 2003; Foote *et al.*, 2009; Morin *et al.*, 2010; Pitman *et al.*, 2011). Resident, transient and offshore killer whale ecotypes have been well characterized since the 1980s in the eastern North Pacific (Bigg *et al.*, 1990).

Further west of the North Pacific, a report identified multiple killer whale subpopulations throughout the Aleutian Islands: one subpopulation in the eastern and one in the central Aleutian Islands, and a third subpopulation ranging from the western Aleutians to Kamchatka and the Kuril Islands, Russia (Parsons *et al.*, 2013). Recent colonization/re-colonization of the western North Pacific by small groups of killer whales originating from the central/eastern North Pacific has been suggested (Filatova *et al.*, 2018). Although the information on this species around Japan is limited, catch records between 1948 and 1957 indicated killer whales were distributed in the coastal waters off Japan from Hokkaido to the Okinawan islands. Researches in different oceans have revealed the existence of sympatric populations displaying morphological, dietary, and genetic diversification e.g., in the Antarctic (Pitman and Ensor, 2003; LeDuc *et al.*, 2008) and the North Atlantic oceans (Foote *et al.*, 2009, 2010; Morin *et al.*, 2010). Currently, the taxonomic status of killer whales is undergoing scrutiny and possible revision (Krahn *et al.*, 2004; LeDuc *et al.*, 2008; Morin, 2010; Bruyn *et al.*, 2013).

One important question for using the skull morphology for classification purposes is whether the skull features have a nature of growth-dependent differences. In the present study, this question was addressed by examining cranial specimens of killer whales collected from different localities in the western North Pacific. This study is the first one to investigate a developmental change in the skull morphology of killer whales.

Materials and methods

Samples

The list of samples used in the present study is shown in Table 1. Skull samples of killer whales were available from different museums, aquariums and other institutions in Japan. Killer whales were from different localities of the Pacific coast of Japan, the Okhotsk Sea, and around the Okinawan Islands. A total of 22 skulls of killer whales (seven females, eight males, and seven individuals with no sex information) were available. Body length information was available for 14 whales.

Morphometric feature

Cranial measurements are given in Table 2. Crania were measured in a straight line using an anthropometer to the nearest 0.1 cm. We did not include the mandible bone in this study because it was lost in several individuals. A total of 24 measurements was used in the statistical analysis (Table 2, Fig. 1). Most of those measurements have been used previously in taxonomic and population identity studies of Delphinidae species (Perrin, 1975; Kitchener *et al.*, 1990). In this study the measurements were identified using the prefix 'Vx' (see Table 2). The body length and sex information were obtained from each museum, aquarium or university storing a specimen when possible. The observation of genital organs determined sex.



Fig. 1. Killer whale *Orcinus orca* cranial measurement points. A: Dorsal view of the cranium, B: ventral view,C: lateral view, and D: posterior view. Measurement points were determined following Perrin (1975) and Kitchener *et al.* (1990) and are abbreviated according to Table 2.

Statistical analysis

The relationships between body length and skull length, and between skull length and each length measurement were examined using the following allometric equation:

$$y = \beta x^{\alpha} \tag{1}$$

where x is body/skull length, y is skull length/each length measurement, β is the intercept of the line on the y-axis, and α is the slope of the line, also known as the allometric coefficient. The allometric coefficients (α) at each measurement site were examined using a t-test for classification of three different growth patterns: positive allometry (α significantly greater than 1), isometric allometry, and negative allometry (α significantly smaller than 1). Analyses by sex were not conducted because of the limited number of whales with identified gender. Although the range of sampling years was vast, we treated them as one sample collection because of the limited number of specimens available.

Results

Relationship between body length (BL) and skull length (condylobasal length CBL)

The relationship between BL and CBL (Fig. 1) was examined in a subset of 14 killer whale samples for which body length data were available. The BLs in these whales ranged from 218 cm to 785 cm, which had CBLs of 43.8 cm and 121.7 cm, respectively (samples No. 15 and 8, respectively in Table 1). The CBL showed a negative growth pattern ($y=-0.37x^{0.78}$, P<0.001) (Fig. 2), indicating that CBL growth is relatively slower than that of BL.

