Skull morphometry of the common dolphin, *Delphinus* sp., from New Zealand waters

A thesis presented in partial fulfilment of the requirements for the degree of

Master of Science in Conservation Biology

Massey University

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Abstract

The short-beaked, *Delphinus delphis*, and long-beaked, *D. capensis*, common dolphin, two morphotypes of the *Delphinus* genus, are recognized as different species. However, to date, species status of the New Zealand common dolphin, among other geographic populations, remains unclear, owing to morphometric and genetic uncertainty. This lack of taxonomic knowledge is one of the reasons preventing adequate threat status assessment. The main objective of the current skull morphometric study, the first to solely focus on New Zealand *Delphinus* sp., was therefore, to obtain further information regarding taxonomy and life history for conservation purposes. In particular, the study aimed (1) to determine age at cranial maturity through the computation of a suture index; and (2) to assess the validity of several cranial parameters as cranial maturity indicators through the determination of a misclassification index. Furthermore, (3) presence of cranial sexual dimorphism was investigated in (i) metric characters through ANOVA and ANCOVA analyses and in (ii) non-metric characters through Chi-Square tests. (4) The taxonomic status was assessed based on the rostrum length to zygomatic width (RL/ZW) ratio, tooth counts, and the Kalya Index. Moreover, (5) Potential regional differences between Hauraki Gulf (HG) and non-HG specimens were investigated through MANOVA analyses (metric characters), Chi-Square tests, and the computation of the mean measure of divergence (non-metric characters). In addition, (6) measurement error of two metric data acquisition methods (callipers *versus* microscribe) was compared through the computation of three precision estimates (variance, mean absolute difference (MAD), and relative error magnitude (REM)). A total of 67 common dolphin skulls from stranded and by-caught individuals were available for analyses. The majority of skeletal material (73.1%, n = 49), had been archived frozen as intact heads following necropsies at Massey University. Those heads were prepared as part of the present study via applying the manure decomposition method. The remaining 26.9% (n = 18) of

skulls were cleaned specimens housed at the Museum of New Zealand Te Papa Tongarewa. Sex was known for 88.1% (n = 59) of specimens (males: 40.7%, n= 24; females: 59.3%, n = 35). Based on age data and the suture index, 46.3% (n = 31) and 53.7% (n = 36) of specimens were regarded as cranially immature and mature, respectively. Sex ratio of immatures was approximately 1:1 (males: n = 16, females: n = 13), while that of mature specimens was almost 1:3 (males: n = 8, females: n = 22). The suture index suggested that New Zealand *Delphinus* sp. obtain cranial maturity at approximately 11 years. Specimens with ≤ 6.8 % of partly worn teeth were between 1 to 3 years and cranially immature, while specimens with any number of rostral teeth worn down to the gum line were physically mature. Sexual size dimorphism, with larger sizes recorded for males, were detected in total body length (TBL) and in 22.7% (n = 15) of cranial characters analyzed, of which 86.7% (n = 13) were width measurements. In total 70.0% (n = 7) of size dimorphic characters that could be allocated to a cranial functional complex were related to the feeding apparatus. RL/ZW ratio (mean: 1.49 ± 0.06 (SD); range: 1.39 - 1.61) and upper tooth counts (45 - 56) of cranially mature New Zealand specimens assessed (pooled for both sexes) overlapped with values published for both the short-beaked and long-beaked form. Values of TBL, condylobasal length (CBL), rostrum length (RL), and zygomatic width (ZW) were also of intermediate status in both sexes. Findings reported herein suggest that New Zealand *Delphinus* sp. should be regarded as a large form of *D. delphis* until further morphometric and genetic data becomes available. No evidence of regional differences between HG and non-HG specimens was detected in either metric or non-metric characters, however, sample sizes were small. Variance of repeated measures was lower in the calliper (range: 0.1 to 0.7%) than in the microscribe (range: 1.1 to 10.7%) data set for all characters assessed (n = 33). High precision between both data sets was detected for 69.7% (n = 23) of characters (MAD below the 1 mm threshold) and REM of 93.9% (n = 31) of character was deemed excellent or good, indicating high compliance between both methods for the majority of characters assessed.

Acknowledgements

This project would not have been possible without the engagement, commitment, and help of many people. I would especially like to thank both of my supervisors, Dr. Karen Stockin and Dr. Sinéad Murphy, for providing continued support, advice, help, feedback, and words of encouragement throughout the length of this Masters project, as well as for passing on invaluable skills and knowledge. In addition, thank you, Karen, for giving me the opportunity to conduct this research, and thank you, Sinéad, for your engagement, for bringing the microscribe component into this project, and for the road trip to the Museum of New Zealand Te Papa Tongarewa.

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Additional sincere and special thanks go to Prof. Xun Xu, Stephen Crawley, and Jos Guerts from University of Auckland for giving me the opportunity to use their microscribe and facilities at no cost, to Mark Delaney for helping with the digitization process of the skulls, and to Anders Jørgensen and Maria Jedensjö for their help and invaluable advice via email correspondence regarding data acquisition with the microscribe.

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Most importantly, this thesis would not have been completed without the tremendous support and invaluable advice I received from my family! It is only because of them that I kept going until the very end, despite numerous challenges encountered between the pages.

THANK YOU!

'Was mich nicht umbringt, macht mich stärker.'

Friedrich Nietzsche

Therefore, I now know that I am able to tackle the next challenge! ☺

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List of Abbreviations

95% CI	=	95% Confidence Interval
ANCOVA	=	Analysis of Covariance
ANOC(R)	=	Length from the right antorbital notch to the right occipital condyle
ANOVA	=	Analysis of Variance
APM	=	Age at physical maturity
ASM	=	Age at sexual maturity
CBL	=	Condylobasal length
cm	=	Centimetres
COH	=	Configuration of the optical hiatus
CPN	=	Contact between premaxilla and nasal bone
CV	=	Coefficient of Variation
DoC	=	Department of Conservation
fr-fr	=	Frontal-frontal suture
fr-in	=	Frontal-interparietal suture
fr-or	=	Frontal-orbitospenoid suture
g	=	Gram
GLG	=	Growth layer groups
GLLPTF	=	Greatest length of the left post-temporal fossa
GWEN	=	Greatest width external nares
GWIN	=	Greatest width internal nares
GWM	=	Greatest width across both maxillae
GWPA	=	Greatest width of the parietal bone
GWPR	=	Greatest width of the premaxillae
GWRM	=	Greatest width of the right maxilla bone
HG	=	Hauraki Gulf
HLM	=	Height left mandible
HMF	=	Height foramen magnum
I.Q.R.	=	Interquartile range
IAS	=	Interalveolar septa
ID	=	Identification
Im	=	Cranially immature
km	=	Kilometres

la-fr	=	Lacrimal-maxilla-frontal suture
LLLAC	=	Length of the left lacrimal bone
LLM	=	Length left mandible
LLSQ	=	Length of the left squamosal bone
LMF	=	Length of the mandibular fossa
LOL	=	Left orbit length
LRM	=	Length right mandible
LWPA	=	Least width of the parietal bone
MAD	=	Mean absolute difference
MANCOVA	=	Multivariate Analysis of Covariance
MANOVA	=	Multivariate Analysis of Variance
Mat	=	Cranially mature
MaxDLTF	=	Maximum diameter of the left temporal fossa
MaxDRTF	=	Maximum diameter of the right temporal fossa
max-fr	=	Maxilla-frontal suture
ME	=	Measurement error
Mio	=	Million
mm	=	Millimetres
MMD	=	Mean measure of divergence
MNC	=	Extension of the maxillae relative to the nuchal crest
mtDNA	=	Mitochondrial DNA
na-fr	=	Nasal-frontal suture
non-HG	=	Non-Hauraki Gulf
NZCDP	=	New Zealand Common Dolphin Project
pa-ex	=	Parietal-exoccipital suture
pa-fr	=	Parietal-frontal suture
pal-max	=	Palatine-maxilla suture
pal-pal	=	Palatine-palatine suture
pa-so	=	Parietal-supraoccipital suture
pers. comm.	=	Personal communication
POOW	=	Postorbital width
premax-max	=	Premaxilla-maxilla suture
PROW	=	Preorbital width
pt-ba	=	Pterygoid-basioccipital suture

pt-pal	=	Pterygoid-palatine suture
REM	=	Relative error magnitude
REXN	=	Distance from tip of rostrum to external nares
RL	=	Rostrum length
RL/ZW ratio	=	Rostrum length to zygomatic width ratio
SD	=	Standard deviation
so-ex	=	Supraoccipital-exoccipital suture
SSD	=	Sexual size dimorphism
SST	=	Sea surface temperature
SW	=	Skull weight
SW/CBL^3	=	Skull weight to condylobasal length ratio
SW/ZW^3	=	Skull weight to zygomatic width ratio
TBL	=	Total body length
TRIN	=	Distance from tip of rostrum to internal nares
unpubl.	=	Unpublished
WBOCS	=	Width between the basioccipital crest at the basioccipital-sphenoid suture
WFM	=	Width foramen magnum
WMF	=	Width of the maxillae relative to the frontal bones
WPT	=	Width of the pterygoid bones
WR1/2	=	Width of rostrum at midlength
WR3/4	=	Width of rostrum at 3/4 length from base
WR60	=	Width of rostrum at 60 mm from base
WRB	=	Width of rostrum at base
ZW	=	Zygomatic width
zy-pa-ex	=	Zygomatic-parietal-exoccipital suture

CHAPTER 1

Introduction

Plate 1.1. Common dolphin, *Delphinus* sp., in the Hauraki Gulf, Auckland, New Zealand. Photograph by S. Dwyer.

1.1 Morphology of the delphinid skull

Both osteology, the scientific study of bones, and morphology, the study of form and structure, form a vital part of evolutionary, taxonomic, ecological, and life history studies of odontocetes (toothed whales) (Perrin, 1975; Rommel, 1990; Fordyce, 2009; Heyning & Lento, 2002; Galatius et al., 2011). The skull is the most frequently assessed skeletal part in morphologic studies, owing to the frequent lack of post-cranial skeletal material. Based on the fossil record, it is thought that modern delphinids appeared approximately 12 to 10 million (Mio) years ago (Fordyce, 2009). Both morphological and molecular evidence indicate that extant toothed whales evolved from terrestrial hoofed mammals (Heyning & Lento, 2002). As a consequence of morphological modifications necessary for the secondary adaptation to an aquatic lifestyle, the size, shape, and position of several cranial bones of delphinids deviate severely from the arrangement of the typical terrestrial mammalian skull, and some features have been lost (Perrin, 1975; Mead & Fordyce, 2009). These morphological modifications are apparent in all five functional complexes of the skull, namely the breathing / sound producing, feeding, hearing and vision apparatus, and the braincase (Perrin, 1975; Mead & Fordyce, 2009).

1.1.1 The breathing and sound producing apparatus

Cranial features associated with the breathing complex include the nares (external and internal bony openings), the nasals, the nasal cavity, and the pterygoid sinus system (refer to Figs. 1.1 to 1.3) (Mead & Fordyce, 2009).

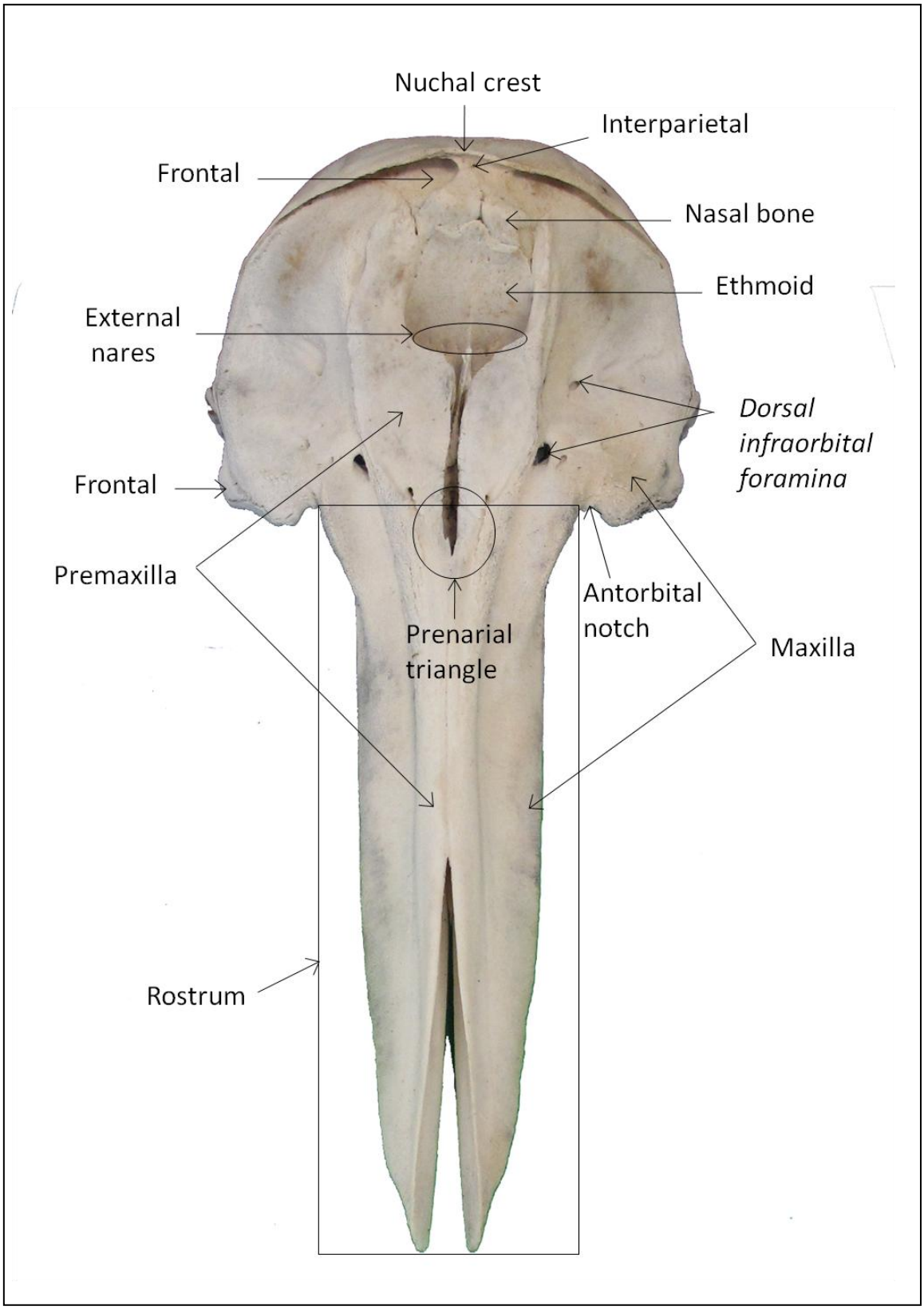

Figure 1.1. Description of a selected number of cranial bones of a delphinid skull in dorsal view adapted from Mead & Fordyce (2009).

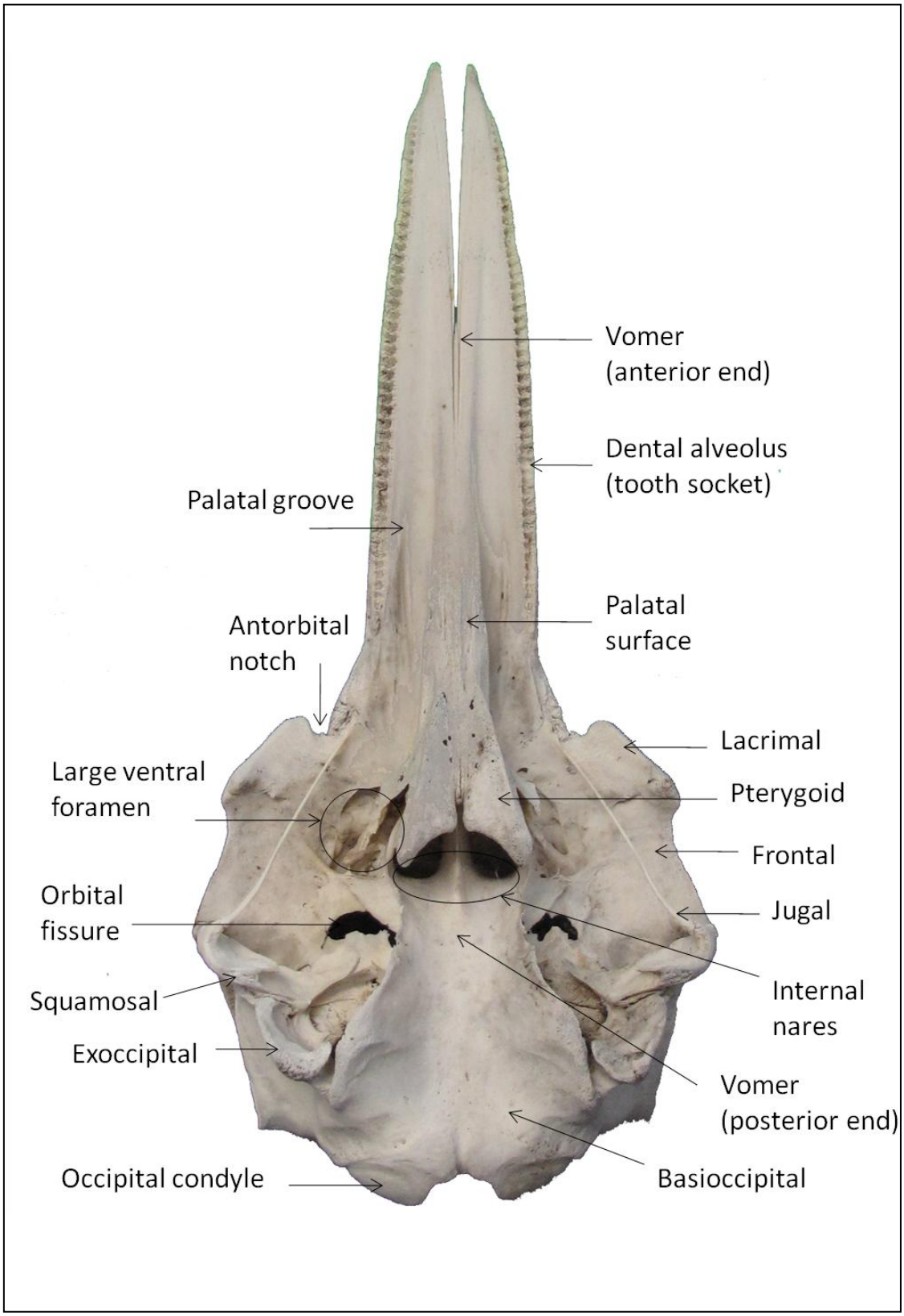

Figure 1.2. Description of a selected number of cranial bones of a delphinid skull in ventral view adapted from Mead & Fordyce (2009) and Perrin et al. (1994).

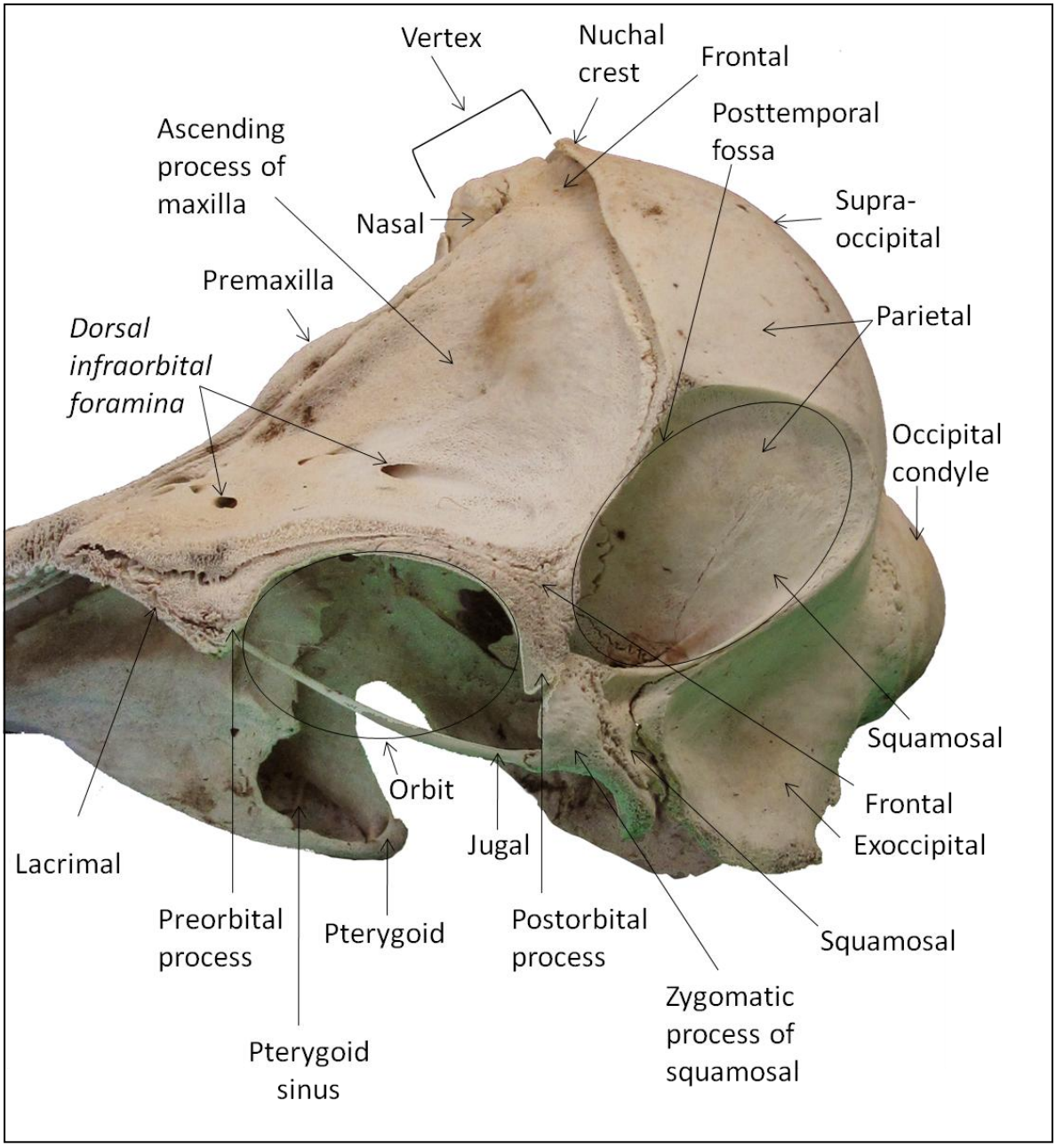

Figure 1.3. Description of a selected number of cranial bones of a delphinid skull in lateral view adapted from Mead & Fordyce (2009).

One of the most obvious modifications of the delphinid skull is the shift of the paired external bony nares to a posterodorsal position within the facial region of the cranium (Fig. 1.1). The dorsal position of the blowhole and the smoothening of the nasal cavity facilitate rapid

exchange of air (Perrin, 1975). The nasal cavity refers to the space between the external bony nares. These are enclosed by the nasals, maxillae, premaxillae and frontals, and the internal bony nares or choanae, which are bounded by the pterygoids, the basiosphenoid, part of the vomer, and the palatines at the ventral side (Mead & Fordyce, 2009). The vertex, which refers to the area between the nasal bones (inclusive) and the nuchal crest (Fig. 1.3), serves as an important attachment site for several muscles related to the nasal passage in delphinids (Mead, 1975). This function of the vertex is a consequence of the dorsoposterior shift of the external nares and deviates from the mammalian skull, where the vertex simply defines the highest point of the cranium without fulfilling a specific role (Mead & Fordyce, 2009). The nasal bones are loose in young individuals, but fuse with age (Rommel, 1990).

Absence of paranasal sinuses in cetaceans is most probably linked to the fact that a rigid-walled system does not allow for expansion of air as a result of pressure differences while diving (Reidenberg & Laitman, 2008). Instead, an airway system referred to the pterygoid sinus system evolved, which includes the presence of air sacs (Fig. 1.4) that allow pressure-related air expansion without risking skull fracture (Reidenberg & Laitman, 2008). Part of this sinus complex contains modified pterygoid bones, which join ventrally onto the palate and enclose the enlarged internal nares (refer to Figs. 1.2 and 1.3) (Reidenberg & Laitman, 2008).

Cranial features that affect sound generation and modification are the posterior parts of the maxillae and premaxillae that form part of the facial area. These bones have become broader and wider to support the melon (Thomas & Kastelein, 1990; Mead & Fordyce, 2009).

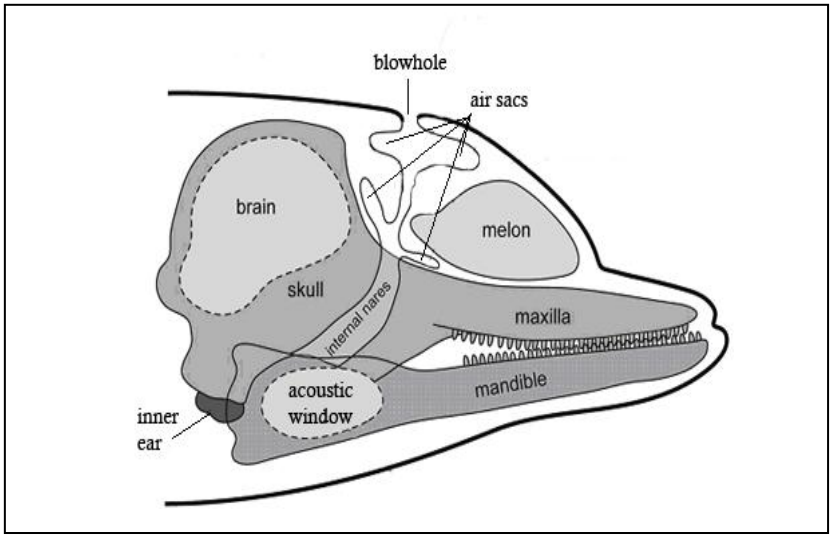

Figure 1.4. Delphinid head showing position of the skull, melon, and air sacs adapted from Cranford et al. (1996).

1.1.2 The feeding apparatus

Cranial features related to the feeding apparatus are the upper jaw (rostrum), lower jaw (mandible), teeth, the zygomatic and postorbital processes, and the post temporal fossae (refer to Figs. 1.1 to 1.3 and 1.5) (Perrin, 1975; Mead & Fordyce, 2009).