Relationship between skull length (CBL) and other cranial measurements

Table 2 shows the results of the allometric analyses for the relationship between CBL and each cranial measurement (see also Appendix).

Skull width, rostral length and width

Four of the five skull width characters (V5, V6, V12, and V13 in Fig. 1 and Table 2) showed a positive growth pattern, though the width at the tip of the antorbital process of the maxilla (V18) was isometric. The rostral width characters (V2–4 and V19) also exhibited positive allometry with the growth of CBL (Table 2). These results showed the braincase becoming relatively shorter, the rostral length

Sample no.	Sex	BL (cm)	CBL (cm)	Age	Location	Year obtained	Sample ID	Sample holder	
1	F	547	98.5	_	East China Sea, Okinawa	1988	M67 (nago-B)	Nago Museum	
2	F	600	99.2	17*	Nemuro Strait, Rausu	2005	kaitaku-AKW6	Hokkaido Museum	
3	F	654	108.6	29*	Nemuro Strait, Rausu	2005	rakuno-AKW9	Rakuno Gakuen University	
4	F	614	103.8		Pacific Ocean, Kii Peninsula, Taiji	2008	1.2.7	Port of Nagoya Public Aquarium	
5	F	589	99.7	>28**	Pacific Ocean, Kii Peninsula, Taiji	2011	Taiji-6	Taiji Whale Museum	
6	F	563	98.3	13*	Nemuro Strait, Rausu	2005	AMP-R20- AKW2	Ashoro Museum of Paleontology	
7	F	550	99.8		Okinawan Island, Japan	1994	SUM071	Okinawa Churashima Foundation	
8	М	785	121.7	—	Seto Inland Sea, Hyogo	1957	Suma-K01	Suma Aqualife Park	
9	М	700	110.7		East China Sea, Okinawa	1988	M66 (nago-A)	Nago Museum	
10	М	704	118.2	—	Soya Strait, Wakkanai	2010	SNH10057	Okhotsk Museum Esashi	
11	М	660	107.9	—	Pacific Ocean, Kii Peninsula, Taiji	1978	Taiji-2	Taiji Whale Museum	
12	М		122.0		Okhotsk, Sakhalin Island, Gulf of Patience	1937	KPM- NF1002979	Kanagawa Prefectural Museum of Natural History	
13	М	690	120.6	—	Pacific Ocean, Kii Peninsula, Taiji	1966	Taiji-1	Taiji Whale Museum	
14	М	410	85.1	—	Boso Peninsula, Japan		O-15	Tobayama's Cetacean Collection/TUMSAT***	
15	М	218	43.8		Boso Peninsula, Japan		O-11	Tobayama's Cetacean Collection/TUMSAT***	
16	Uk	—	96.5	—	Toyokoro-cho, Hokkaido, Japan	2005	AMP-R26	Ashoro Museum of Paleontology	
17	Uk		96.2	—	Taiki-cho, Hokkaido, Japan	2005	AMP-R27	Ashoro Museum of Paleontology	
18	Uk	_	104.2		Japan		ICR-001	Institute of Cetacean Research	
19	Uk		106.8		Kii Peninsula, Japan		Taiji-3	Taiji Whale Museum	
20	Uk		104.9		Kii Peninsula, Japan		Taiji-4	Taiji Whale Museum	
21	Uk		103.4		Kii Peninsula, Japan		Taiji-5	Taiji Whale Museum	
22	Uk		104.6	—	Okinawan Island, Japan		Okinawa-1	Okinawa Churashima Foundation	

 Table 1.
 List of specimens of the killer whales from western North Pacific examined in this study, by sex, age, and locality of sampling. Body length (BL) and skull (condylobasal) length (CBL) are also shown.

*: Age information quoted from Amano et al. (2011).

**: Rearing period.

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(V1) somewhat longer, and the braincase width relatively more comprehensive (Fig. 3). The zygomatic process of the squamosal bone became laterally more protrusive with CBL growth, in qualitative observation, as the space where the temporal muscle passes (the ventrolateral opening of the temporal fossa) was getting more enlarged compared to those of the newborn calf (Fig. 4).