A further obvious difference of the typical delphinid skull, as compared to terrestrial mammals, is the long rostrum, which is formed by the elongated maxillae, premaxillae, and vomer (Mead & Fordyce, 2009). The latter is the only unpaired cranial bone of the odontocete skull. The teeth of odontocetes became conical and simplified in shape in the early evolutionary history of cetaceans (Oelschläger, 1990). This homodentition allowed the number of teeth to increase dramatically (Oelschläger, 1990; Mead & Fordyce, 2009). The La Plata River dolphin, *Pontoporia blainvillei*, marks an extreme example with a total of up to 242 teeth (Mead & Fordyce, 2009). The long rostrum and mandibles in conjunction with the large number of homodont and conical teeth facilitated a switch in foraging technique

from cutting to grasping and swallowing prey whole (Oelschläger, 1990). The zygomatic processes of the squamosal provide the attachment sides for lower jaw bones. The temporal muscles pass through the temporal fossae, which are enclosed by the zygomatic and postorbital processes (Mead & Fordyce, 2009). Nerves and blood vessels transmit through apertures in the bone, called foramina (Rommel, 1990) (refer to Figs. 1.1 to 1.3, 1.5 and 1.6).

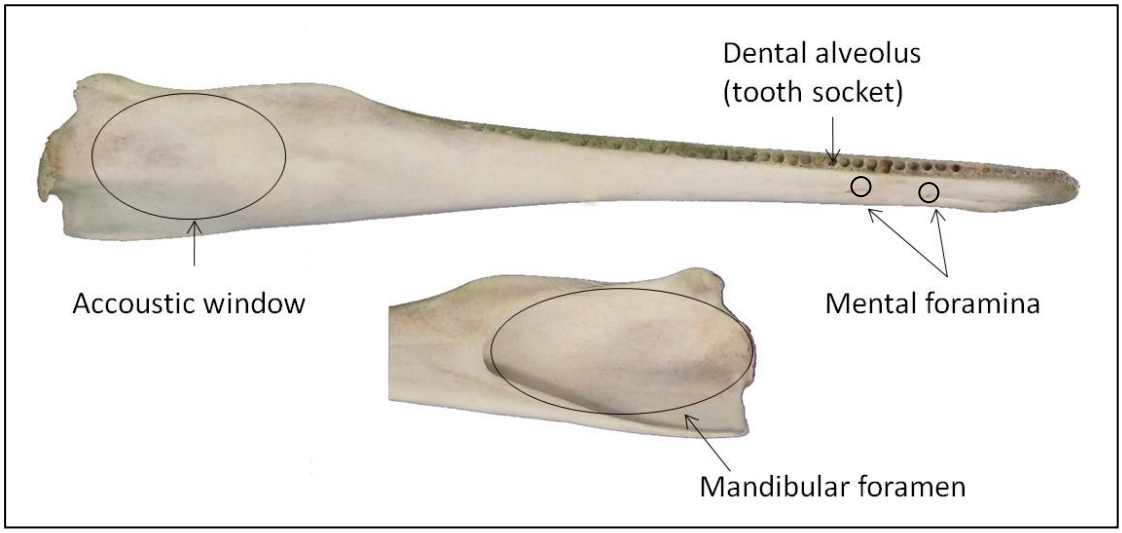

Figure 1.5. Description of a selected number of features of the mandible (lower jaw) adapted from Mead & Fordyce (2009).

A distinct feature of the odontocete skull is its directional, bilateral asymmetry characterized by a larger sized right side of the cranium and a larger right nasal passage in particular (Rommel, 1990). It has initially been assumed that asymmetry of the skull reflects the asymmetry of the associated soft nasiofacial tissue and is related to the production of biosonar (Mead, 1975; Cranford et al., 1996; Yurick & Gaskin, 1988). However, skull asymmetry does not appear to be a prerequisite for biosonar production (MacLeod et al., 2007). In addition, varying degrees of cranial asymmetry have been documented in odontocete species (Ness, 1967), a fact that the biosonar-hypothesis fails to account for. A recent investigation provided

evidence that the directional facial asymmetry in delphinids is a result of an asymmetrically placed larynx, which evolved from the necessity to separate the respiratory and digestive tract in order to allow large prey items to be swallowed whole while preventing damage to the air ways or causing suffocation (MacLeod et al., 2007). The authors reported a significant positive relationship between average cranial asymmetry in different odontocetes and maximum prey size.

A further feature of the delphinid skull is known as telescoping, which is the result of the overlap of several cranial bones (Miller, 1923). Two forms of telescoping are distinguished. First, facial telescoping occurs due to the posterior extension of the maxillae and premaxillae (rostral bones) over the orbits and the frontals, thereby forming part of the facial region (refer to Fig. 1.1) (Miller, 1923; Perrin, 1975; Mead & Fordyce, 2009). Facial telescoping is thought to be related to the posterodorsal shift of the external nares that continues during ontogenetic development (Mead & Fordyce, 2009). Second, supraoccipital telescoping refers to the anterior shift of the supraoccipital during ontogenetic development. This process results in the formation of the nuchal crest (refer to Figs. 1.1 and 1.3) and associated decreased visibility of the interparietal (Miller, 1923; Perrin, 1975; Mead & Fordyce, 2009).

1.1.3 The vision apparatus

The orbit of the typical mammalian skull is enclosed by the frontal, maxilla, and jugal (Mead & Fordyce, 2009). In delphinids, the orbit is predominantly bounded by the frontal, dorsal- and laterally, but is only partially bounded by the thin jugal on the ventral side (refer to Fig. 1.3) (Mead & Fordyce, 2009). The orbital fissure (refer to Fig. 1.2), which transmits cranial nerves, is undivided in immature animals, but tends to become subdivided as the animal ages (Rommel, 1990; Mead & Fordyce, 2009).

1.1.4 The hearing apparatus

The hearing complex of delphinids has been most drastically modified. Cranial features involved in hearing are the mandibles, the middle (tympanic bulla), and inner (periotic bone) ears (Figs. 1.4 and 1.5) (Mead & Fordyce, 2009).

The external ears have been greatly reduced and are located underneath the blubber layer (Thomas & Kastelein, 1990). The role in hearing of those vestigial external ears is unclear, although it is believed that sound is perceived via the mandibles. A significant modification of the lower jaws in delphinids is the presence of a large mandibular foramen (refer to Fig. 1.5), the lumen of which extends to the tip of the mandible (Mead & Fordyce, 2009). It is hypothesized that the fatty material, which fills these foramina and is in contact with the tympanic bulla of the inner ear, acts as an acoustic window, important for the reception and transmission of sound (Thomas & Kastelein, 1990; Mead & Fordyce, 2009).

The ear bone structure in delphinids is known as the tympanoperiotic (Mead & Fordyce, 2009). This complex comprises the middle and inner ear, which are referred to as the tympanic bulla and periotic bone, respectively; both are joined but not fused at their posterior and anterior processes (Mead & Fordyce, 2009). The ear bones have thereby become isolated from the skull, which is related to the sense of hearing (Thomas & Kastelein, 1990; Mead & Fordyce, 2009).

1.1.5 The braincase

The braincase, or cranium, comprises all bones that enclose the brain, namely: the exoccipital, supraoccipital, interparietal, parietal, squamosal, frontal, ethmoid, basioccipital, tympanoperiotic, and sphenoid (Figs. 1.1 to 1.3 and 1.6) (Mead & Fordyce, 2009).

The occipital bones have become wider, flatter and thicker, providing for better attachment of muscles involved in locomotion (Mead & Fordyce, 2009). The foramen magnum, situated at the back of the cranium (refer to Fig. 1.6), is bounded by the basi-, ex-, and supraoccipital bones. The spinal cord and the 'vertebral vascular plexus', which is the primary blood supply to the brain, transmit through this opening (Mead & Fordyce, 2009).

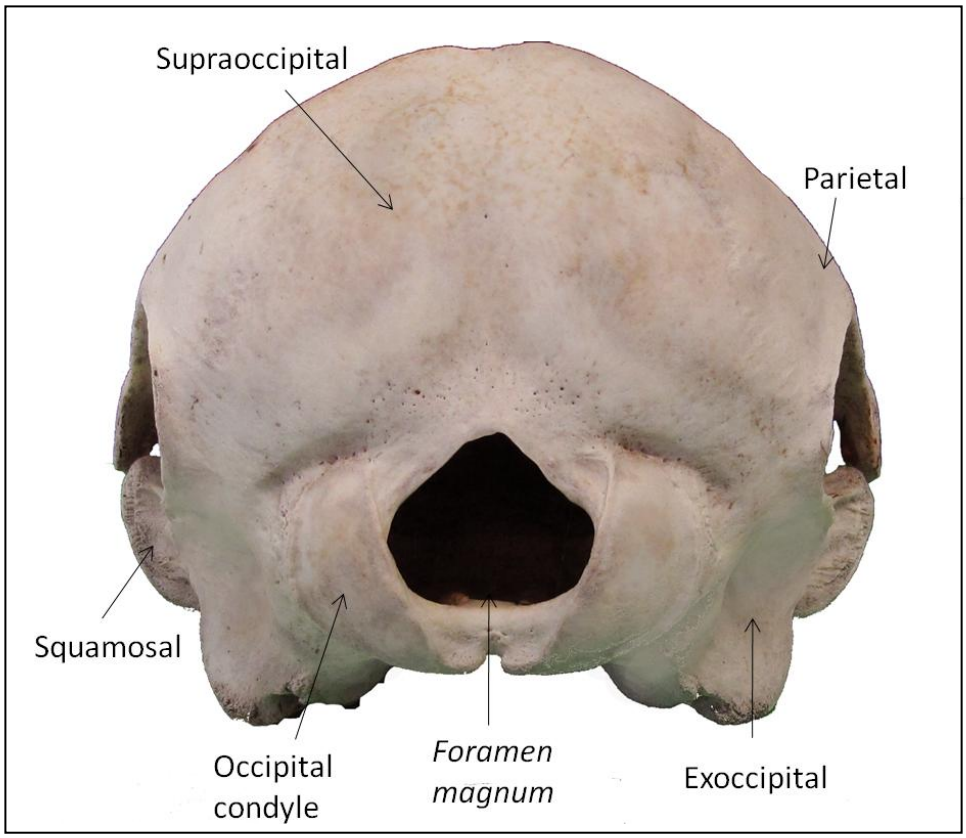

Figure 1.6. Description of a selected number of cranial bones of a delphinid skull in occipital view adapted from Mead & Fordyce (2009).

1.2 Application of cranial morphology as a tool in science

1.2.1 Types of cranial characters

Two different types of skeletal characters are distinguished in morphological studies: metric (quantitative) and non-metric (qualitative) characters (Cheverud et al., 1979).

1.2.1.1 Metric characters

Conventionally, metric characters, which refer to overall differences in size and shape of bones, are measured with vernier and / or digital callipers (Perrin, 1975; Chen et al, 2008). Nowadays, the use of geometric analysis as a tool for morphometrical studies is becoming increasingly widespread (e.g. Marcus et al., 2000; Galatius et al., 2011; Goswami et al., 2010; Nicolosi & Loy, 2010). Geometric morphometrics is based on morphological landmark capture with, for example, a digitizer such as a microscribe, and subsequent data transformation and analyses (Klingenberg, 2011). Several precision estimates (including the mean absolute difference (MAD)) can be computed to assess measurement error (ME) and precision between linear measurements obtained through different data acquisition methods (Weinberg et al., 2004).

1.2.1.2 Non-metric characters

Since the late 1800s, minor variations in cranial and post-cranial skeletal traits such as teeth, ridges, fenestrae, and foramina (openings for blood vessels and nerves) have been increasingly included in anthropologic studies (Ansorge, 2001; Berry, 1975; Cheverud, 1979; Le Double, 1903). These discontinuous skeletal variants are known as non-metric characters

and are coded by state, such as presence / absence, total number, or as relative position to another skeletal feature (Le Double, 1903; Berry, 1975; Perrin et al., 1982).

1.2.1.3 Cranial sutures and skull growth

Cranial bones are still unfused after birth and fuse with age (Rommel, 1990). In addition to the two skeletal characters aforementioned, degree of closure of suture lines is also frequently examined as part of morphological studies to infer a specimen's age and assess maturity status (Van Waerebeek 1993; Gonzalez, 2002; Galatius et al., 2011; Chen et al., 2011). Advancement of suture closure is commonly assessed through scoring, where higher scores are given for more advanced stages of suture fusion (Van Waerebeek, 1993; Galatius et al., 2011). Growth of cranial bones and functional complexes can only be determined for individuals of known age (Perrin, 1975; Noldus & Klerk, 1984).

1.2.2 Addressing taxonomy and geographic variation through cranial morphology

1.2.2.1 Cranial maturity and age estimation

Only skulls from individuals that have ceased growth should be included when determining morphological difference between species, populations, and sexes; and when assessing individual variation in delphinids, because the rostrum and several other cranial features are not fully developed in immature individuals (Perrin, 1993). Fusion of both epiphyses to the vertebral centra provides evidence for physical maturity (Calzada et al., 1997). In the absence of post cranial skeletal material, only cranially mature specimens should

be included for morphometric examination (Perrin, 1975; Perrin & Heyning, 1993). A specimen is said to have attained cranial maturity when growth of the skull has ceased. Distal fusion of the premaxilla with the maxilla (refer to Fig. 1.7) has been determined as a reliable indicator for cranial maturity in several dolphin species (Dailey & Perrin, 1973; Mead & Potter, 1990; Calzada et al., 1997).

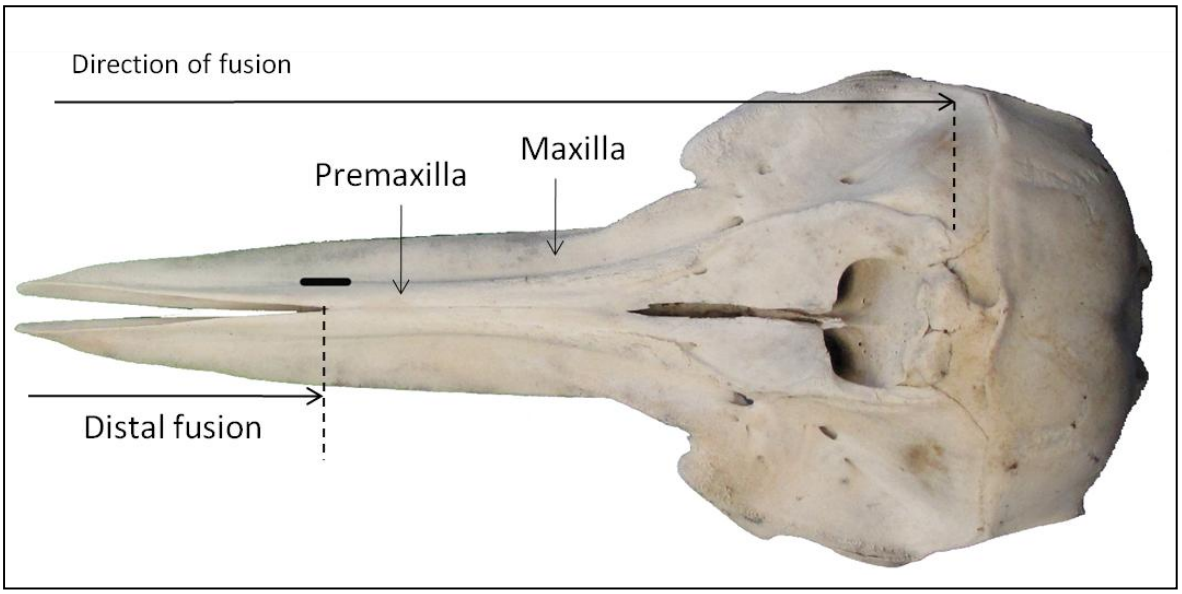

Figure 1.7. Schematic description of rostral fusion on a delphinid skull adapted from Amaha, 1994. Note: Rostral fusion occurs between the premaxilla and maxilla (indicated by horizontal black line) on both sides of the rostrum. Fusion starts at the tip of the rostrum and progressively extends backwards. Distal fusion: Premaxilla-maxilla fusion up to the anterior end of the fusion between the left and right premaxilla.

Distal fusion is, however, not a definite indicator of cranial maturity in some species, including the short-beaked common dolphin, *D. delphis* (Perrin & Heyning, 1993), and Pacific white-sided dolphin, *Lagenorhynchus obliquidens* (Van Waerebeek, 1993). Owing to this uncertainty, biological data such as age, total body length (TBL), and sexual maturity are considered, if available, when deciphering cranially mature specimens (Perrin & Heyning,

1993; Murphy et al., 2006; Westgate, 2007). Condylobasal length (total skull length), premaxilla-maxilla fusion over at least 50% of the length of the rostrum, the overall degree of cranial fusion (e.g. based on a suture index), and developmental status of alveoli have also been included as a criterion for maturity assessment, especially in the complete absence of biological data (Van Waerebeek, 1993; Jefferson & Van Waerebeek, 2002; Murphy et al., 2006; Westgate, 2007; Tavares et al., 2010, Pinela et al., 2011; Juri et al., 2012).

1.2.2.2. Sexual dimorphism

Before addressing taxonomic issues or investigating geographic variation, it is necessary to test morphological samples for sexual dimorphism, as differences in absolute and relative size is evident in metric characters of the cranium in several vertebrate species, including the common dolphin (Samaai, 2005; Murphy et al., 2006). Sex related differences might also be present in non-metric characters (Berry, 1975, Perrin et al., 1994; Brasili et al., 1999).

1.2.2.3 Taxonomy

Historically, species and subspecies status of animals was predominantly determined from morphological and geographical data (Robineau et al., 2007). A quantitative guideline states that separation at the sub-species level is justified if 75% or more members of a population can be distinguished from all (> 99%) individuals of the overlapping population (Amadon, 1949; Patten & Unitt, 2002). However, disagreement still exists about the number of characters to examine when assessing subspecies level and the level of, for example, morphological differences needed that justify discrimination at the species and subspecies level (Patten & Unitt, 2002; Taylor, 2005; Robineau et al., 2007). It is generally accepted that

one or more non-overlapping metric cranial differences validate a species status, while overlapping modal differences support a sub-species status (Westgate, 2007).

Nowadays, molecular analyses are increasingly being employed in taxonomic studies (Reeves et al., 2004). However, one limitation of molecular techniques is the fact that sub-species status is more difficult to determine with molecular markers in conditions of continued genetic exchange (Haig et al., 2006). Furthermore, phylogenetic history might not always be detected in a given genetic locus due to natural selection (Taylor, 2005). As a result, morphological studies continue to remain an important part in taxonomy (Yurick & Gaskin 1988; Heyning & Perrin, 1994; Perrin et al., 1994; Wang et al., 2000), because they complement results from genetic studies and can provide insights into mechanisms driving morphological differentiation (Adams et al., 2004; Natoli et al., 2006).

1.2.2.4 Geographic variation

Non-metric characters are believed to be largely under genetic control and less affected by selection pressure as compared to, for example, metric cranial traits related to the feeding apparatus (Pankakoski & Hanski, 1989). As a result, non-metric characters are regarded as good indicators of the degree of genetic exchange between populations and are widely used in anthropology (Berry, 1975; Cheverud et al., 1979; Brasili et al., 1999). Non-metric characters have also been deemed valuable in other vertebrate studies addressing geographic variation, including studies on cetaceans (Kinze, 1985; Van Waerebeek, 1993; Perrin et al., 1994; Wiig et al., 2012). A common method to determine the degree of separation between populations is to compute the mean measure of divergence (MMD), based on the frequency of trait expression of a set of non-metric characters (Sjøvold, 1977; Green et al., 1979). However, in

odontocete studies, comparison between degree of discriminative power of non-metric and metric characters in geographic variation analyses has rendered different results. While metric characters were found superior in a study addressing geographic variation in the common dolphin (Perrin et al., 1994), the converse trend applied to a study on narwhals, *Monodon monoceros* (Wiig et al., 2012). Perrin et al. (1994) suggested employing both metric and non-metric characters in geographic variation studies.

1.3 The common dolphin, *Delphinus* sp.

1.3.1 Taxonomy

1.3.1.1 Overview

The common dolphin belongs to the *Delphinus* genus within the subfamily Delphininae (Perrin, 1989). Further genera within this subfamily include *Sousa* sp., *Stenella* sp., *Tursiops* sp., and *Lagenodelphis hosei* (LeDuc et al., 1999). All members of this family display typical 'dolphin-shape' characteristics such as a distinct beak and dorsal fin, two or more fused cervical vertebrae, and at least 20 pairs of rostral teeth (Martin, 1990). In the common dolphin, the number of rostral teeth in each tooth row varies from 41 to 67 (Jefferson and Van Waerebeek, 2002; Murphy et al., 2006) and *Delphinus* sp. have 73 or 74 vertebrae (Watson, 1981). A distinct feature of the common dolphin is the presence of palatal grooves on the palate of the maxillae (Heyning & Perrin, 1994) (refer to Fig. 1.2).

Following the initial identification by Artedi, (1738), the common dolphin was classified as *Delphinus delphis* by Linnaeus (1758). Since then, high variability in morphological characters and pigmentation patterns within this cosmopolitan genus has caused taxonomic uncertainty, which has led to the description of over 20 nominal species worldwide

(Hershkovitz, 1966). However, for over 30 years (until 1994) only one highly variable species, *D. delphis* Linnaeus, was officially acknowledged, owing to the lack of studies addressing the issue of geographical variation adequately (Rice, 1977; Ross, 1984; Jefferson et al., 1993).

Over the last two decades, research efforts on common dolphin populations have increased and two morphotypes, the short-beaked-form, *D. delphis,* and the long-beaked-form, *D. capensis,* are currently recognized as two distinct species (Heyning & Perrin, 1994). The short-beaked and long-beaked form had first been described by Banks and Brownell (1969) from the Bay of California in the eastern North Pacific. The authors based the distinction between these two forms on differences recorded in rostral length to zyogomatic width (RL/ZW) ratios. This distinction was rejected by van Bree and Purves (1972), who argued that a similar ratio was recorded in African waters, where it presented a continuous cline. The authors further suggested that both shorter and longer rostra may be present in *Delphinus* populations and that short rostra may, for example, predominate in cooler waters owing to a smaller volume to surface area ratio.

In the mid-1990s, Heyning and Perrin (1994) re-examined the data from California and found evidence for differences in body length, colouration, rostral length (refer to Plate 1.2), and number of teeth between the short-beaked and long-beaked forms. Based on their findings, the authors concluded that these two morphotypes should be recognized as separate species. Genetic analyses using mtDNA and cytochrome *b* sequences confirmed the lack of gene flow between these two genetically distinct forms (Rosel et al., 1994). In addition, results indicated a closer relatedness between short-beaked forms from the eastern North Pacific and the Black Sea than between the former and the long-beaked form occurring sympatrically in the eastern North Pacific (Rosel et al., 1994). Based on published descriptions, Heyning and Perrin

(1994) assigned *D. delphis* Linnaeus to the short-beaked-form. The long-beaked form, which initially had been referred to as the nominal species *D. bairdii* (Dall, 1873) by Banks and Brownell (1969), was renamed as *D. capensis*. The renaming was based on similarities in skull measurements and tooth counts between *D. bairdii* and the nominal species *D. capensis* previously described from South Africa (Gray, 1828), which led to the hypothesis that both morphotypes, short- and long-beaked common dolphin, occurred globally (Heyning & Perrin, 1994).

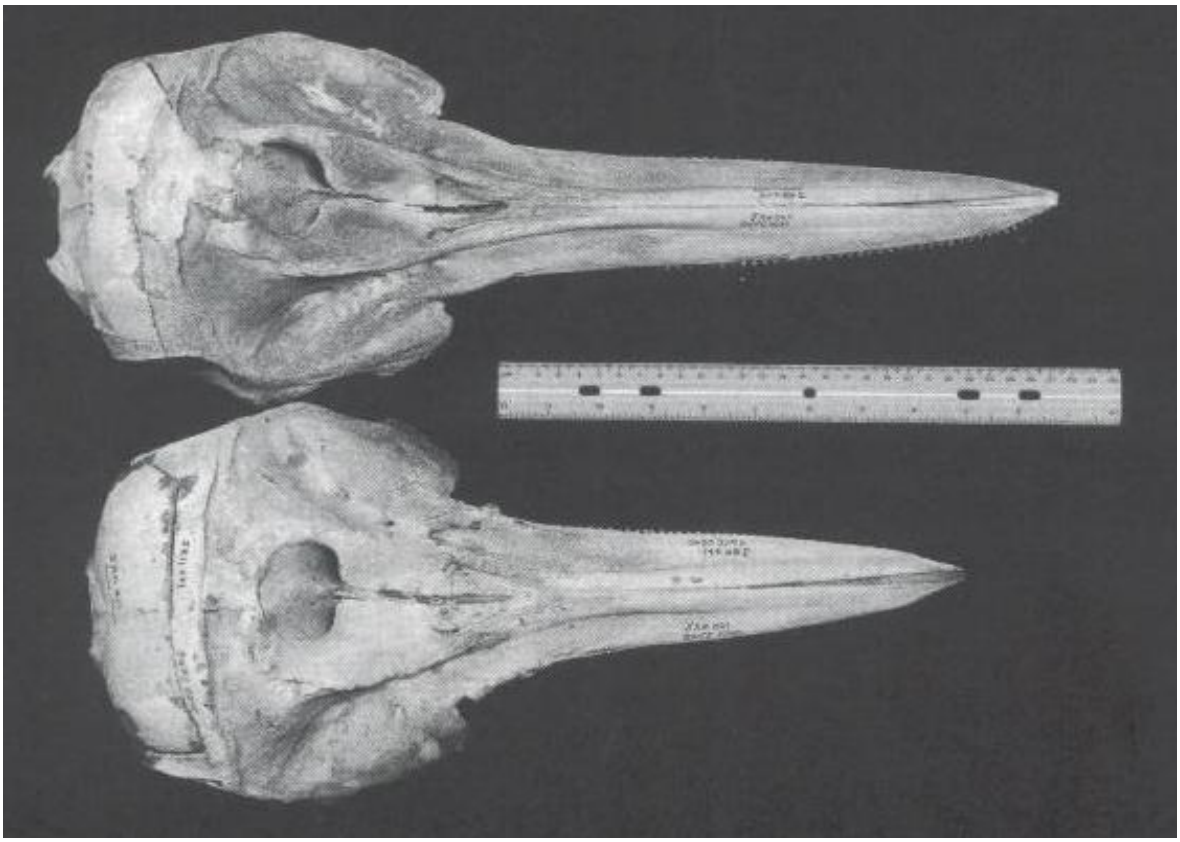

Plate 1.2. Short-beaked, *D. delphis* (bottom) and long-beaked, *D. capensis*, (top) common dolphin male skull specimen from southern Californian waters in dorsal view. Photograph adapted from Evans (1994).

Currently, three common dolphin sub-species, one within *D. delphis* and two within *D. capensis*, have been proposed (Perrin et al., 2009). Based on cranial morphometric evidence and a smaller average body size, *D. d. ponticus,* which inhabits the Black Sea, has been recognized as a sub-species of the short-beaked common dolphin (Barabash, 1935; Perrin & Reilly, 1984; Perrin et al., 1994). Within the Indo-Pacifc region two morphotypes, *D. c. capensis* and *D. c. tropicalis* are proposed as sub-species of *D. capensis* (Jefferson & Van Waerebeek, 2002; Perrin et al., 2009). *D. c. tropicalis* is an extremely long-beaked form that had initially been described by Cuvier (1829) as *D. longirostris* and had later been re-named as *D. tropicalis* by van Bree (1971). The main characteristic features of the population of *D. c. tropicalis*, which stretches from northeast Africa to China, are an extremely long and narrow rostrum and high tooth counts (Jefferson & Van Waerebeek, 2002). In addition, Amaha (1994) reported that the *tropicalis*-form displayed relative narrower skulls and rostra. Initially, these observations led to the suggestion that the *tropicalis*-form should be considered a separate species (Amaha, 1994). However, Heyning and Perrin (1994) hypothesized that the *tropicalis*-form represented an extremely long-beaked form of *D.capensis* and therefore proposed a sub-species status. Their proposal was based on the resemblance in external and skeletal morphology of both morphotypes. The sub-species status was later recognized by Jefferson and Van Waerebeek (2002). The authors found evidence of a clinal variation in rostrum length, which decreased moving both eastwards and westwards, from India towards South Africa in the west or Japan in the east. Based on their results, the authors proposed the hypothesis that variation in rostrum length and tooth counts of the *capensis*- and *tropicalis*-form might be a result of integration and / or hybridisation of both forms in Southeast Asia and South Africa. However, to date, neither morphological nor molecular evidence are in strong support of a sub-species status of either *D. c. capensis* or *D. c .tropicalis* (Smeenk et al., 1996; Amaral et al., 2009; Perrin et al., 2009).

1.3.1.2 Difficulties in the taxonomy of the common dolphin

While the two sympatric populations of the short-beaked and long-beaked morphotypes in the eastern North Pacific could be clearly distinguished as distinct species, based on both morphological and genetic grounds (Heyning & Perrin, 1994; Rosel et al., 1994), non-concordance between morphological and genetic evidence exists for common dolphin populations on a global scale (Natoli et al., 2006; Esteves & Oviedo, 2007; Amaral et al., 2009). The common dolphin in several geographical regions including the eastern North Atlantic, Australia, and New Zealand appear to be an intermediate form between the two recognized species from the eastern North Pacific (Amaha, 1994; Bell et al., 2002; Murphy et al., 2006; Westgate, 2007). All authors reported an overlap in several cranial morphometric measurements with Heyning and Perrin's (1994) published values for both *D. delphis* and *D. capensis* from Californian waters. Values derived for skull size, RL/ZW ratio, and TBL from 110 physically mature eastern North Atlantic common dolphin specimens from the UK, Ireland, Netherlands, Spain, and Portugal, overlapped with published values for *D. delphis* and *D. capensis* in the North Pacific (Murphy et al., 2006). The common dolphin in eastern North Atlantic waters is currently classified as a large-form of *D. delphis*, as specimens from the eastern North Atlantic display a larger skull size, RL/ZW ratio, and TBL as compared to the North Pacific short-beaked common dolphin (Murphy et al., 2006).

Bell et al. (2002) examined a total of 165 mature common dolphin specimens from southern Australian waters. The authors reported that overall, cranial characters were more variable than those for both species in the North Pacific. They further reported that several measurements, including RL/ZW ratio, overlapped considerably with values reported for *D. delphis* and *D. capensis* inhabiting Californian waters. While RL/ZW ratio of the common dolphin in southern Australian waters was within the range reported for male *D. capensis*,

tooth counts from all specimens examined fell within the range for *D. delphis*. Results revealed a significant overlap between potentially three morphological groups of common dolphin in southern Australian waters and the authors thereby concluded that only one, highly variable species, *D. delphis*, is present in southern Australian waters. However, recent genetic analyses demonstrated a fine-scale genetic structure for *D. delphis* off eastern South Australia and New South Wales (Möller et al., 2011).

Results from molecular analyses conducted on 199 common dolphin samples from eight geographic regions, indicated that the long-beaked morphotype may have evolved independently in different geographic regions (Natoli et al., 2006). This finding thereby contests the validity of the assumed monophyly hypothesis of this species. Differences in rostrum length documented between and within *Delphinus* sp. populations might relate to foraging strategies and niche segregation rather than taxonomy (Natoli et al., 2006; Esteves & Oviedo, 2007; Amaral et al., 2009; Pinela et al., 2011).

1.3.1.3 Taxonomic status of the common dolphin in New Zealand waters

To date, no morphometrical study specific to *Delphinus* sp. in New Zealand waters has yet been conducted (Stockin, 2008). Until recently, only the short-beaked form of the common dolphin was assumed to be present in waters off New Zealand. This assumption was predominantly based on the fact that pigmentation patterns of individuals identified in the field matched the description of *D. delphis* (Gaskin, 1968; Webb, 1973) and because New Zealand had not been included into the distributional range proposed for *D. capensis* based on a lack of morphometric analyses (Heyning & Perrin, 1994). Based on an inaccurate citation by Heyning and Perrin (1994), Rice (1998) had noted that individuals of *D. capensis* had been documented in New Zealand waters (Stockin & Visser, 2005).

Observations within the last decade revealed that colouration of New Zealand common dolphin specimens deviates from characteristics typical of *D. delphis* (Stockin & Visser, 2005). Furthermore, morphometric data provide evidence for taxonomic uncertainty (Amaha, 1994). The author investigated geographic variation in *Delphinus* sp. and reported that specimens from New Zealand shared morphological characteristics of both *D. delphis* and *D. capensis* and could not be assigned to either species. The fact that the Amaha's (1994) finding was based on only a limited sample size (n = 15, New Zealand) and pooled with Australian specimens (n = 9), warrants further investigation.

Genetic analyses indicate the importance of such a morphometric study to clarify the taxonomic status of *Delphinus* sp. in New Zealand. A haplotype from the eastern North Pacific long-beaked form was identified in a stranded physically mature New Zealand female common dolphin (WS04-28Dd) through mtDNA analyses (Stockin et al., in press.). High relatedness between this female and another physically mature individual classified as short-beaked form that stranded during the same event was established through genetic analyses. Hybridisation was one possible suggestion that has been put forward as a potential explanation for this finding (Stockin, 2008). However, the recent addition of microsatellite analyses placed the specimen WS04-28Dd within the short-beaked phylogeny (Stockin et al., in press). A high level of genetic diversity has been documented for the New Zealand common dolphin (Stockin et al., in press; Amaral et al., 2012). Stockin (2008) reported that three of the 65 haplotypes identified were shared with short-beaked populations in Argentina, the eastern North Atlantic and South Africa and three haplotypes were also shared with North Pacific and South African long-beaked populations.

Due to these documented morphological and genetic ambiguities among *Delphinus* sp. specimens in New Zealand waters, the common dolphin is currently referred to at the genus

level, as *Delphinus* sp., until the taxonomic status has been clarified in this region (Stockin & Orams, 2009).

1.3.2 Distribution

1.3.2.1 Distributional range of the common dolphin

The common dolphin is one of the most widely distributed delphinids, with populations present in both coastal and oceanic waters throughout the world's oceans between 60°N and 50°South (Di Natale & Mangano, 1983; Jefferson et al., 1993; Evans, 1994; Heyning & Perrin, 1994) (Fig. 1.8). The short-beaked common dolphin, *D. delphis*, has a more extensive distribution than *D. capensis*, with populations recorded in both the eastern and western North and South Atlantic and Pacific Oceans, the Mediterranean, and Black Sea (Di Natale & Mangano, 1983; Amaha, 1994; Heyning & Perrin, 1994) (refer to Fig. 1.8). Distribution of the short-beaked common dolphin in the eastern North Atlantic ranges from approximately 60°N (southwest of Norway) (Evans, 1994) to the southern limit of the western Sahara Equator (Pinela et al., 2011). In the western North Atlantic *D. delphis* occurs in waters off Newfoundland to Florida (Heyning & Perrin, 1994) and in the western South Atlantic it has been recorded off Brazil, Uruguay, and Argentinea (Bastida & Rodríguez, 2006; Tavares et al., 2010; Juri et al., 2012). In the Pacific, the short-beaked form has been documented off southern Japan, southern Australia, and New Zealand (Gaskin, 1968; Amaha, 1994; Bell et al., 2002) (refer to Fig. 1.8). To date, very few *D. delphis* have been recorded from the south-west Indian Ocean (Samaai et al., 2005) and it has not been confirmed from the eastern Indo Pacific region.

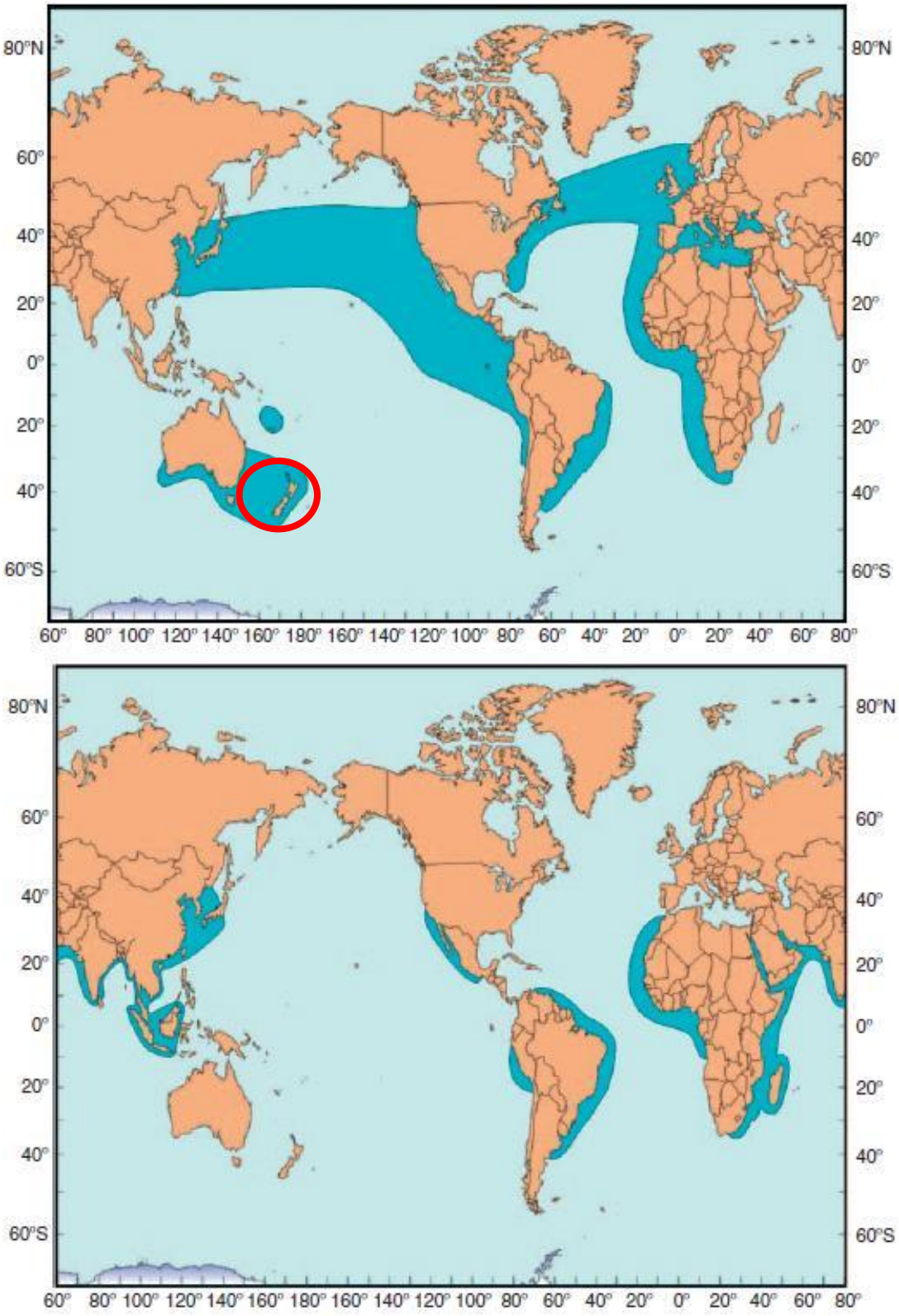

Figure. 1.8. Global distribution of the short-beaked (top) and long-beaked common dolphin (bottom) adapted from Perrin (2009). Note: The circle indicates New Zealand.

It is, however, possible that the species might be present in the Northern Yellow and East China Seas (Wang, 1985; Amaha, 1994). A study conducted within the last decade, has identified 2 out of 72 common dolphin specimens examined from waters south of Madagascar as *D. delphis* (Samaai et al., 2005). Distribution of the long-beaked common dolphin, *D. capensis*, is currently less well known, due to the fact that until 1994 only one species, *D. delphis*, was recognized. In the western South Atlantic, populations occur off the coast of central-eastern Venezuela and the South Brazilian Bight down to Argentina in the south (Heyning & Perrin, 1994; Esteves & Oviedo, 2007, Tavares et al., 2010; Juri et al., 2012). The species has also an extensive distributional range in eastern South Atlantic waters off the west coast of Africa, south of the western Sahara (Jefferson et al., 1997; Natoli et al., 2006) (refer to Fig. 1.8). Populations in the Pacific Ocean are present in waters off Baja California, central / southern California, Peru, Japan, Korea, and Taiwan (Amaha, 1994; Heyning & Perrin, 1994).

Populations of both species, *D. delphis* and *D. capensis*, occur sympatrically off California, Japan, South America, and off the south-western African coastline in waters between the Western Sahara and the Senegal River (Amaha, 1994; Heyning & Perrin, 1994; Natoli et al., 2006; Juri et al., 2012) (refer to Fig. 1.8). However, while *D. delphis* occurs in both inshore and offshore waters, distribution of *D. capensis* appears to be more restricted to coastal and warmer waters (Heyning & Perrin, 1994; Gill & Burke, 1999; Jefferson & Van Waerebeek, 2002).

1.3.2.2 Distribution of the common dolphin within New Zealand waters

In New Zealand, *Delphinus* sp. occurs in most waters around the North Island, particularly along the north-eastern coast between the Bay of Islands and the Bay of Plenty (Stockin, &

Orams, 2009) (refer to Fig. 1.9). The potential existence of three *Delphinus* sp. sub-populations within New Zealand waters, namely: a coastal, an oceanic, and a Hauraki Gulf (HG) population has been investigated through genetic analyses (Stockin et al., in press).

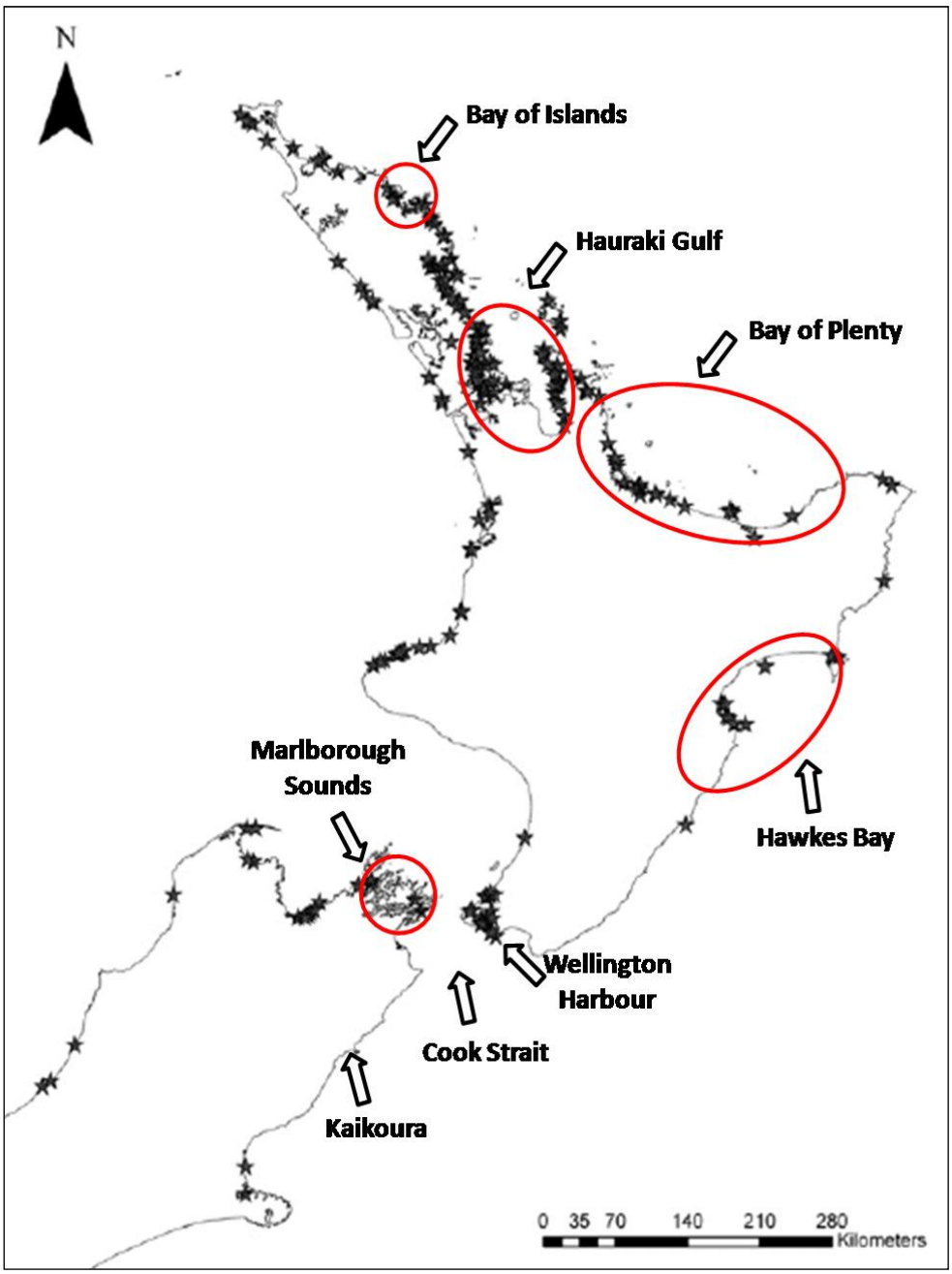

Figure 1.9. Map of New Zealand adapted from Stockin & Orams (2009) displaying distribution of *Delphinus* sp. strandings documented between 1961 and 2003, and regions referred to within the text.

This investigation was initiated based on the fact that the common dolphin is the most frequently observed cetacean within the HG (refer to Fig. 1.9) and the hypothesis that the year round presence in that particular region suggests site fidelity of at least some individuals (Stockin, 2008). Initial mtDNA analysis had identified small significant differences between the potential HG and the putative coastal and oceanic populations, while the latter two were not differentiated (Stockin & Orams, 2009). However, Stockin (2008) had highlighted the constraints of mtDNA data and pointed out that no definite conclusions regarding potential population segregation within New Zealand waters could be drawn in the absence of further molecular analyses. Recently, Stockin et al. (in press) demonstrated high levels of genetic diversity among New Zealand *Delphinus* sp. and suggested that the finding could be a result of potential population sub-structure that had been hypothesized to exist within New Zealand waters (Stockin, 2008). Latest analyses based on microsatellite data provide contrasting results to the mtDNA data (Stockin et al., in press). The authors reported that microsatellite data does not support a population separation of HG *versus* non-HG *Delphinus* sp., but suggests a potential segregation instead between the putative coastal and offshore populations (Stockin et al, in press.).

The common dolphin is further regularly seen in the Wellington Harbour region (refer to Fig. 1.9) and large schools have been sighted in Cook Strait (Gaskin, 1968; Webb, 1973). Occurrence around the South Island appears to be more restricted, with sightings mainly in the Marlborough Sounds (Webb, 1973) and Kaikoura (Gaskin, 1968; Yin, 1999) (refer to Fig. 1.9).

1.3.3 Maturity status

Assessments of important life history traits such as growth and age at sexual maturity (ASM) and age at physical maturity (APM) of *D. delphis* have increased in recent years, especially in the Northern Hemisphere (Perrin & Reilly, 1984; Silva & Sequeira, 2003; Murphy & Rogan, 2006).

1.3.3.1 Sexual maturity in the common dolphin

Several factors that influence the age at which ASM is attained include, but are not limited to, the health status of an individual and the quality and quantity of prey (Miller, 2007). Consequently, ASM for common dolphin populations differs between geographical regions. Early records from the eastern North Atlantic suggest male *D. delphis* in French waters attain sexual maturity TBL between 190.0 and 200.0 cm (Collet, 1981). The author further noted that the onset of sexual maturity in males and females was most likely to occur at the age of ≥ 6 and between 5 and 7 years for both sexes, respectively. More recent results provide evidence that short-beaked common dolphin males pooled from Irish and French waters attain sexual maturity at an average age of 11.9 years (Murphy et al., 2005), while ASM in individuals of the same species and sex is attained at a slightly earlier age (9.5 years) in the western North Atlantic (Westgate & Read, 2007). In contrast, sexual maturity in female *D. delphis* inhabiting Irish, western North Atlantic, and eastern tropical Pacific waters is attained at an average age of 8.2 (Murphy et al., 2009), 8.3 (Westgate & Read, 2007), and 7.9 years (Danil & Chivers, 2007), respectively. Likewise, similar body lengths at ASM have been estimated for females from Irish (188.0 cm, Murphy et al., 2009) and eastern tropical Pacific waters (186.5cm, Danil & Chivers, 2007). In New Zealand, male and female

Delphinus sp. obtain sexual maturity at a TBL of 197.5 and 183.4 cm, respectively and males reach ASM at 9.3 years of age (Stockin et al., 2011). ASM of common dolphin females has not yet been estimated owing to small sample size (Stockin et al., 2011).

1.3.3.2 Physical maturity in the common dolphin

After attaining sexual maturity, odontocetes typically continue to grow for several years until growth ceases and physical maturity is attained (Chivers, 2002). Mean TBL of physically mature *D. delphis* typically ranges between 180.0 and 244.0 cm (Evans, 1994; Murphy & Rogan, 2006), with mature males being approximately five percent larger than females (Evans, 1994; Silva & Sequeila, 2003). Asymptotic body length, indicative of physical maturity, is reached at a total body length of 211.6 and 197.4 cm in short-beaked common dolphin males and females from Irish waters, respectively (Murphy & Rogan, 2006). The authors reported that males and females attain asymptotic lengths at approximately 11 and 9 years of age, respectively. Asymptotic length (215.9 cm) is attained at a much earlier age (between approximately 5 to 6 years) in *Delphinus* sp. from eastern south Brazil (Siciliano et al., 2007). However, the authors were limited by sample size (n = 20) and did not analyze sexes separately. Female short-beaked common dolphins from eastern tropical Pacific waters reach asymptotic lengths at approximately 197.2 cm (Danil & Chivers, 2007). In New Zealand, male and female *Delphinus* sp. attain asymptotic body lengths at an estimated length of 204.5 and 199.9 cm, respectively (Stockin et al., 2011). APM has not yet been determined for this population owing to small sample size (Stockin et al., 2011).

1.4 Conservation significance of this research

1.4.1 Conservation status of the common dolphin

As identified herein, a paucity of knowledge regarding taxonomy and some life history parameters exists for New Zealand *Delphinus* sp. In addition, abundance and density estimates are not yet known (Stockin & Orams, 2009). The common dolphin is subject to several anthropogenic impacts in New Zealand waters, including by-catch and net entanglement (Stockin et al., 2009), tourism (Stockin et al., 2008b), and pollution (Stockin et al., 2007). Despite these factors, the common dolphin is currently regarded as 'not threatened' at the national level (Baker et al., 2010). While it is recognized that low confidence can be placed in this listing owing to 'poor data', the panel justifies the 'not threatened status', as no evidence exists to support a population decline (Baker et al., 2010). As a consequence, no national species-specific action plan exists for the common dolphin (Suisted & Neale, 2004). Due to the reasons listed above, the importance to re-classify New Zealand *Delphinus* sp. as 'data deficient' has been stressed, unfortunately without success (Stockin & Orams, 2009). The importance for population specific threat status assessment is apparent when viewing the conservation status of *Delphinus* sp. on a worldwide scale. While *D. delphis* is classified as a species of 'least concern' by the IUCN globally (Hammond et al., 2008a), the Mediterranean sub-population has been classified as 'endangered' (Bearzi, 2003; Bearzi et al., 2003; Piroddi et al., 2011). Furthermore, *D. d. ponticus*, a sub-species inhabiting the Black Sea, is listed as 'vulnerable' (Birkun Jr., 2008). The 'data deficient' status has been recognized for *D. capensis* (Hammond et al, 2008b). Both subspecies, *D. c. capensis* from the Pacific and Atlantic, and *D. c. tropicalis* from the Indo-Pacific are currently not listed independently (Hammond et al, 2008b).

1.4.2 Potential implications for conservation and management of the common dolphin in New Zealand waters

In order to gain scientific knowledge about *Delphinus* sp. in New Zealand waters, the New Zealand Common Dolphin Project (NZCDP) was initiated in 2002 under the auspices of Massey University (Stockin, 2008). The current morphological study is conducted as part of the NZCDP and is the first morphometric study to solely focus on the New Zealand common dolphin, with the main aim to provide further information on the taxonomic status of *Delphinus* sp. from New Zealand waters.

Should morphometric data be suggestive of potential population segregation, impact of net entanglement and by-catch in the jack mackerel, *Trachurus novaezelandiae*, fishery (Stockin et al., 2009) could be much higher on the common dolphin population in New Zealand waters than originally anticipated. A potential implication for conservation status and management of *Delphinus* sp. in New Zealand waters could be the possible stronger necessity for revision of the national threat status classification of this delphinid, should morphometric data from this study provide evidence suggestive of the presence of (1) individuals with characteristics unambiguous of the long-beaked form; and / or (2) potential population segregation within New Zealand waters.