Braincase

In this study, the braincase was defined as the regions directly covering the brain, including the frontal, maxilla, premaxilla, ethmoid, sphenoid, squamosal, parietal, interparietal and occipital bones (Uekusa *et al.*, 2018). The measurements indirectly describing the braincase size (V22, V23, and V24) showed negative allometry or isometry, though the length of squamosal (V14), which is not directly

Region	Site no.	Measurement character		Based on condylobasal length (CBL)		<i>P</i> - value [†]	Relative growth pattern	Adj. R square
	-			α	lnβ			
Skull width	V13	Greatest width of skull	22	1.13	-1.04	**	positive	0.99
	V5	Greatest preorbital width	22	1.18	-1.44	**	positive	0.97
	V6	Least supraorbital width	22	1.24	-1.75	**	positive	0.98
	V12	Greatest width of maxillaries	21	1.34	-2.19	**	positive	0.91
	V18	Width at tip of anterior process of maxilla	21	1.31	-2.14	0.075	isometry	0.76
Rostral length	V1	Length of rostrum	22	1.13	-1.23	*	positive	0.98
and width	V2	Width of rostrum at base	22	1.28	-2.49	**	positive	0.98
	V3	Width of rostrum at 60 mm anterior to the base of rostrum	21	1.35	-2.78	**	positive	0.89
	V4	Width of premaxillaries at midlength of rostrum	22	1.59	-4.93	**	positive	0.91
	V19	Width of rostrum at 3/4 length, measured from posterior end	20	1.91	-5.81	**	positive	0.93
Braincase	V22	Greatest parietal width at the posterior section of the frontal	21	0.75	0.14	*	negative	0.75
	V23	Greatest occipital width within temporal fossa	20	0.95	-0.76	0.795	isometry	0.54
	V24	Height of skull	11	1.15	-1.52	0.458	isometry	0.79
	V14	Length of zygomatic process of squamosal (right)	22	1.28	-2.95	**	positive	0.98
Temporal fossa	V8	Greatest length of right temporal fossa, measured to external margin of raised suture	22	1.20	-2.01	**	positive	0.97
	V9	Greatest width of right temporal fossa at right an- gles to greatest length	21	1.07	-1.91	0.744	isometry	0.57
	V15	Anteroposterior diameter of the ventrolateral opening of the right temporal fossa	20	1.35	-3.37	*	positive	0.87
	V16	Lateral diameter of the ventrolateral opening of the right temporal fossa	21	1.40	-3.60	0.054	isometry	0.72
Nasal area	V7	Greatest width of external nares	21	0.85	-1.27	0.398	isometry	0.55
	V20	Greatest width of internal nares	20	0.95	-1.52	0.32	isometry	0.95
	V21	Distance from foremost end of junction between nasals to hindmost point of margin of supraoc- cipital crest	19	0.76	-1.19	0.08	isometry	0.65
Orbital region	V10	Length of right orbit from apex of preorbital pro- cess of frontal to apex of postorbital process	22	0.53	0.08	**	negative	0.70
	V11	Length of antorbital process of right lacrimal	22	1.17	-3.12	0.307	isometry	0.72
	V17	The antorbital process thickness: the distance from the ventral surface of the lacrimal to the dorsal surface of the maxilla (right-side)	21	1.84	-5.90	* *	positive	0.79

 Table 2. Relative growth coefficients and growth patterns of each killer whale skull region.

[†]: The significance of deviation of each relative coefficient from a value of 1 (*: P < 0.05, **: P < 0.01).

related to the braincase size, showed positive allometry (Table 2). According to qualitative observations, the parietal bones in the newborn calf's temporal crest were laterally curved convex in posterior view, and the greatest parietal width within the temporal fossa was wide as long as the greatest width of the skull (Fig. 3). However, the temporal surface of the parietal bones concavely curved with CBL growth and development of the temporal crest.