1.5 Research aims and thesis structure

Owing to the relative inaccessibility of the marine habitat, the reliance on infrequently stranded and by-caught individuals for scientific investigations and hence the long timeframes it may take to obtain large enough sample sizes to conduct morphological studies, taxonomic status of several delphinids and their phylogenetic relationships has not yet been clarified (Perrin, 1989; LeDuc et al., 1999; Taylor, 2005; Caballero et al., 2008). The common dolphin, *Delphinus* sp., provides a good example of a cosmopolitan genus with highly confused taxonomy (Amaha, 1994; Smeenk et al., 1996; Jefferson & Van Waerebeek, 2002; Murphy, et al., 2006; Juri et al., 2012). The main purpose of the current skull morphometric study was to provide further information regarding the taxonomic status of this genus in New Zealand waters to aid ongoing conservation and management efforts.

Following the traditional format, this thesis comprises four chapters, namely: Introduction, materials & methods, results, and discussion.

Chapter 1: Introduction

The first chapter provides background information to this study and details the aims of the research.

Chapter 2: Material & Methods

This chapter outlines the skull preparation process, the different manual methods employed for data acquisition, and statistical treatment of the data.

Chapter 3: Results

Chapter three outlines the results of the study. Research questions were addressed in the order outlined in section 1.2.2. The results chapter is comprised of two parts and the set of objectives addressed in each part and associated hypotheses are outlined below.

PART I: Cranial maturity indicators and skull growth

The first part of this chapter investigates cranial development and validity of cranial components as cranial maturity indicators and aims to:

1. Assess the cranial maturation process (suture data)
2. Determine a cranial maturity cut-off point and age at cranial maturity (suture data)
3. Enable cranial maturity status determination and age range estimation for specimens of unknown age and unknown maturity status (suture data)
4. Assess the validity of TBL and cranial elements as indicators of cranial maturity (metric and non-metric data, relative skull weight, and tooth condition)

Hypotheses:

Age at cranial maturity

It is anticipated that New Zealand *Delphinus* sp. attain cranial maturity at approximately the same age as asymptotic TBL is reached in *D. delphis* from Irish waters (males: 11 years, females: 9 years), as determined by Murphy et al. (2006).

Cranial maturity indicators

Given that the developmental status of interalveolar septa has been employed to decipher cranially mature specimens (Tavares et al., 2010) it is assumed that this feature will also display a high discriminative power in the present study.

Skull specimens available for the present study, for which results from the first part of chapter 3 indicated cranial maturity, were included in subsequent analyses. These were in relation to sexual dimorphism, taxonomy, geographic variation, and precision estimates between two metric data acquisition methods in the second part of chapter 3, which are outlined below.

PART II: Sexual dimorphism, taxonomy, geographic variation, and precision of two metric data acquisition methods

The second part of this chapter seeks to investigate:

1. Presence / absence and degree of sexual dimorphism in cranial characters of the New Zealand common dolphin (metric and non-metric data)

2. Whether potential sexual dimorphic features are associated with a certain functional complex of the skull (metric data)

3. The taxonomic status of the New Zealand common dolphin (metric data)

4. Potential geographic variation in cranial features between specimens from HG and non-HG waters (metric and non-metric data)

5. Precision between linear measurements obtained with vernier / digital callipers and through landmark digitization with a microscribe (metric data)

Hypotheses:

Sexual dimorphism

Based on Amaha (1994), it is anticipated that a high degree of cranial sexual dimorphism, particularly in the feeding apparatus, will be identified in the present study.

Taxonomy

It is assumed that RL/ZW ratios of New Zealand specimens are of 'intermediate status' between the two currently recognized species (Amaha, 1994; Stockin & Visser, 2005).

Geographic variation

Due to small sample size, limited confidence is placed in detecting significant geographic variation among *Delphinus* sp. from New Zealand waters.

Precision of two metric data acquisition methods

A high degree of precision between calliper and microscribe recordings is anticipated to be associated with measurements for which landmarks were unambiguously locatable on the

skull (e.g. a point where 2 or 3 sutures meet). A lesser degree of precision is expected for characters with less easily identifiable reference points.

Chapter 4: Discussion

Results are discussed. Suggestions and recommendations for future research are also provided based on findings and limitations of the present study.

CHAPTER 2

Materials & Methods

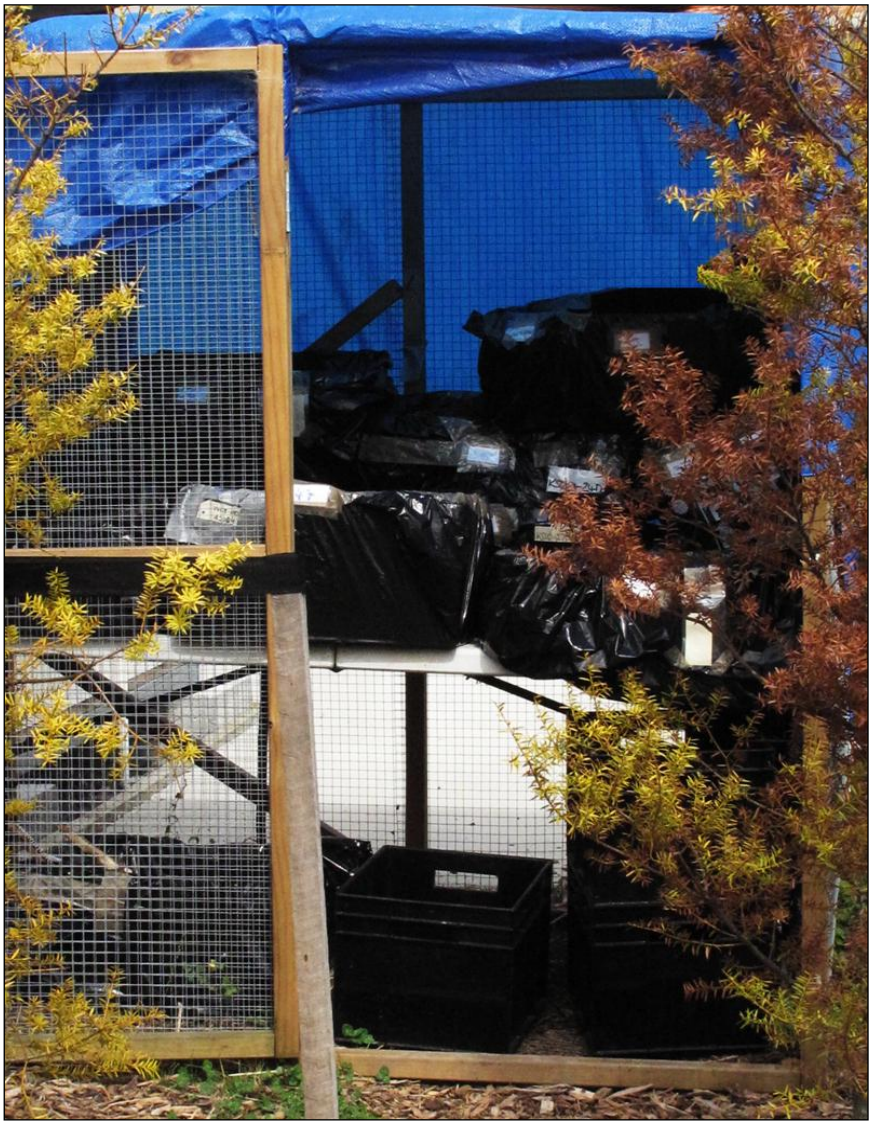

Plate 2.1. Enclosure in which *Delphinus* sp. skull specimens from New Zealand waters were kept in boxes immersed with horse manure to aid the final decomposition of flesh after manual removal of most superficial tissues.

2.1 Materials

2.1.1 Skull specimens

Skeletal material for the current study was obtained from two sources (1) intact frozen *Delphinus* sp. heads dissected during necropsies at Massey University; and (2) cleaned skulls provided by the Museum of New Zealand Te Papa Tongarewa, Wellington. The former samples required removal of tissues and subsequent cleaning prior to morphometric analyses.

2.1.2 Additional biological data

Information on sex, reproductive developmental status (i.e. sexually immature and mature), total body length (TBL), and location of the stranded or by-caught common dolphin were available from the NZCDP database (Massey University, unpubl. data) for the majority of skulls stored at Massey University, as well as for some specimens housed at the Museum of New Zealand Te Papa Tongarewa and included in the present study. As outlined in Stockin et al. (2011), sexual maturity status assessment on reproductive organs had been conducted following Murphy et al. (2005; 2009). TBL for the majority of specimens had been determined during necropsies conducted at Massey University or by Department of Conservation (DoC) officers in the field.

Age data, information on whether females had been lactating or pregnant, and cause of death were available for some specimens. Age had been obtained by counting growth layer groups (GLG) in dentine as part of an ongoing life history study under the NZCDP. Biological information for some skull specimens housed at the Museum of New Zealand Te Papa Tongarewa was available from the Museum's database. In total, three of the skulls available had been obtained from females that had been captured and held captive in Marineland, Napier, Hawkes Bay for 11 to approximately 30 years.

2.2 Manual Methods

2.2.1 Initial examination (tooth condition)

Prior to preparation of the Massey University samples, heads were defrosted in labelled plastic crates for a minimum duration of 24 hours. Tooth counts were conducted on each jaw. In addition, the general condition of each individual tooth in both the maxillary and mandibular bones was recorded on a data sheet according to seven predefined categories: Not erupted, partly erupted, normal (fully intact), partly worn, worn to gum line, broken, and missing (refer to Appendix 1).

Ten teeth, preferentially from the lower left jaw / mandible and always from the mid-lower jaw region (assuming no damage), were carefully extracted with a knife and stored in ethanol for the purpose of life history analyses. When removing teeth, effort was undertaken, where possible, to leave tooth sockets intact in order to enable subsequent tooth socket counts on cleaned jaw bones.

2.2.2 Skull preparation

Eyes and most of the superficial flesh, blubber, and brain mass were manually removed from each skull with a knife and scalpel. The mandibles were left attached to the skull to prevent bone damage. Identification (ID) tags were attached to each stripped skull and each mandible with thin metal wire to enable correct identification at a later stage. Stripped and labelled skulls were subsequently left to drain in numbered plastic crates for a total duration of 24 hours (refer to Plate 2.2).

Plate 2.2. New Zealand *Delphinus* sp. skull specimen left to drain after manual removal of most superficial tissue.

To aid the decomposition process of the remaining flesh, each stripped skull was immersed in horse (*Equus* sp.) manure. For this purpose, cardboard boxes measuring approximately 50 x 30 x 30 cm were wrapped into two refuse bags measuring 83.8 x 101.4 cm and securely taped to protect boxes from precipitation when placed outdoors. The bottom of each box was filled with a ca. 3 - 5 cm thick layer of horse manure onto which the stripped, drained, and labelled skull was placed. Each skull was then completely immersed in horse manure and the lids loosely closed, leaving a gap to ensure necessary air circulation. Boxes were labelled with consecutive numbers and with the ID of the respective dolphin skull. All boxes were placed into a locked wire-meshed enclosure for security and further protection from the environmental elements. Both the roof and back wall of the enclosure were covered with

plastic mats in order to prevent rain entering the boxes, yet allowing maximum air circulation (refer to Plate 2.1).

Skulls were recovered after a period of three to four weeks of immersion, depending on the size of the skull and degree of remaining tissue on the skull at immersion (refer to Plate 2.3).

Plate 2.3. Recovery of a New Zealand *Delphinus* sp. skull specimen after immersion in horse manure for several weeks to aid the final decomposition of remaining flesh attached after manual removal of most superficial tissue.

Loosened teeth were removed and placed into labelled sealable plastic bags for ageing. The tympanoperiotic were also stored dry. At this stage of the decomposition process, the mandibles of most skulls had become detached. Each skull and respective mandibular bones were placed back into the boxes and re-covered with fresh horse manure. Water was added to keep the top layer of manure moist in order to aid the final stages of the decomposition process. After a further five-week period, each skull and associated lower jaw bones were retrieved and cleaned of the horse manure using tepid water, a nylon brush, toothbrush, and

pincers. Cleaned skulls were arranged outside in the sun to allow the bones to dry and bleach. To prevent the bones from soaking in the rain, each skull and associated mandibles were placed onto a piece of wire-mesh measuring approximately 50 x 30 cm and placed on top of the empty wrapped-up cardboard boxes. After four weeks, the bones were inverted to facilitate drying / bleaching of the ventral side. Following another four-week period, the bleached skulls were moved indoors for three days to ensure that the bones were completely dry prior to being wrapped in bubble wrap and securely stored in cardboard boxes until morphometrical analyses commenced.

2.2.3 Cranial sutures

Degree of fusion of 16 cranial suture lines (after Van Waerebeek, 1993; González, 2002; Chen et al., 2011; Galatius et al., 2011) were recorded for each skull specimen separately for both sides of the skull (Table 2.1; Figs. 2.1 and 2.2). For the majority of sutures, the degree of fusion was categorized using a scoring system differentiating three fusion stages (adapted from Van Waerebeek, 1993). In addition, a forth suture stage category was introduced following Galatius et al., 2011 (Table 2.2). Only two fusion stages were differentiated for sutures 1 - 3 due to difficulties in discriminating fusion stages 1 and 2 (refer to Table 2.2). Examples of the different stages of fusion of a selected number of sutures are displayed in Appendices 2 and 3.

Table 2.1. List of cranial sutures assessed for cranial maturity status determination of *Delphinus* sp. skulls from New Zealand waters. Note: Nr. = number; Abbr. = abbreviation; l/r = left and right side of the skull, respectively; m = suture located along midline of the skull; Ref. = reference; VW = Van Waerebeek, 1993; Go = González, 2002; C = Chen et al, 2011; G = Galatius et al. 2011.

Nr.	Abbr.	Side	Cranial sutures	Ref.
1	max-fr	l/r	maxilla-frontal	Go
2	premax-max	l/r	premaxilla-maxilla	Go
3	na-fr	l/r	nasal-frontal	Go
4	fr-fr	m	frontal-frontal	Go
5	fr-in	l/r	frontal-interpariatal	Go
6	fr-or	l/r	frontal-orbitospenoid	G
7	la-fr	l/r	lacrimal-maxilla-frontal	VW
8	pa-ex	l/r	parietal-exoccipital	G
9	pa-fr	l/r	parietal-frontal	G
10	pal-max	l/r	palatine-maxilla	VW
11	pal-pal	m	palatine-palatine	Go
12	pa-so	l/r	parietal-supraoccipital	G
13	pt-ba	l/r	pterygoid-basioccipital	VW
14	pt-pal	l/r	pterygoid-palatine	VW
15	so-ex	l/r	supraoccipital-exoccipital	C
16	zy-pa-ex	l/r	zygomatic-parietal-exoccipital	VW

Table 2.2. Suture scoring system employed for assessing cranial maturity status of *Delphinus* sp. skulls from New Zealand waters. Note: Ref. = Reference; VW = Van Waerebeek (1993); G = Galatius et al. (2011); T.S. = devised in this study.

Fusion stage	Description Sutures 1 - 3	Ref.
0	No fusion, elements can be moved freely	T.S.
3	Fused, elements cannot be moved	T.S.
	Sutures 4 - 16	
0	No fusion, cranial elements can be moved freely	VW
1	Limited fusion, cranial elements cannot be moved, sutures lines clearly visible at all points	VW
2	Partial obliteration of suture line	VW
3	Complete obliteration of suture line	G

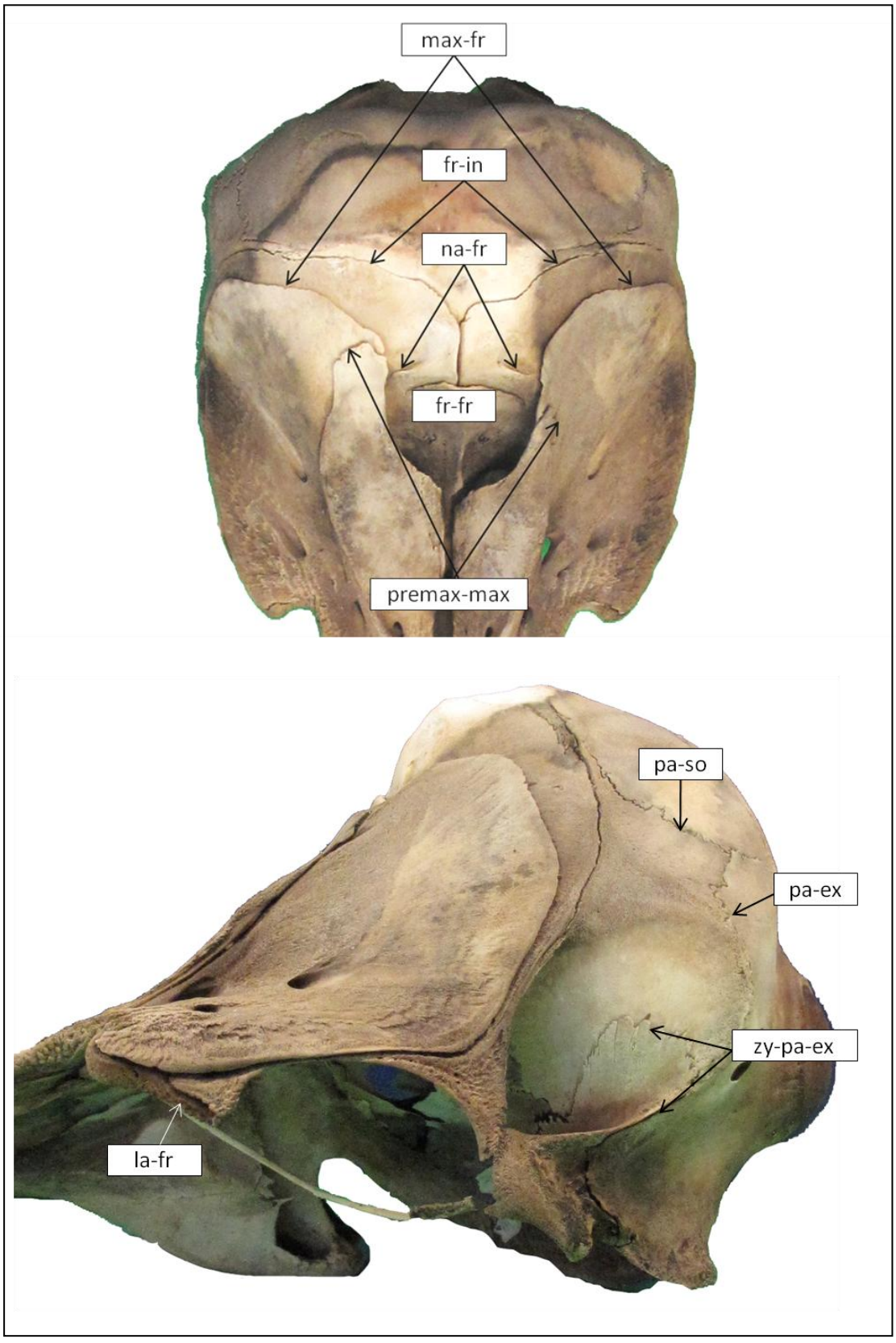

Figure 2.1. Selection of cranial sutures for cranial maturity determination in *Delphinus* sp. skulls from New Zealand waters in dorsal (top) and lateral (bottom) view. For suture abbreviation refer to Table 2.1.

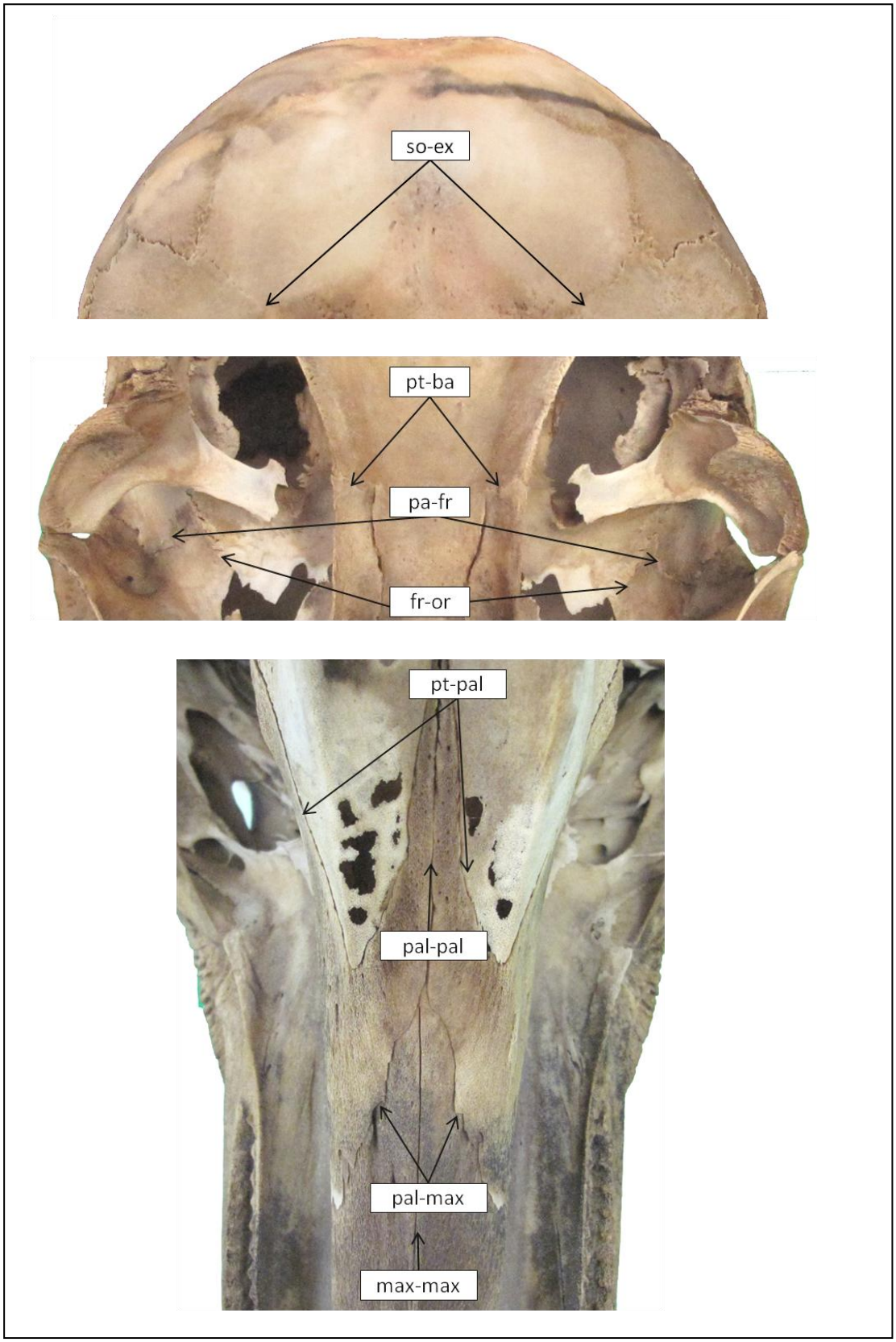

Figure 2.2. Selection of cranial sutures for cranial maturity determination in *Delphinus* sp. skulls from New Zealand waters in occipital (top) and ventral (middle and bottom) view. For suture abbreviation refer to Table 2.1.

The extent of rostral fusion was classified according to 5 categories (Table 2.3) in order to assess the validity of different degrees of premaxilla-maxilla fusion as cranial maturity indicator for *Delphinus* sp. from New Zealand waters. Distal fusion was not included as a category, given that it has been determined as an unreliable indicator of cranial maturity in the common dolphin (Heyning & Perrin, 1993). The category 'fusion up to the end of the premaxilla fusion' employed by Amaha (1994) was not adapted in the present study, owing to the author's statement that high individual variability exists in the length of premaxilla fusion. Instead categories 3 and 4 (refer to Table 2.3), were devised in the present study.

Table 2.3. Categories of rostral fusion differentiated in the present study. Note: A = Amaha (1994); J&VW = Jefferson &Van Waerebeek (2002); T.S. = devised in this study.

Category	Description of extent of rostral fusion	Ref.
1	< 50% of the length of the rostrum	J & VW
2	= 50% of the length of the rostrum	J & VW
3	> 50%, but < 75% of the length of the rostrum	T.S.
4	> 75%, but < base of rostrum	T.S.
5	to base of rostrum	A

2.2.4 Metric measurements

Prior to taking linear measurements, rostrum condition of each specimen was graded based on the damage to the rostrum tip using criteria devised in this study (Table 2.4; Fig. 2.3).

Table 2.4. Rating criteria for assessing rostrum intactness of *Delphinus* sp. skulls from New Zealand waters devised in the present study.

Category	Description
1	Fully intact rostrum
2	Tip of the tooth row missing, but anterior most projection of at least one premaxilla fully intact
3	Minor damage to tips of both premaxillae
4	Major damage to tips of both premaxillae

Figure 2.3. Rostrum tip ratings for *Delphinus* sp. skulls from New Zealand waters. Categories 1 to 4: (1) Fully intact rostrum; (2) Fully intact premaxillae, but protrusion of the tooth rows is damaged; (3) Minor damage to premaxillae tips; (4) Major damage to premaxillae tips.

To avoid inter-observer bias all cranial measurements were taken by the author. Following Purdie (1994) and Murphy et al. (2006), all initially proposed cranial characters (taken from the literature and devised by the author) were repeatedly taken on a number of randomly allocated skulls (n = 5) to determine whether the proposed measurements could be measured consistently. During this test phase, several metric measurements were discarded due to difficulties in determining points of reference and because the measurement error (ME) exceeded 0.5 mm. Following this process, a total of 71 metric measurements were deemed appropriate for reproduction and obtained from each skull. Of those, 60 were previously taken by Perrin (1975), Amaha (1994), Bell et al. (2002), Murphy et al. (2006), Westgate (2007), and Miramontes Sequeiros et al. (2010). The remaining 11 characters were devised by the author (refer to Table 2.5, Figs. 2.4 to 2.8).