Temporal fossa

The anteroposterior length (V8) and the dorsoventral width (V9) of the temporal fossa showed positive allometry and isometry, respectively (Table 2). Hence, the temporal fossa size became rela-



Fig. 2. Relationship between body length and condylobasal length (CBL). Black and white circles indicate males and females, respectively. The solid line indicates the prediction line from allometry analysis.

tively broader with CBL growth (i.e., horizontally with a long, elliptic shape) (Fig. 4). In qualitative observations, the dorsal and lateral views of the skulls showed that the posterior ends of the temporal crest are located far anterior to the posterior end of the occipital condyles in the newborn calf (Fig. 3). However, along with the growth of the CBL, the posterior ends of the temporal crest were extended in a posterior direction, and the crest of the temporal fossa clearly developed, becoming thick and conspicuously ridged.

The anteroposterior diameter (V15) and the lateral diameter (V16) of the ventrolateral opening border of the temporal fossa showed positive allometry and isometry, respectively. These growth patterns represented an extension of the space where the temporal muscle passes (Fig. 4). The posterior view of the skull clearly showed the development of the temporal crests and an exoccipital and squamosal extension with CBL growth (Fig. 3).



Fig. 3. Dorsal (upper) and posterior (lower) view of four male killer whale crania. Condylobasal length (CBL) and width of these crania scaled to the actual length.

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Fig. 4. Ventral (upper), diagonally right rear (middle) and lateral (lower) views of the newborn calf and adult killer whale cranium. Orange arrows show the measurement points of the ventrolateral opening border of the temporal fossa, which consists of the zygomatic process of the squamosal bone posteriorly and the postorbital process of the frontal bone anteriorly (V15 and V16 in Table 2 and Fig. 1). Orange shades cover the estimated area where the temporal muscle is attached.

Nasal area

The width of the nares (V7 and V20) and the anterior junction of nasal to posterior margin of supraoccipital crest length (V21) displayed isometry (Table 2). According to qualitative observations, the adult animals' nasal and surrounding areas (frontal, parietal, and occipital bones) were particularly protruded in a dorsal direction, which differed from those of the newborn calf (Fig. 4). Frontal and intraparietal bones were hardly visible as they were covered by maxillary and supraoccipital bones.

Orbital region

The orbit length from the apex of the preorbital process of the frontal bone to the apex of the postorbital process, represented by V10, exhibited negative allometry (Table 2). The antorbital process thickness defined as the distance from the ventral surface of the lacrimal to the dorsal surface of the maxilla (V17) indicated positive allometry (Table 2). The relative length of the antorbital process of the lacrimal bone (V11) showed isometry with CBL growth, and it was thick and sturdy throughout the growth of a newborn into an adult whale (Fig. 4). The surface of the antorbital process, represented by the maxilla bone, remarkably developed in a dorsal direction.

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Discussion

Relationship between CBL and BL

The ratio of CBL to BL of killer whales declined with growth, and negative allometry was detected (Fig. 2). According to previous studies, the growth rate of some delphinid species' skull decreases with growth, and they stop growing when their BL reaches a plateau at a certain age (Perrin, 1975; Ito and Miyazaki, 1990; Kitchener *et al.*, 1990; Miyazaki and Amano, 1994). Therefore, the results of the present study agree with those previous studies. Differences in physical maturity of BL between sexes are known in some whale species (e.g., short-finned pilot whale *Globicephala macroryhnchus* (Miyazaki, 1990), false killer whale *Pseudorca crassidens* (Baird, 2002; Ferreira *et al.*, 2014)). Killer whales exhibit a difference in size according to sex (adult males are longer than females). Sexual dimorphism (especially in external morphology) is evident in the killer whales. For example, profound sexual dimorphism was observed in the dorsal fin and flipper size (males have larger structures) (Heyning and Dahlheim, 1988). Therefore it is expected that such sex differences in the relationship between CBL and BL also occur in the killer whales, and future studies should consider comparisons between females and males.

Utility of skull measurements as classification criteria

Isometric changes in some particular skull measurements mean that such measurements can be employed as criteria for sex and/or species/subspecies classification as they are not affected by changes in the skull size. While other measurements also showed an isometric character, the authors consider that the best candidates to be used as taxonomical classification criteria are the lacrimal bone length (V11) and the width of the internal nasal cavity (V20) because these measurements showed isometry (Table 2).