All linear measurements were taken to an accuracy of 0.1 mm using digital callipers (Measurmax, 300 mm) for measurements of ≤ 300 mm and standard manual vernier callipers (Measurmax, 600 mm) for measurements > 300 mm in length. Following Westgate (2007) each skull was securely fixed to a table using blu-tack and all measurements were taken with the rostrm tip resting on the tabletop. All metric characters, except for condylobasal length (CBL), rostrum length (RL), distance from tip of rostrum to external (REXN), and internal (TRIN) nares, were recorded directly on each specimen. Both points of reference (tip of rostrum and the most posterior point of occipital condyle) for the CBL measurement could not directly be recorded on the skull with the callipers, but had to be transferred onto paper that had been securely fixed on the table underneath the specimen. This was necessary, as the depth of the manual calliper was not deep enough to be placed over the skull and both points of reference were therefore marked on paper using metal rulers (S. Murphy, pers. comm.). RL measurements (tip of rostrum to base of rostrum) were recorded in a straight line from the

midpoint of the base of the rostrum to a line marked down on paper between both premaxillae tips, representing the most anterior point of the rostrum. This was necessary as (1) the position of the antorbital notches, which marked the reference points for the base of the rostrum, was slightly asymmetrical; and (2) length of the left and right tip of the premaxillae differed slightly in most specimens (refer to Fig. 2.4). The most anterior tip of the premaxillae was also marked on paper in order to determine REXN and TRIN given that the tip of the rostrum also did not fall in a straight line with the respective reference point at the external and internal nares for determining those to metric characters (refer to Figs. 2.4 and 2.6).

Each calliper measurement was taken three times on each skull that had been stored at Massey University to assess measurement error (ME). Owing to the low ME associated with individual characters (variance: < 0.001 - 0.079) and time constraints of the study, all metric measurements on skull specimens housed at The Museum of New Zealand Te Papa Tongarewa were only taken once.

Table 2.5. Description of metric measurements conducted on *Delphinus* sp. skulls from New Zealand waters. Note: L. = location on skull; Nr. = number; Abbr. = abbreviation; l = left side of the skull = r = right side of the skull; m = at midline of skull; w = width measurement; Ref. = reference; P = Perrin (1975); A = Amaha (1994); Bell et al., 2002; M = Murphy (2006); W = Westgate (2007); MS = Miramontes Sequeiros et al. (2010); T.S. = devised in this study.

L.	Nr.	Abbr.	Side	Definition of character abbreviations	Ref.
	1	CBL	m	Condylobasal length: Tip of rostrum to most posterior point of occipital condyles	P
	2	RL	m	Rostrum length: Tip of rostrum to base of rostrum (line across posterior limit of antorbital notches)	P
	3	ANOC(L)	l	Length between antorbital notch to midpoint between occipital condyles	M
	4	ANOC(R)	r	Length between antorbital notch to midpoint between occipital condyles	T.S.
	5	LANFC (L)	l	Length between antorbital notch to frontal crest	T.S.
	6	LANFC (R)	r	Length between antorbital notch to frontal crest	T.S.
	7	REXN	r	Distance from tip of rostrum to anterior base of external nares (to mesial end of posterior margin of naris)	P
	8	ANFPR	m	Distance from posterior limit of antorbital notches to posterior end of fusion of premaxillae	A
	9	LFPR	m	Length of fusion of premaxillae	A
D	10	WRB	w	Width of rostrum at base: Along line between posterior limit of antorbital notches	P
O	11	WPRB	w	Width of premaxilla at base: Along line between posterior limit of antorbital notches	A
R	12	WTB	w	Width of triangle at base: Along line between posterior limit of antorbital notches	T.S.
S	13	WT30	w	Width of triangle 30 mm anterior to base	T.S.
A	14	WR60	w	Width of rostrum 60 mm anterior to base	P
L	15	WPR60	w	Width of premaxilla 60 mm anterior to base	M
	16	WR1/2	w	Width of rostrum at midlength: Measured from posterior end	P
	17	WPR1/2	w	Width of premaxilla at midlength of rostrum: Measured from posterior end	P
	18	WR3/4	w	Width of rostrum at 3/4 length: Measured from posterior end	P
	19	WPR3/4	w	Width of premaxilla at 3/4 length: Measured from posterior end	M
	20	LSOW	w	Least supraorbital width	P
	21	GWPR	w	Greatest premaxillae width: Measured adjacent to external nares	P
	22	GWLPR	l	Greatest width of right premaxilla: Measured adjacent to external nares	A
	23	GWRPR	r	Greatest width of left premaxilla: Measured adjacent to external nares	A
	24	GWM	w	Greatest width across both maxillae	T.S.

Table 2.5 continued.

L.	Nr.	Abbr.	Side	Definition of character abbreviations	Ref.
	25	GWLM	l	Greatest width of maxilla: Measured to suture with premaxilla	T.S.
	26	GWRM	r	Greatest width of maxilla: Measured to suture with premaxilla	T.S.
	27	GWEN	w	Greatest width of external nares	P
	28	GLLPTF	l	Greatest length (height) of post-temporal fossa (to external margin of raised suture)	P
L	29	HLPTF	l	Vertical height of post-temporal fossa	P
A	30	WLPTF	l	Horizontal width of post-temporal fossa	M
T	31	LOL	l	Orbit length: Measured from apex of preorbital process to apex of postorbital process	P
E	32	GLRPTF	r	Greatest length (height) of post-temporal fossa (to external margin of raised suture)	W
R	33	HRPTF	r	Height of post-temporal fossa	W
A	34	WRPTF	r	Width of post-temporal fossa	W
L	35	ROL	r	Orbit length: Measured from apex of preorbital process to apex of postorbital process	P
	36	MaxDLTF	l	Maximum diameter of temporal fossa	P
	37	MaxDRTF	r	Maximum diameter of temporal fossa	P
	38	LLUTR	l	Length of upper tooth row: From hindmost margin of hindmost alveolus to tip of rostrum	P
	39	LRUTR	r	Length of upper tooth row: From hindmost margin of hindmost alveolus to tip of rostrum	P
	40	TRIN	m	Distance from tip of rostrum to internal nares (to midpoint between mesial end of posterior margin of pterygoids	P
	41	GLLPT	l	Greatest length of pterygoid	P
V	42	GLRPT	r	Greatest length of pterygoid	P
E	43	WPT	w	Width of pterygoids	P
N	44	GWIN	w	Greatest width of internal nares	P
T	45	PROW	w	Greatest preorbital width	P
R	46	POOW	w	Greatest postorbital width	P
A	47	ZW	w	Greatest width across zygomatic process of squamosal	P
L	48	WBOC	w	Width of basioccipital measured at crests btw jugular notches	W
	49	WBOCS	w	Width between basioccipital crests at basioccipital-sphenoid suture measured at top of margins	P
	50	LLSQ	l	Greatest length of squamosal measured from lower limit of suture of squamosal and exoccipital	T.S.

Table 2.5 continued.

L.	Nr.	Abbr.	Side	Definition of character abbreviations	Ref.
	51	LRSQ	r	Greatest length of squamosal measured from lower limit of suture of squamosal and exoccipital	T.S.
	52	LLLAC	l	Length of antorbital process of lacrimal	P
O	53	LRLAC	r	Length of antorbital process of lacrimal	P
C	54	WPA	w	Width of parietal at suture with maxilla and frontal crest	P
C	55	GWPA	w	Greatest width of parietal between temporal fossae	W
I	56	LWPA	w	Greatest width of parietal measured at raised suture of temporal fossae	B
P	57	GWEX	w	Greatest width of exoccipital measured at sutures with squamosals	T.S.
I	58	GWEXL	l	Greatest width of exoccipital measured from foramen magnum to rim of post-temporal fossa	MS
T	59	GWEXR	r	Greatest width of exoccipital measured from foramen magnum to rim of post-temporal fossa	MS
A	60	HBC	m	Vertical external height of braincase from frontal crest to basioccipital at condyle	P
L	61	HFCFM	m	Vertical external height of braincase from frontal crest to top of foramen magnum	M
	62	HFM	m	Greatest height of foramen magnum	MS
	63	WFM	w	Greatest width of foramen magnum	A
M	64	LLM	l	Greatest length of mandible (ramus)	P
A	65	HLM	l	Greatest height (depth) of mandible at right angles to greatest length	P
N	66	LMF	l	Length of mandibular fossa: Measured to mesial rim of internal surface of condyle	P
D	67	LLLTR	l	Length of lower tooth row: From hindmost margin of last alveolus to tip of mandible	P
I	68	LRM	r	Greatest length of mandible (ramus)	P
B	69	HRM	r	Greatest height (depth) of mandible at right angles to greatest length	P
L	70	RMF	r	Length of mandibular fossa: Measured to mesial rim of internal surface of condyle	P
E	71	LLRTR	r	Length of lower tooth row: From hindmost margin of last alveolus to tip of mandible	P

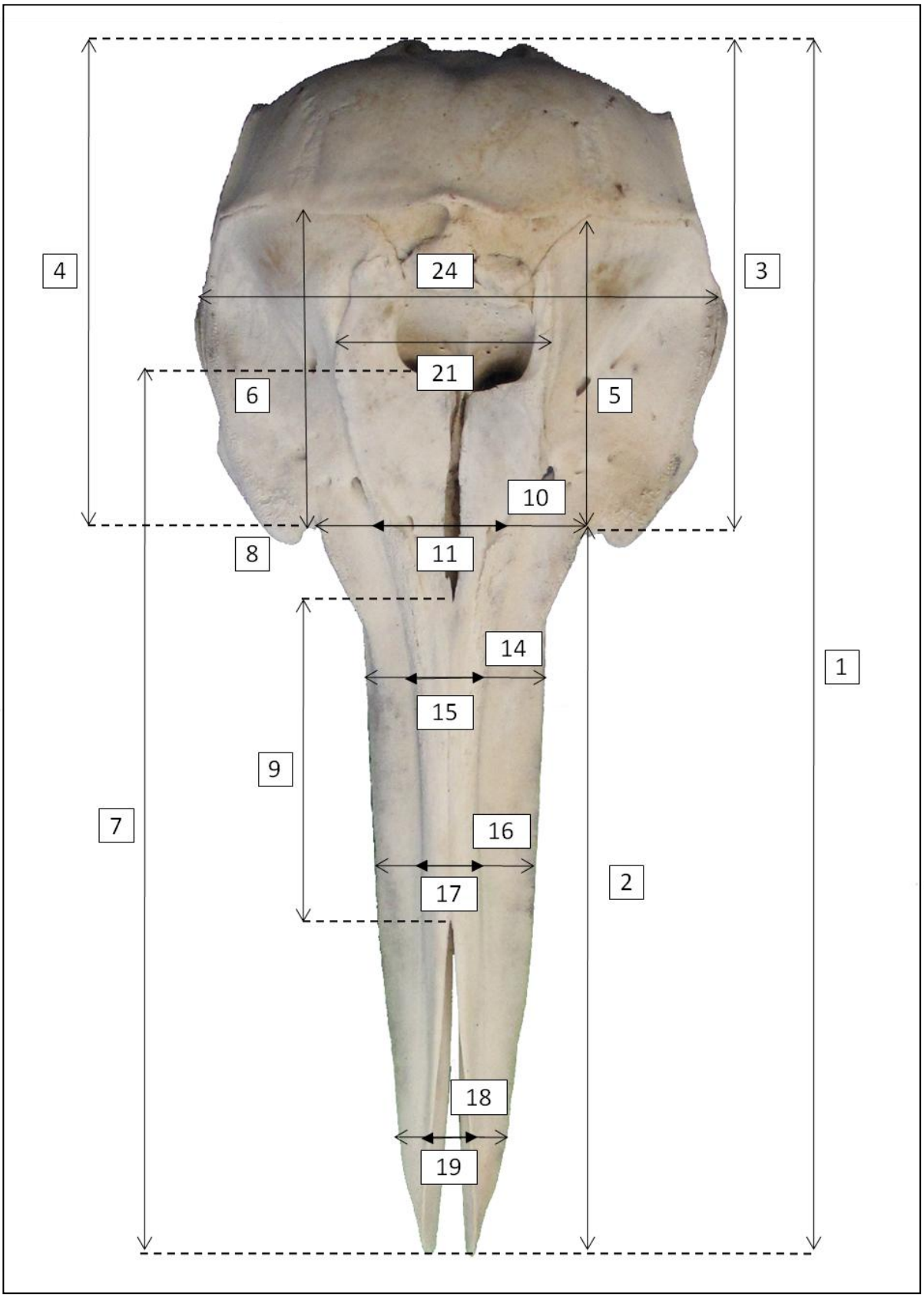

Figure 2.4. Selection of metric measurements taken on *Delphinus* sp. skulls from New Zealand waters in dorsal view. For character definitions refer to Table 2.5.

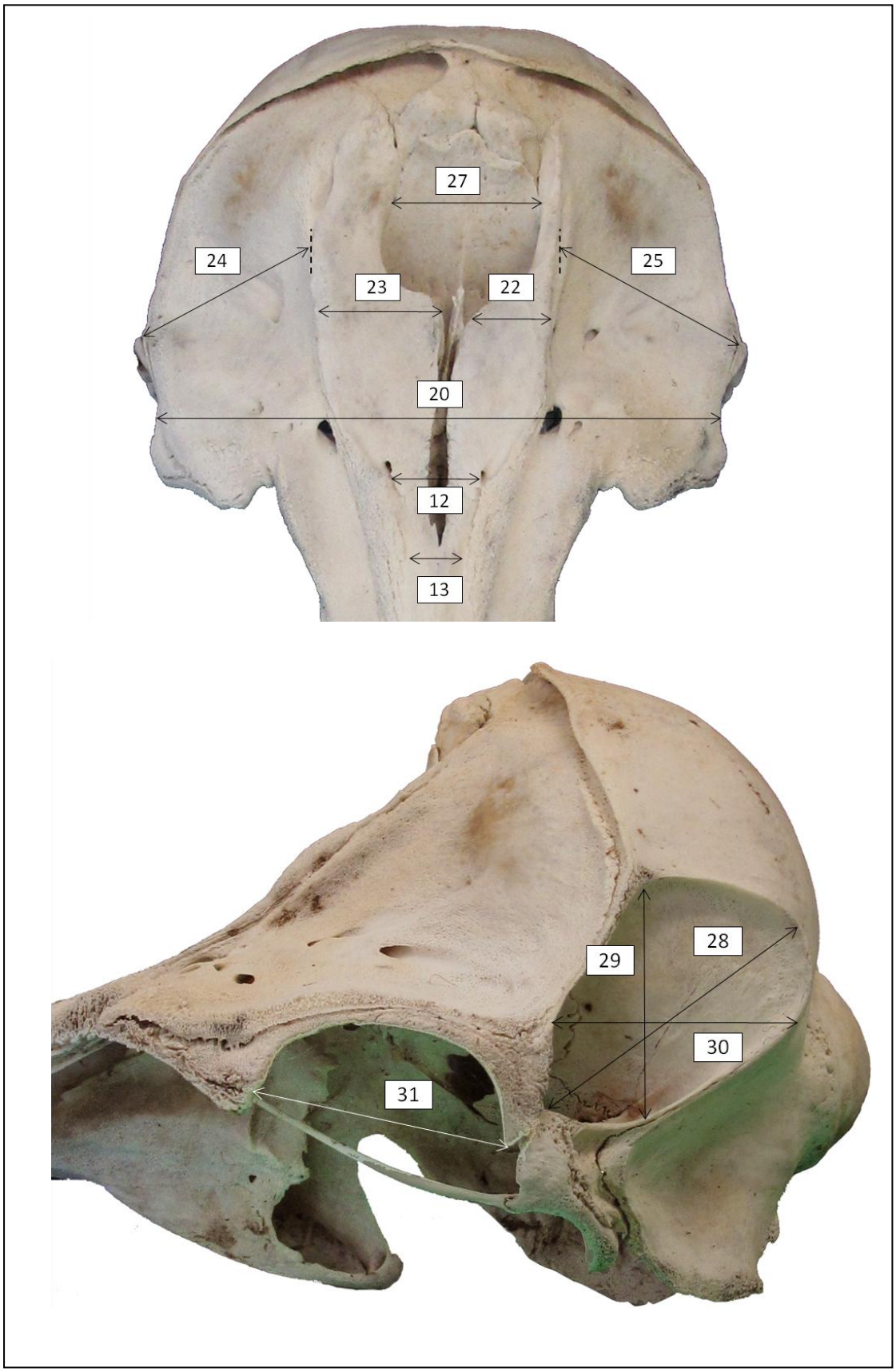

Figure 2.5. Selection of metric measurements taken on *Delphinus* sp. skulls from New Zealand waters in dorsal (top) and lateral (bottom) view. For character definitions refer to Table 2.5.

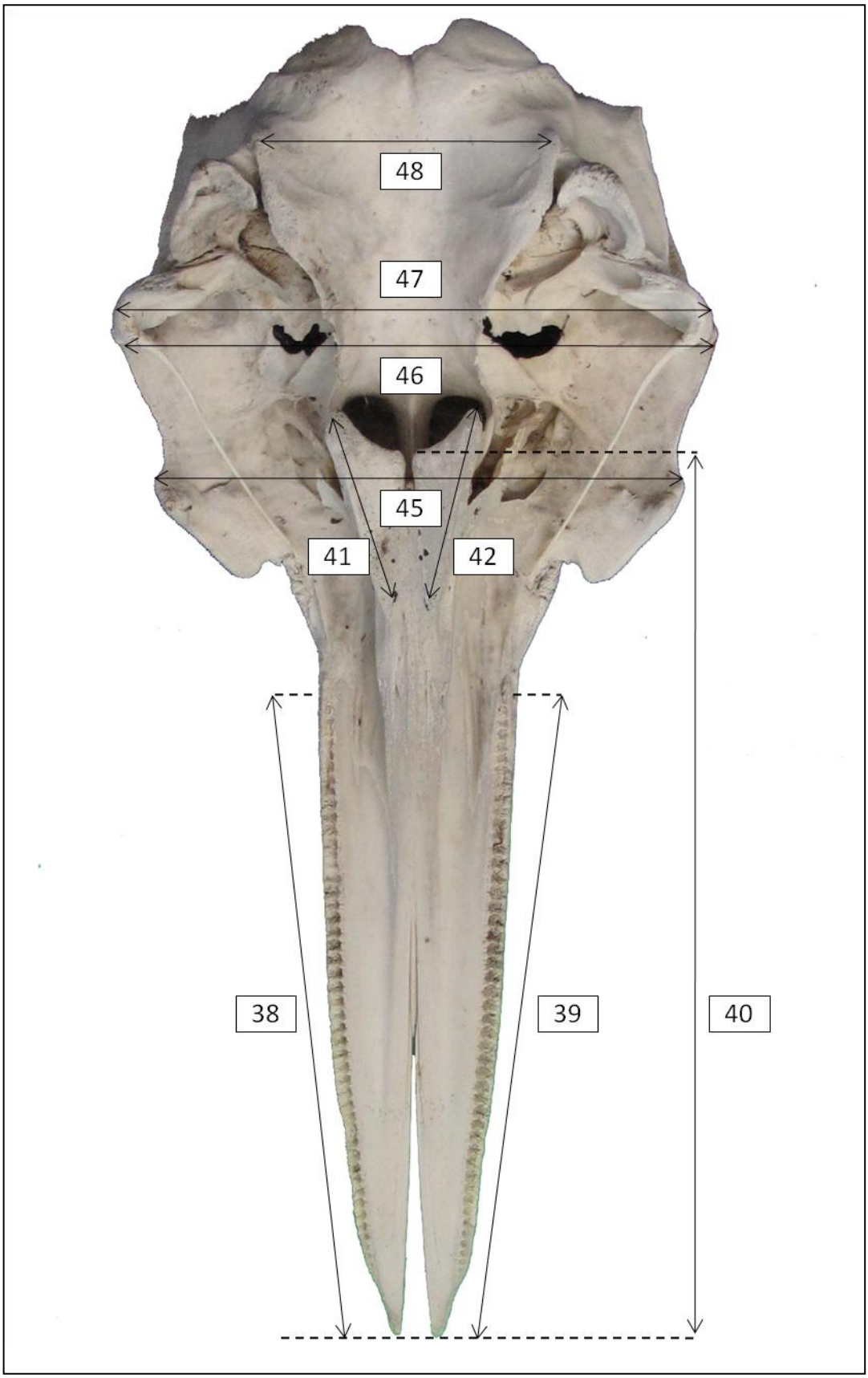

Figure 2.6. Selection of metric measurements taken on *Delphinus* sp. skulls from New Zealand waters in ventral view. For character definitions refer to Table 2.5.

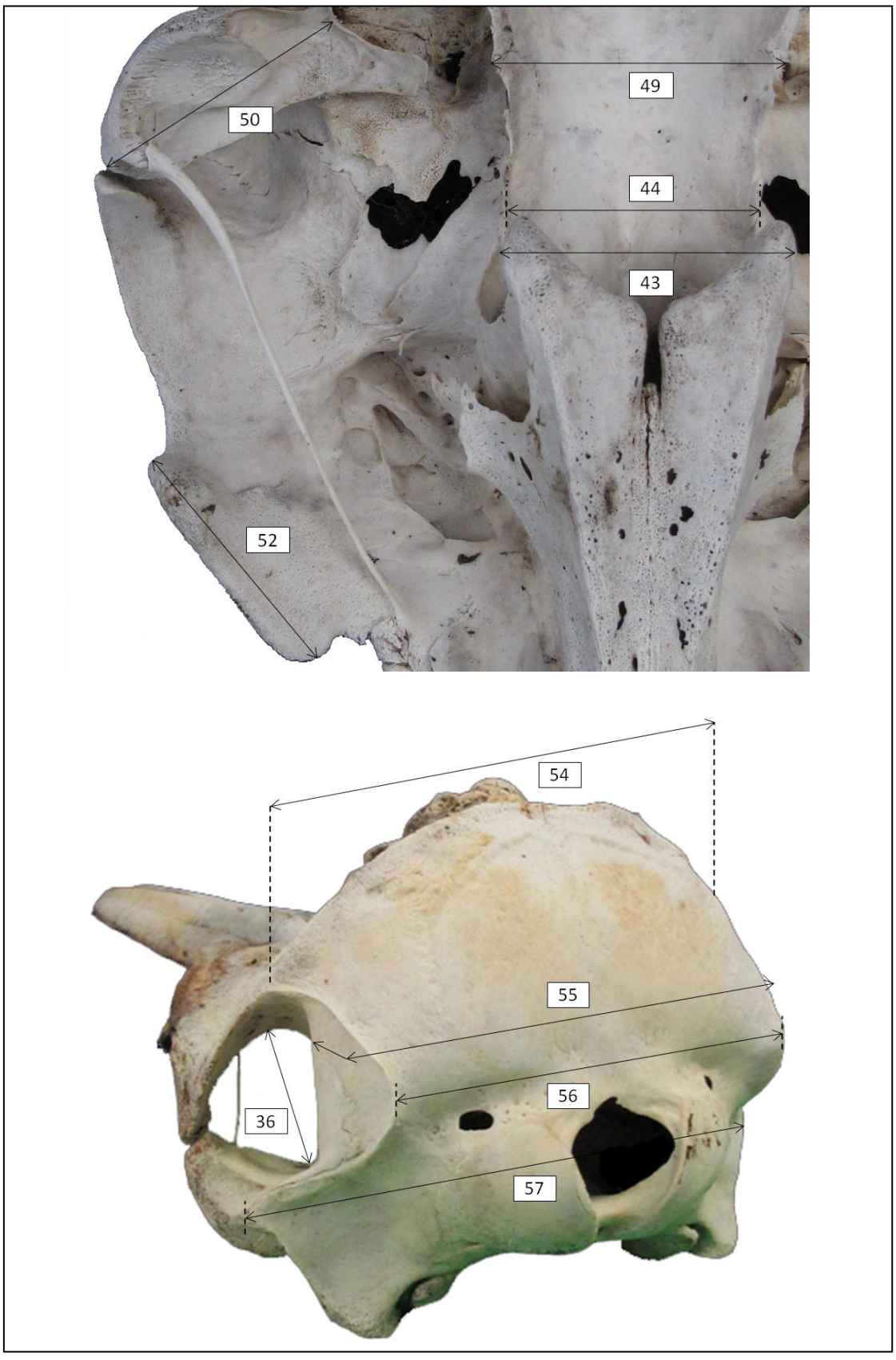

Figure 2.7. Selection of metric measurements taken on *Delphinus* sp. skulls from New Zealand waters in ventral (top) and occipital (bottom) view. For character definitions refer to Table 2.5.

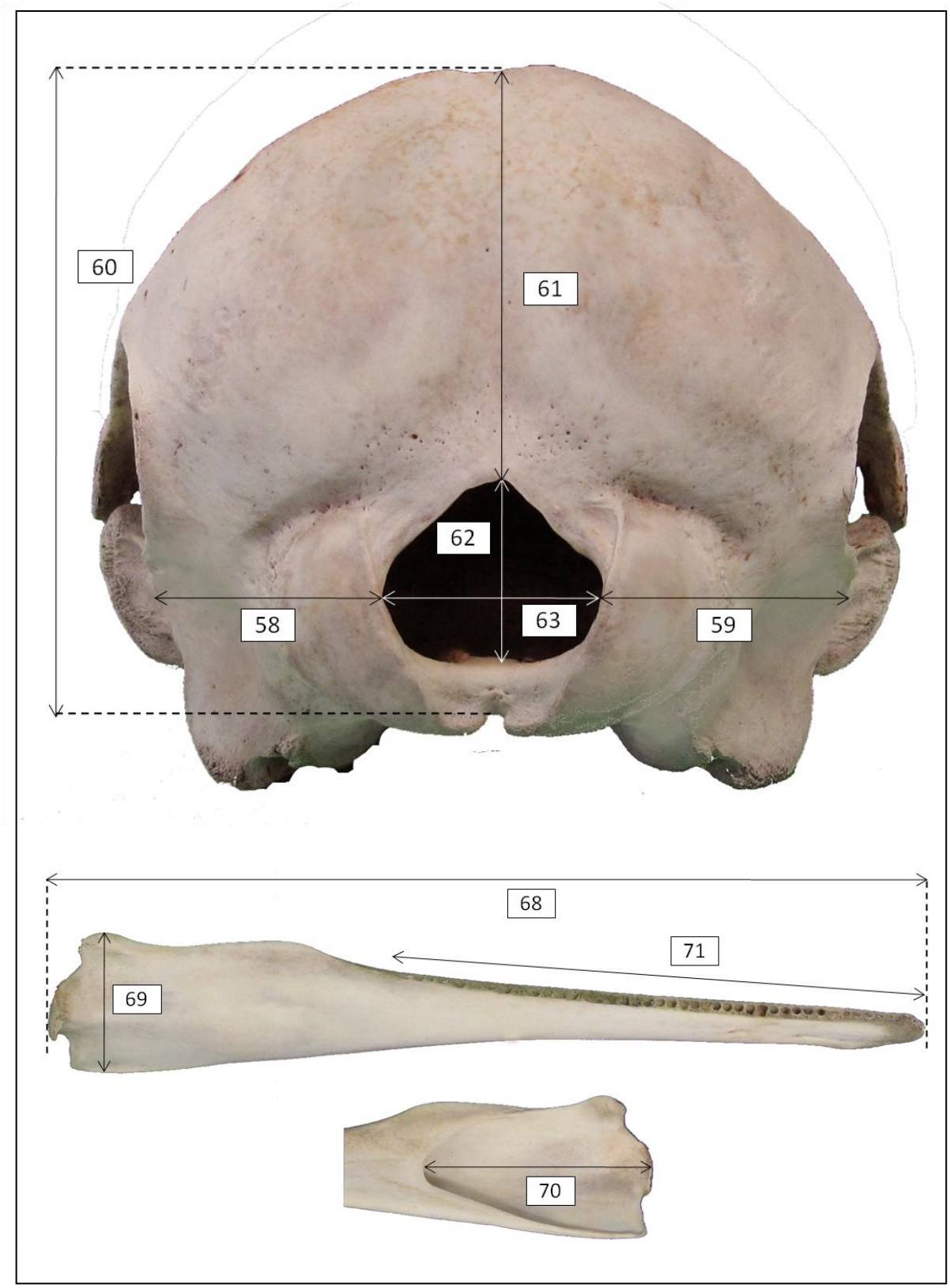

Figure 2.8. Selection of metric measurements taken on *Delphinus* sp. skulls from New Zealand waters in occipital view (top) and on the mandibles (bottom). For character definitions refer to Table 2.5.

2.2.5 Skull weight

The weight of only fully intact skull specimens (including rostrum rating 2 - 3), which had no major pieces of flesh or teeth remaining, was determined to the nearest gram using a digital scale. Each skull was only measured twice, given that the exact same value was obtained for a given specimen.

2.2.6 Non-metric cranial characters

Alveoli (tooth socket) counts were conducted on each jaw with fully intact tooth rows (Table 2.6). Following Amaha (1994), maximum number of tooth sockets was also recorded.

Table 2.6. Tooth socket counts for both sides of upper and lower jaws and maximum tooth socket counts for upper and lower jaws of *Delphinus* sp. skulls from New Zealand waters. Note: Nr. = number; Abbr. = abbreviation; l = left; r = right; Ref. = reference; P = Perrin (1975); A = Amaha (1994).

Nr.	Abbr.	Side	Description	Ref.
1	TUL	l	Number of rostral tooth sockets	P
2	TUR	r	Number of rostral tooth sockets	P
3	TLL	l	Number of mandibular tooth sockets	P
4	TLR	r	Number of mandibular tooth sockets	P
5	MUTC		Maximum number of rostral tooth sockets	A
6	MLTC		Maximum number of mandibular tooth sockets	A

A further 25 non-metric characters were obtained from each skull. Of these, 21 were adapted from Kinze (1985), Perrin et al.(1994), Fettuccia et al. (2009), and Tavares et al. (2010) and the remaining five were devised by the author (Table 2.7; Figs. 2.9 and 2.10). Trait expression of characters 7 and 25 were related to ontogeny and were included to assess the characters' validity to decipher cranial maturity status of skull specimens. Examples of the different trait expressions of characters 7, 11, 14, 16, 19 - 20, and 23 - 25 are given in Appendices 4 to 9.

Table 2.7. Description of non-metric characters recorded on *Delphinus* sp. skulls from New Zealand waters. Note: L. = location on skull; occi. = occipital; l,r = left and right side of the skull, respectively; m = at midline of skull; Nr. = number; S. = side of the skull; Abbr. = abbreviation; B = Bell et al. (2002); F = Fettuccia et al. (2009); P = Perrin et al. (1994); T = Tavares et al. (2010); T.S. = devised in this study.

L.	Nr.	Abbr.	S.	Code	Definition of character abbreviations	Ref.
DORSAL	1	PMIOF	l	1 = anterior; 2 = posterior; 3 = at level or uncertain	Position of anterior edge of mesial infraorbital foramen relative to level of anteriormost projection of antorbital process	P
	2	PLIOF	l	1 = anterior; 2 = posterior; 3 = at level or uncertain	Position of posterior edge of lateral infraorbital foramen relative to posterior edge of mesial infraorbital foramen	P
	3	DPM	m	1 = below; 2 = above; 3 = at level or uncertain	Dorsal projection of mesethmoid between premaxillae near base of rostrum in relation to surface of premaxillae	P
	4	CPPT	m	1 = present; 2 = absent	Contact or near contact (1-mm gap) between premaxillae (or exposed maxillae) in prenarial triangle	P
	5	HMTPR	m	1 = below; 2 = above; 3 = uncertain	Relative height of maxillae at anterior most projection of antorbital process relative to height of premaxillae	T.S.
	6	MNC	l/r	1 = anterior; 2 = at or posterior	Relative extension of ascending process of the maxilla in relation to the nuchal crest	T.S.
	7	WMF	l/r	1 = maxillae wider; 2 = equal or frontal wider	Width of maxillae relative to frontals above the orbit	T.S.
	8	HV	m	1 = below 2; = above; 3 = at level or uncertain	Height of vertex in relation to frontal crest	T.S.
	9	CPN	l/r	1 = present; 2 = absent	Contact between premaxilla and nasal (no intervening bones),	P
	10	EAPLPR	l	1 = anterior to 2 = posterior; 3 = at level to or uncertain	Relative extension of ascending process of left premaxilla in relation to anterior edge of nasal	P
OCCI.	11	SFM	m	1 = piriform; 2 = smooth oval/ circle	Shape of foramen magnum	P
	12	O	m	1 = present; 2 = absent	Presence of distinct dorsal notch	P
	13	NFOCEX	l/r	1 = 1; 2 = 2; 3 =3;... 9 = 0	Number of fenestrations in occipital (near foramen magnum) and exoccipital	P
	14	GOCC	m	1 = narrow; 2 = wide; 3 = uncertain	Groove between occipital condyles	P
	15	SB	m	1 = umbrella; 2 = square; 3 = uncertain	Shape of braincase	B
VENTRAL	16	FBOCV	m	1 = present; 2 = absent	Small foramen between occipital condyles in ventral view	P
	17	MFBOCC	m	1 = present (natural); 2 = absent / post-mortem damage	Mesial fenestration in basioccipital	P
	18	PPEV	m	1 = posterior; 2 = in line or anterior	Position of posterior end of vomer relative to line connecting mesial ends of sutures between alisphenoids and basisphenoid	P
	19	VS	m	1 = narrow; 2 = wide; 3 = uncertain	Shape of vomer	F
	20	LFV	l/r	1 = present; 2 absent	Lateral fenestration in vomer	P
	21	MFV	m	1 = present; 2 = absent	Mesial fenestration in vomer	P
	22	PIOSF	l	1 = posterior; 2 = anterior; 3 = at or uncertain	Position of interior opening of supraorbital foramen relative to frontal trabeculum	P
	23	PAELVF	l/r	1 = anterior; 2 = posterior; 3 = at edge or uncertain	Position of anterior edge of large ventral foramen in maxilla relative to posterior edge of base of jugal	P
	24	OF	l/r	1 = undivided >1mm; 2 = divided; 3 = uncertain	Configuration of the orbital fissure (referred to as anterior lacerate foramen by Fettucia et al., 2009)	F
	25	IAS	l/r	1 = not / partly developed; 2 = fully developed	Developmental status of the interalveolar septa of maxillary and mandibular toothrows	T

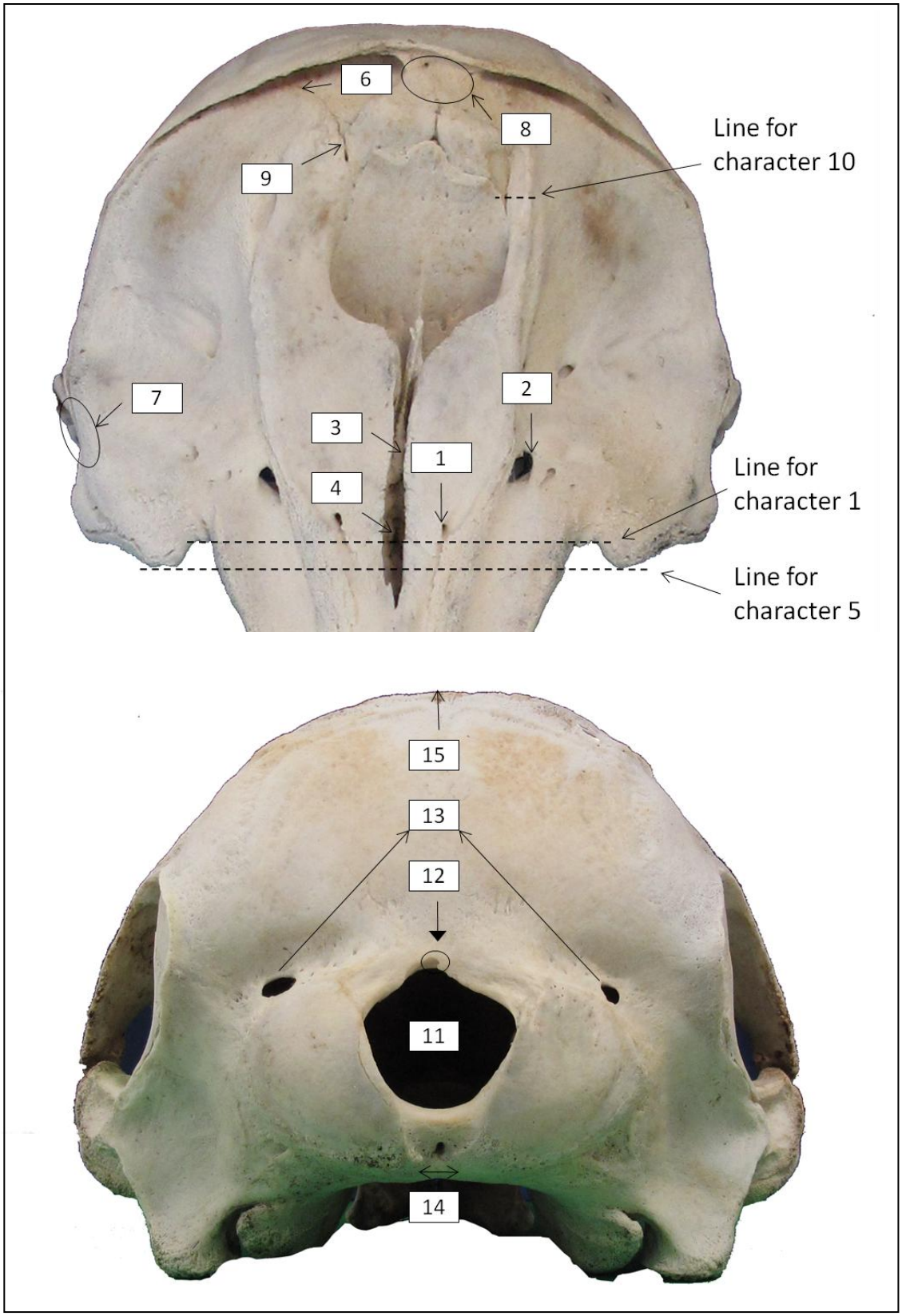

Figure 2.9. Selection of non-metric characters recorded on *Delphinus* sp. skulls from New Zealand waters in dorsal (top) and occipital (bottom) view. For character definitions refer to Table 2.7.

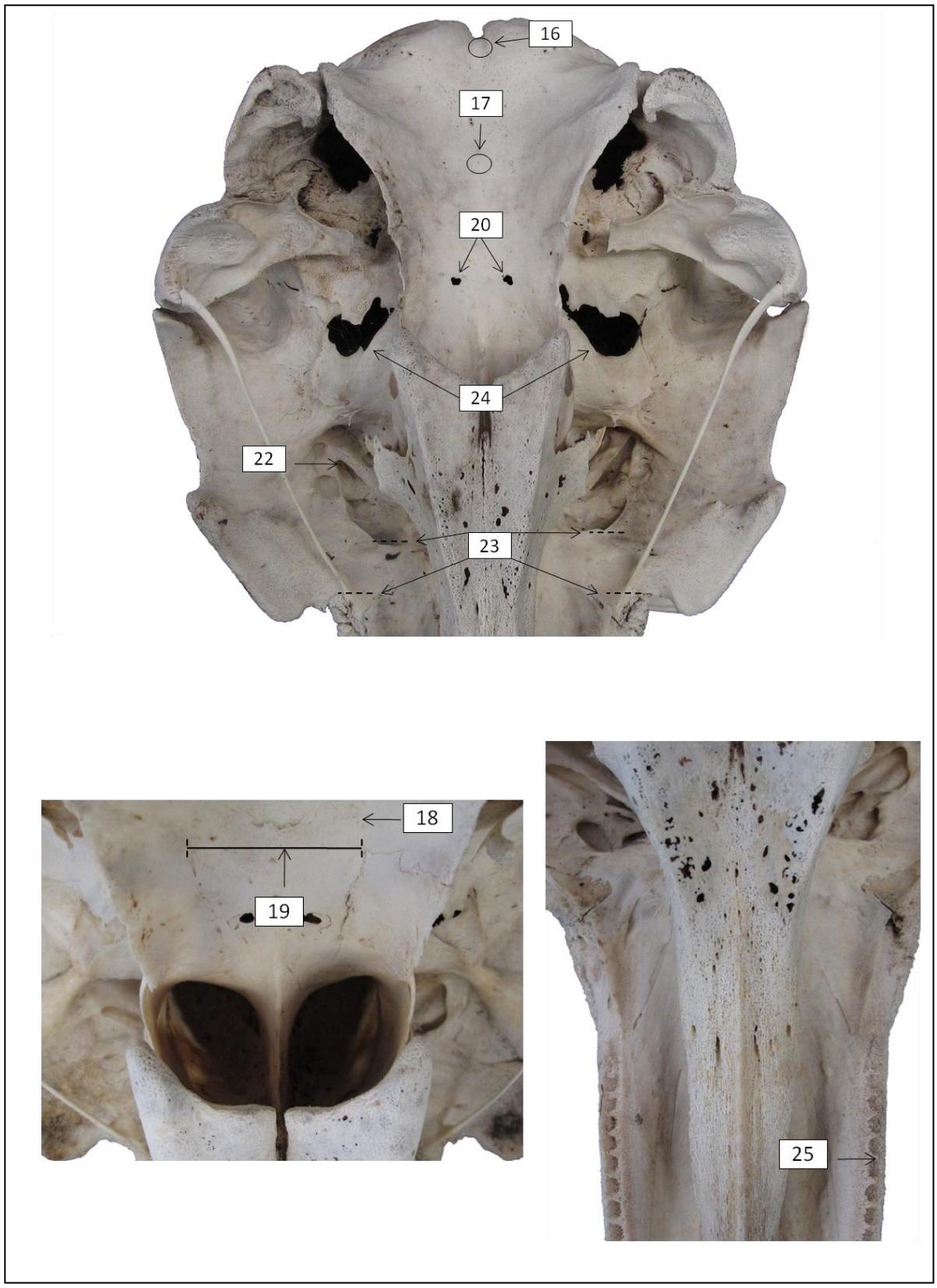

Figure 2.10. Selection of non-metric characters recorded on *Delphinus* sp. skulls from New Zealand waters in ventral views. For character definitions refer to Table 2.7.

2.2.7 Landmark digitization

An electronic 3D contact digitizer (Immersion Microscribe 3DX) was used for capturing landmarks on a subsample of cranially mature *Delphinus* sp. skulls from New Zealand waters. Following Westgate (2007), each skull was securely fixed to a table with blu-tack to prevent any movement during data acquisition (refer to Plate. 2.4).

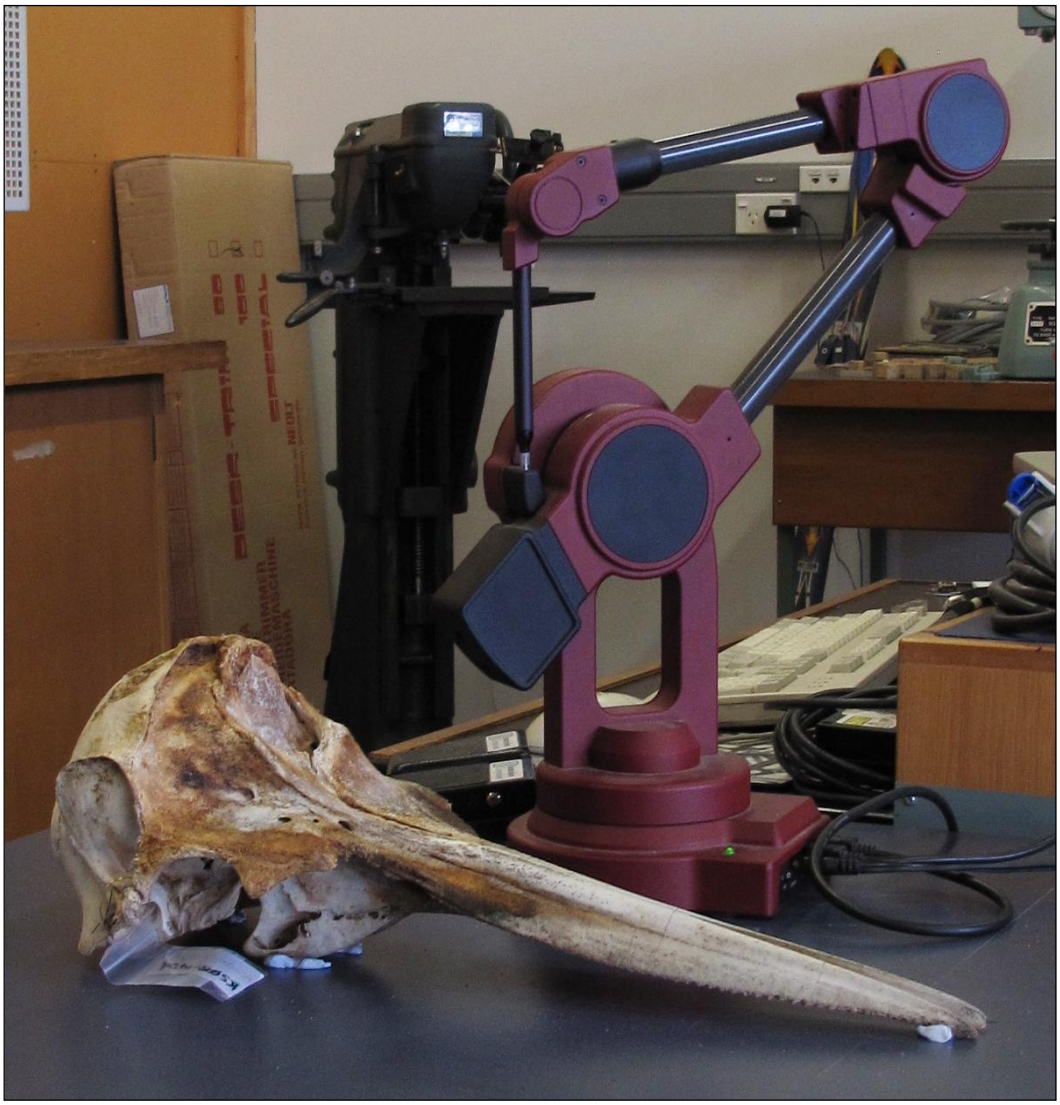

Plate 2.4. Setup for the digitization process of cranial landmark acquisition on *Delphinus* sp. skull from New Zealand waters with a microscribe.

The microscribe was connected to a computer and for landmark digitization, the tip, or stylus, was placed onto the point of interest on the skull. The given landmark was then captured and saved as a x, y, and z co-ordinate directly into a Notepad file by pressing a foot-pedal. During the initial test phase, several landmarks were discarded due to difficulties in determining points of reference. Following this process, a total of 62 three-dimensional landmark coordinates (Table 2.8; Figs. 2.11 to 2.12) were selected for digitization on each specimen. Three reference points were marked with blu-tack (i.e. at the tip of rostrum, the tip of left postorbital process, and the left occipital condyle) and digitized prior to acquiring landmarks in dorsal, lateral, and occipital view with the skull facing up. The skull was then turned and fixed to the table with the ventral side facing up. The reference points were re-taken and landmarks 31 to 62 digitized in ventral view. Because data collection with a microscribe is spatially referenced, re-digitizing the reference points enables to obtain one complete data set, rather than two separate data sets (dorsal and ventral), that would have required to be combined (M. Jedensjö, pers. comm.). Following Sztencel-Jabłonka et al. (2009), all cranial landmarks were taken three times per skull to assess measurement error (ME) between linear distances recorded with callipers and obtained with the microscribe. Following this assessment, landmarks on specimens housed at The Museum of New Zealand Te Papa Tongarewa (n = 9) were digitized only once. Finally, a total of seven landmarks were taken from the left mandible, if present. Each mandible was securely fixed to the table with blu-tack and the lingual surface was arranged uppermost, as all landmarks could be digitized in this view. To avoid inter-observer bias, all landmarks were digitized by the author.

Table 2.8. Description of three-dimensional landmarks that have been digitized on skulls and left mandibles of *Delphinus* sp. from New Zealand waters. Note: L. = location; occip. = occipital; mand. = mandible; Nr. = number of landmark; Abbr. = abbreviation; S. = side of the skull; l/r = left and right side of the skull, respectively; m = at midline of skull; t/b = top and bottom, respectively; W = Westgate (2007); N = Nicolosi & Loy et al. (2010); G = Galatius et al. (2011); T.S. = devised in this study.

L.	Nr.	S.	Definition of landmarks	Ref.
D	1-2	l/r	Anterior tip of premaxilla	W
O	3-4	l/r	Point at interior most margin of premaxilla at base of rostrum	W
R	5	m	Posterior point of fusion of premaxilla	N
S	6	m	Anterior point of fusion of premaxilla	N
A	7-8	l/r	Deepest point of antorbital notch at base of rostrum	W
L	9-10	l/r	Point at outside margin of premaxilla at base of rostrum	T.S.
	11-12	l/r	Anterior point of lacrimal	W
	13-14	l/r	Point at outside of rostrum at 60 mm from the base	T.S.
	15-16	l/r	Point at outside of rostrum at ½ length from the base	W
	17-18	l/r	Point at outside of rostrum at ¾ length from the base	W
	19	r	Posterior most rim of the right premaxillae at external nares	W
O	20	m	Point at nuchal crest in line with tip of dorsal notch of foramen magnum	W
C	21-22	t/b	Points at largest vertical distance of the foramen magnum	T.S.
C	23	m	Medial point of the intercondylar notch of the basioccipital	W
I	24-25	l/r	Widest point at horizontal margins of the foramen magnum	T.S.
P	26-27	l/r	Most outward point of occipital condyles	W
.	28-29	l/r	Supraoccipital-exoccipital-parietal suture at post-temoral fossa	G
	30-31	l/r	Widest point of braincase within post-temporal fossa	W
V	32-33	l/r	Outerior most point at zygomatic process	W
E	34-35	l/r	Ventral point of postorbital process of the frontal	W
N	36-37	l/r	Widest point at postorbital process	W
T	38-39	l/r	Ventral point of preorbital process of the frontal	W
R	40-41	l/r	Widest point of preorbital process	W
A	42-43	l/r	Suture of pterygoid and basioccipital at lateral margin of bones	G
L	44-45	l/r	Deep point of the Eustachian notch (internal nares)	G
	46-47	l/r	Posterior point of lacrimal	W
	48-49	l/r	Posterior tip of pterygoid bones	W
	50-51	l/r	Point at mesial end at posterior margin of pterygoids	W
	52-53	l/r	Anterior point of pterygoid-palatine suture	W
	54-55	l/r	Posterior most margin of caudal most alveoli of rostral tooth row	W
M	56	l	Posterior most point of mandible	W
A	57	l	Posterior most point at rim of mandibular fossa	W
N	58	l	Anterior most point of mandibular fossa	W
D	59-60	t/b,l	Outerior most points across left ramus	W
.	61	l	Posterior most margin of caudal most alveoli of mandible	W
	62	l	Anterior most point at tip of mandible	W

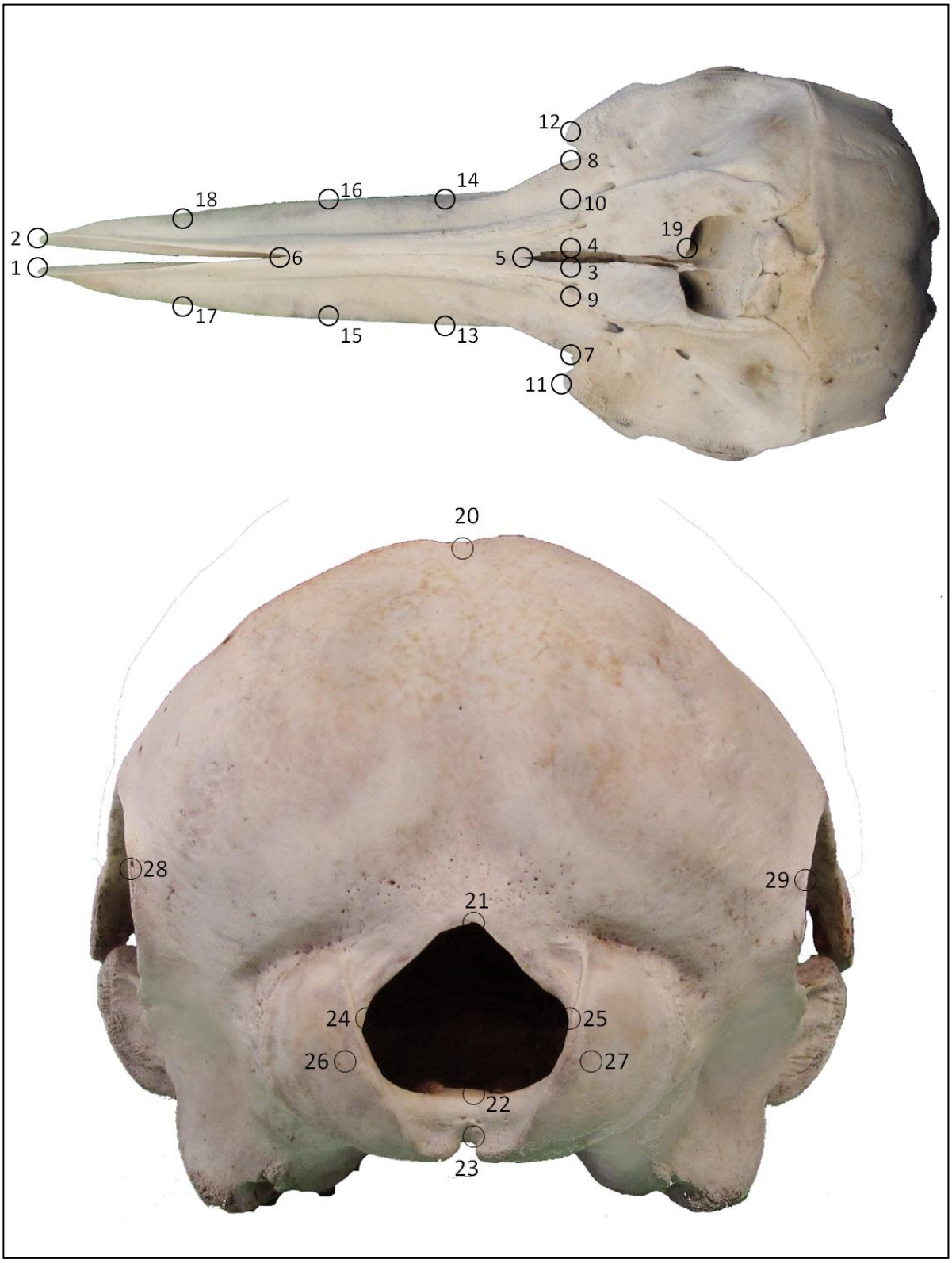

Figure 2.11. Landmarks digitized with a microscribe on *Delphinus* sp. skulls from New Zealand waters in dorsal (top) and occipital (bottom) view. For definition of landmarks refer to Table 2.8.