Lacrimal bone length (V11)

The proportion of V11 to the CBL did not change from newborn calf to adult, thus showing that it might be helpful for sex prediction analysis in all age stages. A previous study that used only adult killer whales from the western North Pacific reported that the lacrimal bone length was useful for sex prediction in this species (Takahashi *et al.*, 2019). The study used linear discriminant analysis and a Random forest algorithm. However, the authors recommended caution in interpreting their results as the true sexual dimorphism for the population because the number of samples used in the study was limited. The present study used a comparatively larger sample size, adding calf killer whales and gaining results to support this measurement character's utility for classification criteria: e.g., sex classification. Kitchener *et al.* (1990) reported a significant difference in this measurement between sexes in the false killer whale *P. crassidens*. This would be collateral evidence supporting our results. Therefore, we conclude that the killer whale lacrimal bone length might be useful for sex prediction regardless of specimen age.

Width of the internal nasal cavity (V20)

The width of the internal nasal cavity presented an isometry pattern with a high adjusted R square value (>95%). This measurement character might be used as novel criterion to discriminate species and subspecies of killer whales because 1) the measurement presented a low individual variance, and 2) the proportion of the measurement never changes with growth. Point 2) makes possible that all available samples can be used for discriminatory purposes. With larger sample sizes, this measurement character might be helpful to discriminate between sexes as well.

Maturity and sex information are usually used in studies on taxonomy based on morphometry. The body shape (not only the skull shape) of immature animals usually differs from that of mature animals. Such studies require a considerable number of samples to deal with several factors (e.g., sex, maturi-

ty). However, materials of this kind are hard to obtain in cetaceans. For this reason, the information on growth-independent changes of some skull measurements in the present study is essential for future taxonomical studies of the killer whales.

Effect of ontogenetic growth on cranial shape

The allometry of the cranium of the killer whale was examined to clarify the effects of size (i.e., ontogenic growth) on cranium shape. Only the width at the posterior section of the frontal bone (V22) showed clearly negative allometry, although other features related to skull width (e.g., V13) showed positive allometry. The analyses suggest that the upper maxillaries width (V12) indicates negative allometry while it represents the dorsal part of the braincase, i.e., it is restricted by the brain size. In contrast, the skull width (V13) and the horizontal diameter of temporal fossa proper (V16), which are not determined by brain size, showed positive allometry, creating space for the temporal muscle to pass. In other words, the temporal muscle can be developed with CBL growth.

The temporal muscle is a fan-shaped muscle situated within the temporal fossa of the skull. The primary function of this muscle is to produce the movements of the mandible at the temporomandibular joint and thus facilitate the act of mastication. In the case of cetaceans, the temporal muscle is also known as one of the most developed muscles for mouth-closing (Seagars, 1982; Herring, 2007; Kim et al., 2018). A site of origin for the temporal muscle is the temporal fossa represented by V8 and V9 in our study. Although the width of the temporal fossa in a dorsoventral direction (V9) had no positive allometry, the length in an anteroposterior direction (V8) showed a high development with CBL growth without being limited in a space produced by brain size. By qualitative observation, the posterior ends of these bones consisted of the temporal fossa extending in a posterior direction, over the posterior end of the braincase. These results indicate an extension of the surface and the crest where the temporal muscle originates (Fig. 4). In addition, the results showed that the space where the temporal muscle passes were expanded with positive allometry and isometry (V15, 16; Fig. 4). Therefore, the temporal fossa and temporal crest expansion may be caused by the development of muscle thickness. Especially, the posterior extension of the temporal crest might also increase the length of the muscle itself and increase the area of temporal muscle attachment. In the case of the bottlenose dolphin, the allometry of the temporal fossa implies the development of the temporal muscle with CBL growth, and similar trends in the allometry of these characters between mature and immature specimens indicate that the development of temporal muscle occurs not only in ontogeny but also in larger specimens among mature individuals (Kurihara and Oda, 2009). In other words, the feeding habit affects this morphological feature during both the immature and mature stages. This previous study speculated that the same tendency might occur in the killer whales since they have a habit of catching and shearing/biting prey (Ford, 2018). Therefore, if this tendency also occurs in mature killer whales having different feeding habits (i.e., ecotype), this morphological feature should be further examined for a more sophisticated understanding and increased application in taxonomy.