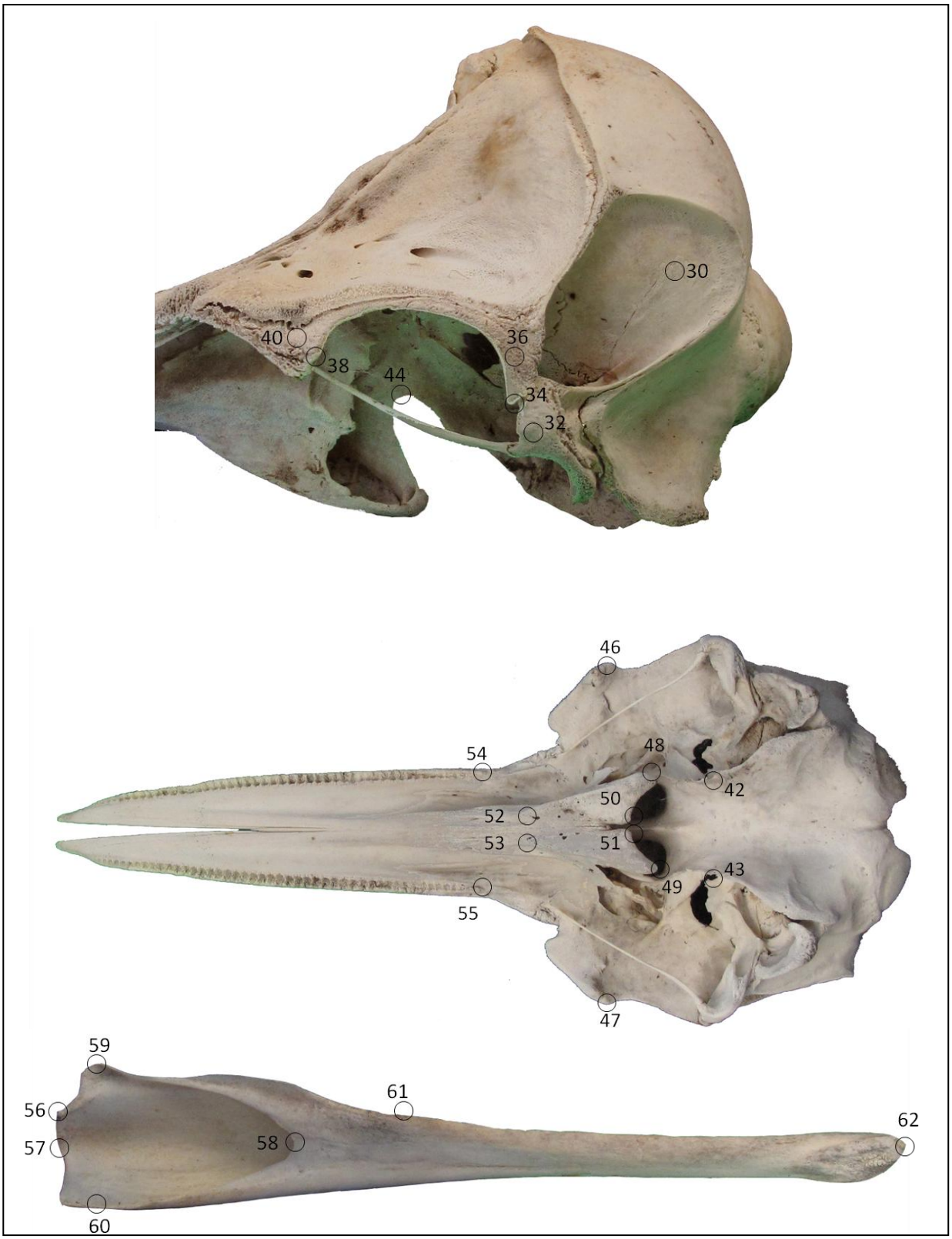

Figure 2.12. Landmarks digitized with a microscribe on *Delphinus* sp. skulls from New Zealand waters in lateral (top) and ventral (middle) view and on the left mandible (bottom). For definition of landmarks refer to Table 2.8. Note: Landmarks with odd numbers in lateral view are not shown, as taken on the right side of the skull.

2.3 Statistical analyses

2.3.1 General remarks

Analyses were conducted in Excel and the statistical software packages SPSS (Version 19; © IBM) and Minitab (Version 15; © Minitab Inc.) The software ArcGIS (Version 9.2; © ESRI Inc.) was used to visually depict carcass location of stranded and by-caught common dolphins of which the skulls were included in the present study.

Following Amaha (1994), statistical analyses were conducted when sample size was more than five per variable. Tests were deemed significant at the α 0.05 level.

Following Wiig et al. (2012), Kendall's tau correlation was used throughout the analyses when non-parametric correlations were undertaken, because sample size was small and owing to the suggestion that Kendall's tau is likely a better estimate of the population than Spearman's Rank Order correlation (Howell, 1997).

Values were expressed as means ± SD (standard deviation) and medians with the associated I.Q.R. (interquartile range) for parametric and non-parametric tests, respectively. P-values were two-tailed.

PART I: Cranial maturity indicators and skull growth

2.3.2 Suture index

2.3.2.1 Data preparation

Before the suture index could be calculated to determine an individual's cranial maturity status, it was necessary to test each suture for (1) bilateral asymmetry (Chen et al., 2011); and (2) correlation with age (Gonzáles, 2002). In addition, a misclassification index (Chen et al., 2011) was calculated to exclude sutures that were not good discriminators between immature and mature individuals.

2.3.2.1.1 Bilateral asymmetry and correlation with age

To test for bilateral asymmetry in the degree of suture fusion between the right and left side of the skull, non-parametric Wilcoxon matched-pairs signed-rank tests were run for each suture using suture scores recorded on both sides for a given suture (after Chen et al., 2011). The palatine-palatine (pal-pal) and frontal-frontal (fr-fr) sutures did not require assessment, given that both sutures run along the midline and not the sides of the skull.

Kendall's tau b correlations were conducted for each suture to determine whether degree of fusion was correlated with age. Only specimens with exact ages were included for analyses in the non-parametric test. However, minimum age of the two oldest (both captive) specimens (WC06-10Dd: 31 years and WC06-08Dd: 33 years) was regarded as exact age, as suture fusion was assumed to have ceased in animals at that old age. In order to visually depict pattern of fusion for each cranial suture in relation to age, it was necessary to pool some ages (6 - 8 years, 9 - 11 years, and 12 - 14 years) due to small sample sizes. Since the degree of suture closure was not expected to differ substantially among the oldest skulls, specimens

aged ≥ 18 years were additionally pooled, which allowed individuals with minimum ages of 18 years to be included.

2.3.2.1.2 Relationship between suture fusion and cranial maturity status

Following Chen et al. (2011), the efficiency of the degree of fusion of individual sutures as an indicator for maturity status was assessed. For this purpose, it was necessary to preliminarily classify all skull specimens as either cranially immature or mature. Specimens were preliminarily regarded as cranially mature if two of the criteria listed in Table 2.9 were met. Although asymptotic TBL has been determined for both male and female *Delphinus* sp. from New Zealand waters (Stockin et al., 2011), it was decided to decipher maturity status primarily based on sexual maturity status and the degree of the premaxillae-maxillae fusion following Perrin & Heyning (1993) and Van Waerebeek (1993), due to the low sample size in the Stockin et al. (2011) study. The asymptote was, however, regarded as a secondary criterion for maturity determination, if data on sexual maturity status was not available. This decision was made, given that estimates for both sexes were comparable to asymptotic lengths determined for male (206.0 cm, n = 170) *D. delphis* from Irish and French waters based on Gompertz growth curves (Murphy et al., 2005) and for female (202.0 cm, n = 510) *D. delphis* from European waters based on Richard's model (Murphy et al. 2009). In the absence of age at physical maturity (APM) for both sexes of *Delphinus* sp. from New Zealand waters (Stockin et al., 2011), APM determined for male (11.9 year) *D. delphis* specimens pooled from Irish and French waters (Murphy et al., 2009), and estimated for female (9 years) *D. delphis* from Irish waters (Murphy & Rogan, 2006) was adapted as a secondary criterion for both sexes in the present study, given that asymptotic lengths of both populations are comparable.

Table 2.9. Criteria for preliminary cranial maturity determination of *Delphinus* sp. skulls from New Zealand waters. Specimens were preliminarily regarded as cranially mature if two or more criteria were met. Note: TBL = total body length; Ref. = reference.

Sex	Criteria	Criteria description	Ref.
Male	Cranial	**Primary criteria:** - Fusion of premaxillae to maxillae ≥ 50% of the length of the rostrum	Jefferson & Van Waerebeek, 2002
	Sexual	- Testes assessed as sexually mature (evidence of spermatogenesis)	Perrin & Heyning, 1993
	Physical	**Secondary criteria:** - TBL ≥ 204.0 cm	Stockin et al.,2011
		- ≥ 12 years of age	Murphy et al., 2005
Female	Cranial	**Primary criteria:** - Fusion of premaxillae to maxillae over at least 50% of the length of the rostrum	Jefferson & Van Waerebeek, 2002
	Sexual	- Ovaries assessed as sexually mature (evidence of ovarian scars)	Perrin & Heyning, 1993
	Physical	**Secondary criteria:** - TBL ≥ 199.9 cm	Stockin et al., 2011.
		- ≥ 9 years of age	Murphy & Rogan, 2006

Following Chen et al. (2011), suture fusion stages 0 and 1 were classified as limited fusion (representative of immature specimens) and fusion stages 2 and 3 were classified as advanced fusion (representative of mature specimens) (refer to Table 2.2). Based on these groupings, three misclassification indices (% of immatures misclassified, % of matures misclassified, and total % misclassified) were calculated for each suture, where advanced and limited suture fusion documented for immature and mature specimens, respectively, was regarded as 'misclassified' (Mead & Potter, 1990).

The dataset violated Chi-Square test assumptions. Consequently, Fisher's Exact tests were therefore run independently for each cranial suture to assess whether degree of suture fusion (limited fusion *versus* advanced fusion) differed significantly with maturity status.

2.3.2.2 Suture index computation

A scoring system that differentiated three degrees of suture fusion was adapted from González (2002) in order to compute a suture index with the aim to determine a cut-off point for cranial maturity. For this purpose, fusion stages 0 (no fusion) and 1 (limited fusion) scored 0 and 0.5, respectively. Fusion stages 2 and 3 (advanced fusion) were pooled and scored 1.

Following González (2002), scores recorded on the left and right side of the cranium for a given suture were averaged for sutures that did not display significant bilateral asymmetry. The suture index for each specimen was determined by calculating the sum of the averaged scores from sutures that:

1. Were significantly correlated with age (after González, 2002)
2. Displayed a significant difference in the degree of suture fusion between mature and immature specimens; and (this study)
3. For which all three misclassification indices were < 50% (this study)

2.3.2.3 Deciphering cranial maturity status

Given that the suture index was computed based on count data, a non-parametric Mann-Whitney U test was applied to examine whether the median suture index differed significantly between cranially immature and mature specimens. Kendall's tau b correlations were carried out to determine whether the suture index was correlated with dolphin age.

2.3.2.4 Age class allocation of specimens of unknown age

Age classes employed by González, (2002) were also deemed appropriate and adapted for analyses in the present study, given that all specimens aged 1 - 3 were sexually immature, the youngest sexually mature individual was 6 years of age, and all specimens ≥ 11 years were cranially mature. Skull specimens of known age were therefore grouped into the following three age classes: I (1 - 3 years), II (6 - 10 years), and III (≥ 11 years). Individuals with the ages 4 and 5 were not available for the present study. In the current study:

- Age class I individuals were characterized by suture fusion stage 0 (elements can be moved freely) in respect to the maxilla-frontal, premaxilla-maxilla, nasal frontal, and frontal-interparietal sutures
- Age class II specimens displayed variable degrees of suture fusion
- Age class III individuals were characterized by advanced suture fusion

A Kruskal-Wallis test was applied to examine whether the median suture index differed significantly between age classes. Specimens of unknown age were assigned to one of the three age classes based on their total suture scores. Specimens for which more than two sutures could not be scored, due to missing osteological elements or remaining flesh, were excluded from age class allocation.

2.3.2.5 Re-assessment of cranial maturity status of individual skull specimens

Based on results obtained from cranial suture index data, the criteria for cranial maturity status determination of New Zealand *Delphinus* sp. specimens were re-defined (Table 2.10)

and cranial maturity status of each *Delphinus* sp. specimen was re-assessed. TBL was no longer considered as a criterion owing to the high percentage (47.6%, n = 10) of cranially mature female specimens below the asymptote (refer to section 3.3).

Table 2.10. Criteria for cranial maturity status determination of *Delphinus* sp. specimens from New Zealand waters. Specimens were regarded as cranially mature if at least two of the criteria were met. Note: GLG = growth layer groups; P & H = Perrin & Heyning (1993); T.S. = devised in this study.

Criteria	Criteria description	Ref.
1	Assessed as sexually mature	P & H
2	Rostral fusion ≥ 75% of the length of the rostrum	T.S.
3	Suture index ≥ 8	T.S.
4	≥ 11 years (as determined from GLG in dentine)	T.S.

2.3.3 Metric data

2.3.3.1 Data preparation

Prior to statistical analyses, all metric characters were checked for transcription errors and outliers. First, data for each character were visually inspected for obvious outliers, which were re-measured and corrected if required. Second, all metric characters for specimens with rostrum length (RL) categories 1 to 3 (refer to Table 2.4) were regressed against condylobasal length (CBL) and each regression *versus* fit plot was investigated for data points deviating more than four standard residuals from the fitted line. Such extreme outliers were re-taken and corrected, if the measurement had been obtained incorrectly. Measurements for specimens with rostrum category 4 were regressed against mandible length, if available, owing to the high correlation between CBL and mandible length determined in this study (right mandible length: R^2 value = 0.979; left mandible length: R^2 value = 0.965). Preferentially, the right mandible length was chosen owing to the slightly higher correlation with CBL. If either right

or left mandible lengths were not available, measurements were re-taken to ensure accuracy of the measurements.

All metric data were tested for normality and equal variance using Kolmogorov-Smirnoff and Levene's test, respectively. A Welch correction was applied to data that violated the assumption of equal variance and characters that violated the assumption of normality were log transformed (log10(x)). If data still violated normality after a log-transformation, a non-parametric test was chosen instead.

2.3.3.2. Metric characters in relation to total body length and age

Owing to lack or small sample size in one or more rating categories (refer to section 2.2.4) of immature and mature males as well as immature females, ANOVA was only applied to the mature female data set to investigate differences between rostrum rating categories 1 to 3. Due to small sample size, the immature male data sets violated the assumption of normality after a log transformation. A Kruskal-Wallis test was therefore conducted to determine whether significant differences existed in median CBL and RL between immature and mature specimens, pooled for rostrum categories 1 and 2.

CBL and RL were plotted against TBL and age by maturity status and sex to investigate growth patterns. In addition, three further cranial characters (length of fusion of premaxillae (LFPR), and length (LLM), and height (HLM) of left mandible) were plotted against age. Owing to the lack of very young female specimens, no growth curves could be fitted through CBL and RL data as a function of age. Instead, lines of best fit were fitted through the data sets independently for both sexes.

2.3.3.3 Relative skull weight

CBL and zygomatic width (ZW) values were cubed to adjust the measures of length in millimetres (mm) to the measure of mass (weight) in grammes (g), as (1) volume increases as the cube of length; and (2) because volume is directly proportional to mass.

To adjust for skull size, skull weight was plotted against both skull length (CBL^3) and skull width (ZW^3) independently for each sex. A linear regression was then conducted to determine whether skull weight was positively correlated with skull size. SW/CBL^3 and SW/ZW^3 ratios were calculated for each specimen.

Pearson product moment correlations were conducted to test whether SW/CBL^3 and SW/ZW^3 were correlated with TBL and specimen age, separately for each sex, including and excluding captive specimens. Owing to small sample size, sexes had to be pooled to test for a correlation between relative skull weight and age.

Unpaired t-tests were run to investigate whether means of SW/CBL^3 and SW/ZW^3 ratios differed significantly between the sexes. Owing to small sample size, captive females were excluded from this analysis, as it was unknown whether the long duration in captivity (> 30 years) may have had an effect on bone density, and thereby relative skull weight.

2.3.4 Non-metric cranial characters for cranial maturity assessment

Characters displaying a complete lack of difference in trait frequency between all specimens were excluded from analyses. All bilateral characters were tested for asymmetry in trait expression using the equation from Green et al. (1979):

$$\chi^2 o = (b-c)^2 / (b+c)$$

where: b = left presence only and c = right presence only.

Statistical significance was determined using the critical Chi-Square value for 1 degree of freedom (significant if > 5).

Correlation between sides for bilateral traits was assessed using the following equation from Green et al. (1979):

$$\emptyset = \{(ad-bc)^2 / (a+b)\,(a+c)\,(b+d)\,(c+d)\}^{1/2}$$

where: a = bilateral presence, b = left presence only, c = right presence only, and d = bilateral absence.

In further analyses, bilateral characters that displayed no significant asymmetry in trait expression and in which correlation between sides was ≥ 0.8 were represented by the left side of the skull only. This was necessary for consistency, as, following Perrin et al. (1994), some bilateral characters had only been recorded on the left side (refer to Table 2.7). Both sides were considered independently for all bilateral characters, for which a significant asymmetry in trait expression was detected.

Chi-square tests between immature and mature specimens were conducted independently for each non-metric character to investigate whether trait expression was dependent of maturity status. Fisher's Exact tests were run when sample size of any cell was < 5. Only characters for which a significant difference in trait frequency expression was detected were included for further analyses in this part of the study. All characters, in which trait expression could be assigned to a maturity status (refer to Table 2.11), were assessed for their efficiency as an indicator of cranial maturity. For this purpose three misclassification indices (% of immatures misclassified, % of matures misclassified and total % misclassified) were calculated for each

character where specimens were regarded as 'misclassified' when displaying a trait expression representing the opposite maturity status (adapted from Mead & Potter, 1990).

Table 2.11. Trait expression / developmental status of non-metric characters assigned to cranial maturity status in order to assess the character's efficiency as cranial maturity indicator in *Delphinus* sp. skull specimens from New Zealand waters. Note: Ref. = reference; M & F = Mead & Fordyce (2009); T = Tavares et al. (2010); T.S. = devised in this study.

Character	Immature	Mature	Ref.
COH	Undivided	Divided	M & F
IAS	Partly developed	Fully developed	T
WMF	Maxilla wider	Frontal wider	T.S.
MNC	Maxillae anterior to nuchal crest	Maxilla at or posterior to nuchal crest	T.S.

2.3.5 Tooth condition

For consistency and to maximize the number of specimens to be included for analyses, statistical analyses were only based on rostral teeth from both the right and left jaw, because (1) approximately 10 or more teeth, predominantly from the lower left jaw, had been removed from the majority of skull specimens for aging prior to commencing recordings of tooth condition; and (2) mandibles of several specimens were missing.

Proportion of rostral teeth in each of the seven tooth condition categories (refer to section 2.2.1) was determined for each individual specimen. Non-parametric Mann-Whitney tests were applied to determine whether the median percentage per tooth condition category differed significantly with maturity status and age class.

PART II: Sexual dimorphism, taxonomy, geographic variation, and precision of two metric data acquisition methods

2.3.6 Sexual dimorphism

2.3.6.1 Metric characters

Please refer to sections 2.3.1 and 2.3.3.1 for statistical software used and metric data preparation, respectively. Following Amaha (1994), mature *Delphinus* sp. skulls were examined for evidence of sexually dimorphic features using both t-test and Univariate Analysis of Covariance (ANCOVA). The majority of studies (e.g., Amaha, 1994; Murphy et al., 2006; Chen et al., 2011) employ condylobasal length (CBL) as a covariate in order to adjust for the effect of skull size on each metric character. However, because of the minor damage frequently found in *Delphinus* sp. skulls (Pudie, 1994; Westgate, 2007), which was also present in the majority of rostra tips in the present study, CBL could not be determined in all cases (for specimens with rostrum categories 3 and 4). Instead, owing to the high correlation between CBL and mandible length as reported by Purdie (1994) and determined in this study, mandible length was also used as a covariate for statistical analyses. Two sets of ANCOVA analyses were performed using:

1. CBL as a covariate on skulls with intact rostra and
2. Mandible length as a covariate for adult skulls with rostra graded 1 and 2.

Following Bell (2001), percentage difference between the mean measurements of male and females was calculated for each sexual dimorphic cranial character using the following equation:

*(mean (m) – mean (f) / average mean) * 100*

where (m) = male; (f) = female and average mean = mean (m) + mean (f) / 2 for a given character.

2.3.6.2 Functional complexes

Following Perrin (1975), metric characters were assigned to one of four functional complexes of the delphinid skull (braincase, breathing / sound producing, feeding, and vision apparatus). The fifth complex, the hearing apparatus, was not analyzed, as the tympanoperiotic had not been included due to time constraints in the present study. Following Perrin (1975), individual variation of each cranial character that could be allocated to a functional complex was represented by the coefficient of variation (CV) that was calculated separately for each sex. CVs from all characters of a given functional complex were pooled. Given that the data did not pass the normality test after log transformation, a Kruskal-Wallis test was performed to test for significant differences in variation between functional complexes.

2.3.6.3 Non-metric characters

Chi-square test between males and females were conducted separately for each non-metric character that was independent of maturity status (as determined in section 2.3.4) to investigate whether trait expression was independent of sex. Fisher's Exact tests were run when sample size of any cell was < 5.

2.3.7 Taxonomy

Following Banks and Brownell (1969), Amaha (1994), Heyning and Perrin (1994), and Jefferson and Van Waerebeek (2002), taxonomic status was assessed based on the rostrum length to zygomatic width (RL/ZW) ratio and tooth counts. Specimens with rostrum ratings 1 and 2 were included for RL/ZW ratio calculations, while tooth counts were only conducted on specimens with fully intact rostra.

Unpaired t-tests were used to examine for significant differences in the RL/ZW ratio between sexes and regions (Hauraki Gulf (HG) *versus* non-HG), given that the ratio data was derived from continuous data and passed the normality test.

Following Miramontes Sequeiros et al. (2010), the Kalya Index was calculated for each skull specimens using the following equation:

*((Width right exoccipital + width left exoccipital + width of foramen magnum) / width parietal)*100*

2.3.8 Geographic variation

2.3.8.1 Metric measurements

All metric data were tested for normality, homogeneity (refer to section 2.3.3.1), and were log(10)-transformed. Sexes could not be pooled due to the presence of sexual dimorphic cranial characters. Males had to be excluded from analyses owing to small sample size. Consequently, geographic variation analyses were conducted on mature females only. Multivariate analysis of variance (MANOVA) does not allow missing values. As such, it was decided to omit specimens and metric characters with missing values from analyses rather

than to estimate missing values with analyses methods available in SPSS, owing to biases and anomalous results that may be associated with estimated values (Scheffer, 2002; von Hippel, 2004). Inaccuracy of the regression missing value option in SPSS was confirmed in the present study when using this option to estimate CBL of specimens with rating category 3, using mandible length as the predictor variable (correlation with CBL: r = 0.979). Results of CBL estimates of some specimens with rostrum rating category 3 were less than the actual measurements taken. In order to maximise the number of specimens to be included for analyses, two new complete data sets were created: (1) excluding and (1) including characters related to the length of the rostrum. This division was made, due to the fact that a larger number of values were missing in characters related to length measurements of the rostrum. Only characters determined as good discriminators between geographic regions in common dolphin females by Murphy et al. (2006) and Westgate (2007) were included for analyses. Multivariate Analyses of Variance (MANOVA) was conducted on each set of characters to test for significant cranial size differences between mature females from HG and non-HG waters. In addition, Multivariate Analysis of Covariance (MANCOVA), with CBL employed as a covariate to correct for skull size, was run to test whether a significant difference in skull shape was present between females from both regions. MANCOVA could only be conducted on the second data set in which CBL was available for all specimens.

2.3.8.2 Non-metric characters

All characters independent of maturity status and sex were included for geographic variation analyses, which allowed immatures and matures as well as males and females to be pooled. Following Van Waerebeek (1993) and Wiig et al. (2012), Chi-square tests were applied to each character to test for significant differences in non-metric trait expression between

regions (HG *versus* non-HG individuals) both pooled and separately for each sex. Fisher's Exact tests performed when sample size in any cell was < 5.

Following several authors (e.g. Kinze, 1985 and Brasili et al., 1999), the mean measure of divergence (MMD) was computed based on non-metric character trait frequencies, to assess whether a significant degree of divergence existed between HG and non-HG skull samples (both pooled and separately for both sexes). Harris and Sjøvold (2004) suggested that ideally all characters displaying no significant difference in trait expression frequency in at least one sample pair investigated (e.g. determined via independent Chi-Square tests), should be omitted from the MMD computation. Owing to small sample size this recommendation could not be followed in the present study and it was decided to only exclude characters for which a p-value of 1 was obtained. Due to the fact that MMD estimates are only directly comparable when based on the exact same set of characters (Harris & Sjøvold, 2004), it was necessary to omit all characters for which a p-value of 1 was obtained in any of the three data sets investigated (set 1: sexes pooled, set 2: males only, set 3: females only).