Killer whale's rostral length and width characteristics showed positive allometry in this study, which appears to be related to the development of the feeding apparatus. Several studies using a sufficient number of skull samples, e.g., bottlenose dolphin (Kurihara and Oda, 2009), baleen whales (Nakamura *et al.*, 2012), have concluded that the positive allometry of rostral length is related to the feeding apparatus, i.e., it reflects the growth for extension of the range for prey catching (Costa *et al.*, 2016). For the rostral width, it might have been affected by the development of the lateral rostral muscles inserted at the lateral side at the rostrum. Mead and Fordyce (2009) concluded that the posterior areas of the rostrum (V2 and V3 in this study) and its attached rostral muscles are involved in the feeding apparatus. Hence these features can reflect differences in feeding habits between populations.

In addition to the width of the rostrum, the present study results suggested that the width from the ventral surface of the lacrimal bone (i.e., ventral surface) to the top of the maxillae bone showed positive allometry. Also, the surrounding area, i.e., the antorbital process of the maxillae bone and the preorbital process of the frontal bone, became thick, tough, sturdy, and the maxillary crest became more remarkable with CBL growth. The posterior areas of the rostrum and the area surrounding the antorbital process of the maxilla are suggested that it is involved in the generation and modification of acoustic signals (Mead, 1975; Huggenberger *et al.*, 2009). These portions are covered by the anterointernus muscle and *M. maxillonasolabialis anteroexternus*, relating the nasal apparatus structure (Huggenberger *et al.*, 2009). Huggenberger *et al.* (2009) concluded that these muscles might exert a pulling force on the connective tissue dorsal to the anterior nasofrontal sac and the rostral bursa cantantis. The lateral region of the *M. maxillonasolabialis anterointernus* attaches to connective tissue dorsal to the angle and the inferior vestibulum and may control air movement and pressure in the angle and the nasofrontal sac.

Moreover, Cranford *et al.* (2011) concluded that all extant toothed whales generate sonar signals using phonic lips and these muscles and tissues. In the killer whales, various and high-frequency acoustic behaviors are known, and they can be considered as one of the survival strategies or habits by population/ecotype (Miller and Bain, 2000; Deecke *et al.*, 2005, 2011; Simon *et al.*, 2006). Therefore, the apparent developmental change in this area might be considered one of the crucial features of each killer whale population/ecotypes, and combining previous studies and our morphological report could provide valuable evidence on taxonomic studies.

Acknowledgements

The authors thank Dr. Kazutoshi Arai, Mr. Hiromi Saeki, Dr. Hiroshi Katsumata, Dr. Etsuko Katsumata and the other members of the Kamogawa Sea World; Dr. Hiroshi Sawamura, Director of the Ashoro Museum of Paleontology; Mr. Taira Usui, Curator of the Okhotsk Museum of Art; Dr. Hajime Taru, Chief Curator of the Kanagawa Prefectural Museum of Natural History; Ms. Kiyomi Nakamura, Curator of the Kobe City Suma Marine Aquarium; Mr. Katsuki Hayashi, Director and Ms. Tamaki Nakae, Curator of the Whale Museum, Taiji Town; Ms. Haruna Okabe and Dr. Nozomi Kobayashi and the other members of the Okinawa Churashima Foundation; Mr. Naofumi Murata, Curator of the Nago Museum; Mr. Makoto Soichi, former Director, Nagoya Port Aquarium; Dr. Miki Mizushima, Curator, Hokkaido Museum; and Dr. Yoshikazu Sato, Professor, Rakunogakuen University and Dr. Takeharu Bando and Dr. Satoko Inoue of the Institute of Cetacean Research. Comments from anonymous reviewers significantly improved this manuscript.

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Received: January 31, 2021 Accepted: August 5, 2021 Published online: December 22, 2021

Appendix

Changes in the proportion of each measured character to the CBL of killer whales in the western North Pacific. Black, white, and gray indicate male, female, and sex-unknown, respectively. The solid line indicates the prediction line from allometry analyses. Skull morphometric feature measurements are abbreviated according to Table 2.





Appendix (Continued).