MMD values were computed using the equations from Sjøvold (1977) and Green et al. (1979) as detailed in Brasili et al. (1999):

$$MMD = 1/r\sum_{j=1,r} (\theta_{1j} - \theta_{2j})^2 - V_{12j}$$

where: r = number of characters used, θ is equal to:

$$\theta = \tfrac{1}{2} \arcsin (1-2x / (n+1)) + \tfrac{1}{2} \arcsin (1-2(x+1) / (n+1))$$

where: x = number of times the trait is present, and n = number of available sides for the character.

V_{12j} = variance correction term is equal to:

$$V_{12j} = 1 / (n_{1j} + 0.5) + 1 / (n_{2j} + 0.5)$$

where: n_{1j} = number crania investigated for *j*th character in sample *1*, and n_{2j} = number crania investigated for *j*th character in sample *2*.

The computed MMD values were tested for statistical significance using the following equation Green et al. (1979):

$$SD_{MMD} = \sqrt{Var_{MMD}} = \sqrt{2 / r^2} \sum_{j=1,r} V^2_{12j}$$

Samples compared were statistically significantly divergent if the calculated SD_{MMD} value was > 2.

2.3.9 Precision of two metric data acquisition methods

2.3.9.1 Microscribe data preparation

Linear distances between landmarks digitized with a microscribe were obtained using the following equation (morphomet.morphometrics.org):

$$d = \sqrt{(((x2 - x1)^2) + ((y2 - y1)^2) + ((z2 - z1)^2))}$$

where: 'd' is the distance between coordinates of landmark 1 (x1, y1 and z1) and of landmark 2 (x2, y2, z2).

The largest value obtained for CBL and RL computed for the left (landmarks for CBL: 1 and 27; RL: 2 and 4) and right (landmarks for CBL: 2 and 26; RL: 1 and 3) side of the skull were

included for analyses and the smaller value was discarded, as greatest values of CBL and RL required determination.

2.3.9.2 Measurement error

Following Weinberg et al., 2004, repeated measures were averaged for a given character separately for both types of data acquisition method for each specimen. Measurement error (ME) between calliper and microscribe recordings was assessed independently for each character through three commonly employed types of precision estimates (after Gordon & Bradtmiller, 1992; Hayasaki, et al., 2005; Muñoz-Muñoz & Perpiñan, 2010; Fourie et al., 2011; Gornick, 2011):

1. Variance of repeated measures was determined for each character in both data sets (calliper and microscribe data sets) (after Hayasaki et al., 2005; Muñoz-Muñoz & Perpiñan, 2010).

   Furthermore, Pearson correlation analyses were applied to both calliper and microscribe data sets to assess the relationship between variance and mean character size.

2. Following Weinberg et al. (2004), mean absolute difference (MAD) in millimetres between both data acquisition methods was determined for each character. For this purpose, differences in millimetres between calliper and microscribe recordings were determined for each specimen for a given character and those differences were averaged. Following Gronick (2011), the threshold level of significance was set to 1 mm. This threshold value had been set by the author based on clinical and practical relevance and was also deemed appropriate for the present study, as calliper precision

was lower (0.1 mm) than the 1 mm threshold value. The 95% Confidence Interval (95% CI) was computed for each MAD value and a significant degree of measurement error was said to exist between both data acquisition methods for a given character, if the bounds of the 95% CI exceeded the 1 mm significance threshold (after Gornick, 2011). MAD values (in mm) were reported as mean ± SD and associated 95% CI of the mean.

3. Following Weinberg et al. (2004), relative error magnitude (REM), which represents a measure of the error magnitude relative to character size expressed as a percentage, was computed by dividing the MAD value for a given character by the overall mean of that character and multiplying the result by 100. In the present study, the overall mean was computed from the calliper and microscribe mean measurement (mean of repeated measures) for a given character. Higher precision between measurements are represented by smaller percentages. REM values were classified according to precision categories outlined in Weinberg et al., (2004), where: < 1.0%: excellent, 1.0 - 3.9%: very good, 4.0 - 6.9%: good, 7.0 - 9.9%: moderate and ≥ 10%: poor.

All three types of precision estimates, variance (%), MAD (mm) and REM (%) were determined to an accuracy of 0.1.

2.3.9.3 Measurement error in relation to taxonomy and sexual size dimorphism

RL/ZW ratios were calculated twice for each skull specimens based on both (1) calliper; and (2) microscribe measurements to determine deviation in the ratio between both data sets.

Unpaired t-tests were applied independently for each cranial character for each data set (calliper and microscribe) to test for the degree of identical test results (significant or non-significant) obtained for the presence / absence of sexual dimorphism in each cranial character. ANCOVA analyses were not performed in this part of the study, given that all characters tested for sexual shape dimorphism in section 3.10.1 were non-significant. Likewise, it was not necessary to repeat MANOVA and MANCOVA analyses, as no significant geographic variation had been detected in section 3.12.1 based on a larger sample size.

CHAPTER 3

Results

Plate 3.1. Cranially immature (top) and mature (bottom) *Delphinus* sp. male specimen from New Zealand waters included in the present study.

PART I: Cranial maturity indicators and skull growth

3.1 Additional information

A total of 67 common dolphin (*Delphinus* sp.) skull specimens, collected from stranded and by-caught individuals from New Zealand waters, were available for morphometrical examination and analyses (Appendix 10; Fig. 3.1). Of those, 73.1% (n = 49) were collected, and archived frozen at Massey University over a period of 12 years (1999 - 2011). The remaining 18 skull specimens (collection dates between 1932 and 2004), were housed at the Museum of New Zealand Te Papa Tongarewa, Wellington, and additionally included for analyses.

Sex was known for 88.1% (n = 59) of skull specimens, of which 40.7% (n = 24) were male and 59.3% (n = 35) were female. Total body length (TBL) ranged from 133.0 to 241.0 cm in males and from 159.0 to 212.0 cm in females. Exact ages (lowest resolution: 1 year interval) were available for 38.8% (n = 26) skull specimens ranging from 1 to 29 years (NZCDP, unpubl. data). Minimum age was known for 11 (16.4%) individuals ranging from > 10 to > 33 years (Murphy et al., in review). Of these, the two oldest dolphins were captive females. In total, 37.3% (n = 25) of specimens had been assessed as sexually mature, of which 24.0% (n = 6) and 76.0% (n = 19) were males and females, respectively. Of the latter, 52.6% (n = 10) had been pregnant and / or lactating. Rostral fusion extended to ≥ 50% of the length of the rostrum in 74.6% (n = 50) of skulls available.

Based on the above information, 34.3% (n = 23) and 46.3% (n = 31) of skull specimens were preliminarily regarded as cranially immature and mature, respectively. Preliminary cranial maturity status could not clearly be determined for 19.4% (n = 13) of individuals, because either biological data were missing (n = 9, museum specimens) or degree of premaxilla-maxilla fusion and biological data were contradictory (n = 4).

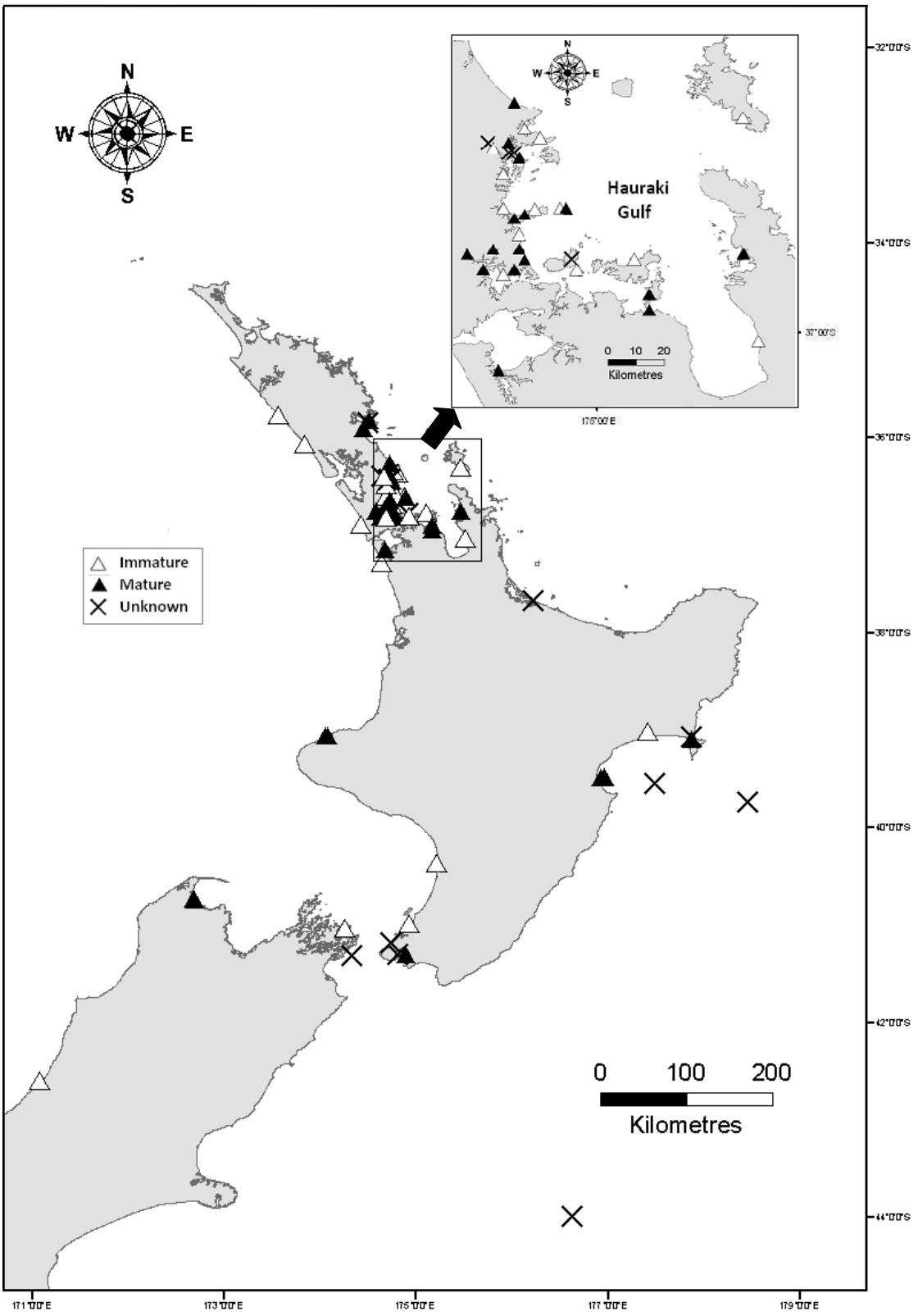

Figure 3.1. Stranding and by-catch location of *Delphinus* sp. skull specimens from New Zealand waters available for the present study. Note: Maturity status (immature, mature, and unknown) refers to the preliminary cranial maturity status that had been assigned to each specimen based on the criteria listed in section 2.3.2.1.2.

3.2 Cranial maturity determination based on the suture index

3.2.1 Suture data preparation

3.2.1.1 Bilateral asymmetry

The degree of suture fusion in 16 cranial sutures was investigated. Bilateral asymmetry in the degree of suture fusion could be assessed in 87.5% (n = 14) of sutures (refer to section 2.3.2.1.1). For 16 individuals the degree of suture fusion of one or more sutures (one: n = 7, two n = 4, three: n = 4, six: n = 1) could not be determined owing to bone damage and remaining flesh. As a result, sample size between sutures differed. Wilcoxon matched-pairs signed-ranks tests revealed no significant difference ($p > 0.05$) in the median degree of fusion between the left and right side for any suture investigated (n = 14) (Table 3.1).

Table 3.1. Wilcoxon matched-pairs signed-ranks tests for bilateral asymmetry of the degree of fusion of cranial sutures assessed on *Delphinus* sp. from New Zealand waters. Note: n = total number; % = percentage of pairs that differed in the degree of fusion between the right and left side for a given suture; W = sum of signed ranks, where positive and negative values indicate more advanced fusion on the right and left side of the skull, respectively; n/a = test was not conducted, because all pairs were equal. For suture abbreviation refer to section 2.2.3.

Cranial suture	n	%	W	p
fr-in	59	15.3	15	0.426
fr-or	66	0.0	0	n/a
la-fr	61	1.6	1	>0.999
max-fr	66	6.1	10	0.125
na-fr	67	7.5	3	0.813
pa-ex	62	8.1	-3	0.813
pa-fr	65	15.4	0	>0.999
pa-so	65	7.7	-5	0.625
pal-max	64	1.6	-1	>0.999
premax-max	67	14.9	-11	0.625
pt-ba	64	14.1	-25	0.164
pt-pal	65	1.5	1	>0.999
so-ex	65	0.0	0	n/a
zy-pa-ex	65	20.0	7	0.839

3.2.1.2 Correlation with age

The degree of fusion was significantly ($p < 0.001$) and positively correlated with specimen age in all sutures except for the supraoccipital-exoccipital (so-ex) suture, in which suture obliteration was recorded in specimens aged 1 year (Table 3.2; Fig. 3.2). Specimens aged 4 - 5 and 15 - 17 years were not available for the present study.

Table 3.2. Kendall tau b correlation results for degree of suture fusion in relation to age for individual sutures of *Delphinus* sp. skull specimens from New Zealand waters. Note: n = sample size; c.coef = correlation coefficient; p = p-value; * = < 0.001. For suture abbreviation refer to section 2.2.3.**

Cranial suture	n	Kendall tau b c.coef	p
fr-in	26	0.710	***
fr-fr	26	0.652	***
fr-or	28	0.653	***
la-fr	25	0.698	***
max-fr	28	0.565	***
na-fr	30	0.767	***
pa-ex	28	0.707	***
pa-fr	28	0.705	***
pa-so	28	0.641	***
pal-max	27	0.632	***
pal-pal	28	0.584	***
premax-max	28	0.545	***
pt-ba	28	0.777	***
pt-pal	28	0.679	***
so-ex	30	0.270	0.057
zy-pa-ex	27	0.570	***

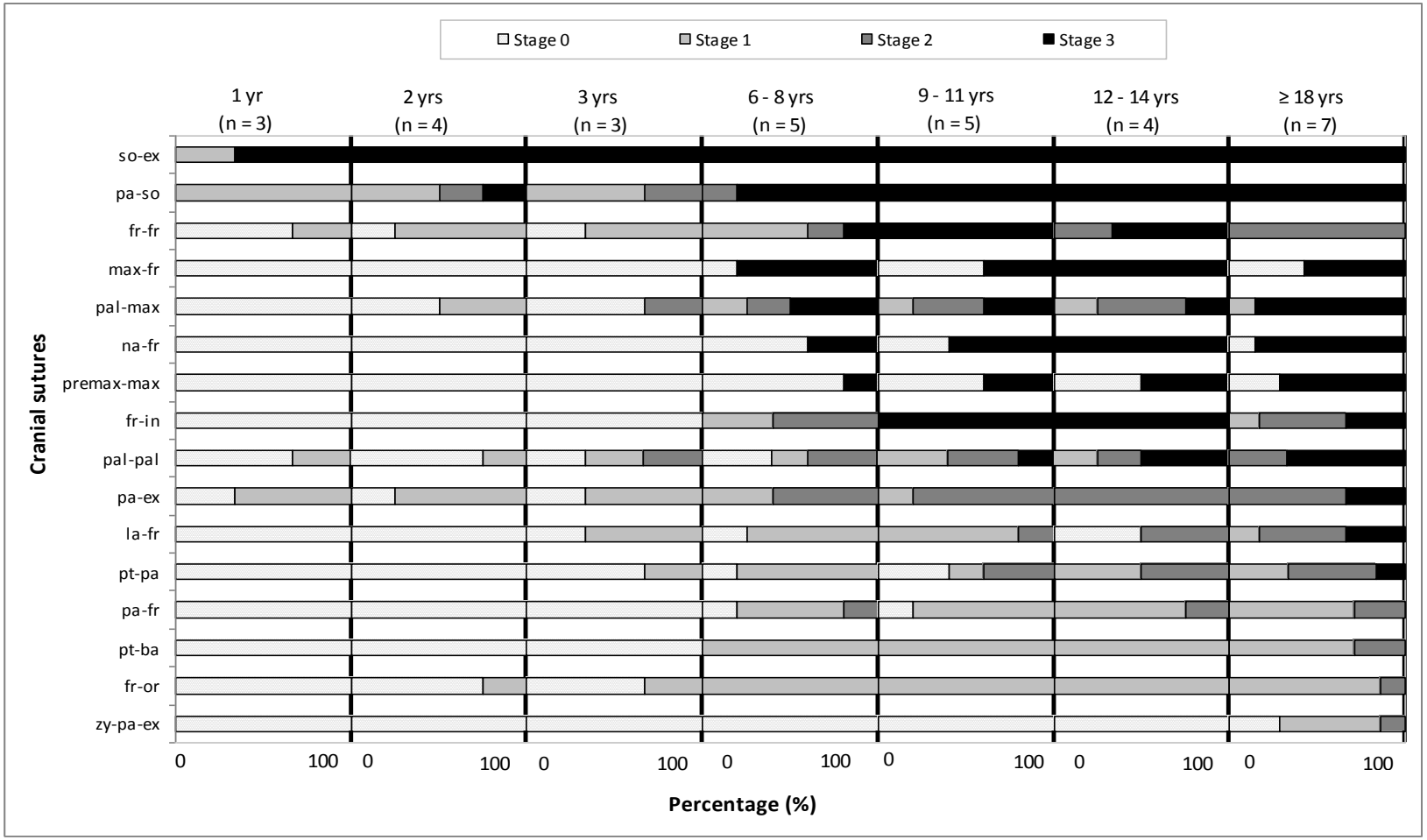

Figure 3.2. Degree of suture fusion, given as a percentage, per age class for 16 cranial sutures recorded on *Delphinus* sp. skull from New Zealand waters. Note: Stage 0 = elements can be moved freely; Stage 1 = no movement and suture lines clearly visible; Stage 2 = partial obliteration; Stage 3 = complete obliteration; yr = year; yrs = years. Specimens aged 4 to 5 and 15 to 17 years were not available for the present study. Sutures arranged according to trend of fusion with age class (top to bottom = early fusion, progressive but variable degree of fusion, and late fusion). For suture abbreviation refer to section 2.2.3.

Although degree of suture closure was positively correlated with age in the remaining sutures (n = 15), the pattern of fusion was not uniform between them. For example, the zygomatic-parietal-exoccipital (zy-pa-ex) suture was characterized by delayed suture fusion, which only occurred in 71.4% (n = 5) of animals aged ≥ 18 years and fusion stage 3 was never recorded (Fig. 3.2). In three sutures (i.e. the fr-or, pterygoid basioccipital (pt-ba), and parietal-frontal (pa-fr)) fusion stage 3 was not recorded for any of the specimens investigated (aged 1 to > 33 years (n = 31). This indicated that complete obliteration of those suture lines may never occur (Fig. 3.2). In contrast, early suture closure and partial / complete obliteration of the so-ex and parietal-supraoccipital (pa-so) already occurred in 100% (n = 5) and 50.0% (n = 2) of specimens of two year of age. The remaining 10 sutures displayed a progressive, but variable, advance in the degree of suture fusion with age (Fig. 3.2). For example, complete obliteration was recorded in individuals aged 6 - 8 years for five sutures (i.e. fr-fr, maxilla-frontal (max-fr), nasal-frontal (na-fr), palatine-maxilla (pal-max), and premaxilla-maxilla (premax-max) suture), while this suture fusion stage occurred only in specimens aged ≥ 18 years for the lacrimal-frontal (la-fr), pa-ex, and pterygoid-palatine (pt-pal) sutures.

3.2.1.3 Misclassification index

The degree of closure in 68.8% (n = 11) of sutures investigated differed significantly ($p < 0.05$) between immature and mature specimens, with the latter having a more advanced degree of suture fusion (Fig. 3.3). Overall, no significant difference ($p > 0.0.5$) was documented in the degree of suture closure between specimens preliminary classified as cranially immature and mature for 31.2% (n = 5) of cranial sutures (i.e. the fr-or, pa-fr, pt-ba, so-ex, and zy-pa-ex) assessed. Lack of significant difference in four of these sutures (fr-or, pa-fr, pt-ba, and zy-pa-ex) resulted from a very low percentage (3.3% (n = 1) to 13.3%

(n = 4)) of advanced degree of suture closure, characterized by partial or complete suture line obliteration, in mature specimens (Fig. 3.3). Conversely, early suture closure, was recorded for the so-ex suture, with advanced stages of fusion documented in 95.7% (n = 22) of immature specimens, as had already been presented in Fig. 3.2.

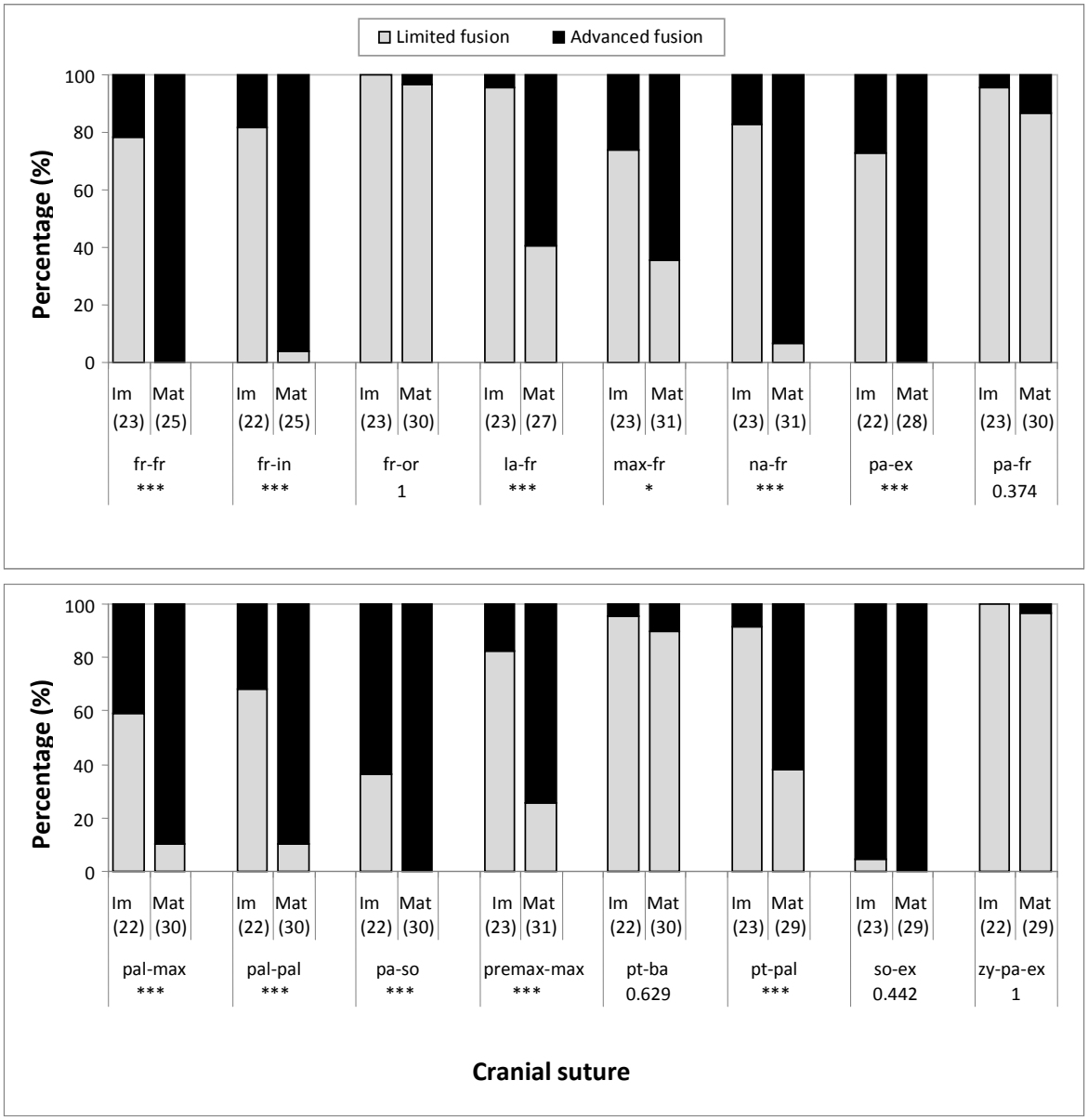

Figure 3.3. Percentage frequency of the degree of suture fusion (limited *versus* advanced) of 16 cranial sutures (listed alphabetically) for immature (Im) and mature (Mat) *Delphinus* sp. skull specimens from New Zealand waters. Note: Limited fusion = fusion stages 0 and 1; advanced fusion = fusion stages 2 and 3); numbers in parentheses represent sample size. Fisher's Exact test results for differences in the state of suture fusion between specimens preliminary classified as cranially immature and mature are also given where: * = p < 0.01; *** = p < 0.001. For suture abbreviation refer to section 2.2.3.

The fr-fr and frontal-interparietal (fr-in) sutures displayed the lowest total misclassification index (10.4% and 10.6%, respectively) for immature and mature specimens combined (Table 3.3). Total misclassification of the remaining seven sutures ranged from 11.3% (na-fr) to 54.9% (zy-pa-ex). Overall, percentage misclassification of 10 sutures (fr-fr, fr-in, pa-ex, na-fr, premax-max, pal-pal, pal-max, la-fr, pt-pal, and max-fr) within both the immature and mature category was < 50% (Table 3.3). Based on the criteria listed in section (2.3.2.2) a total of 62.5% (n =10) of cranial sutures (fr-fr, fr-in, la-fr, max-fr, na-fr, pa-ex, pal-max, pal-pal, premax-max, and pt-pal), were deemed appropriate for the computation of the suture index.

Table 3.3. Efficiency of individual sutures as cranial maturity indicator for *Delphinus* sp. skull specimens from New Zealand waters as determined by percentage misclassification for specimens preliminary classified as cranially immature, cranially mature, and total misclassification (combined for immatures and matures). Note: n = sample size. Immature and mature individuals were regarded as misclassified for a given suture when scores of 2 or 3 (advanced fusion) and 0 or 1 (limited fusion) were recorded, respectively. For suture abbreviation refer to section 2.2.3.

Cranial suture	Percentage misclassified					
	Immature		Mature		Total	
	n	%	n	%	n	%
fr-fr	23	21.7	25	0.0	48	10.4
fr-in	22	18.2	25	4.0	47	10.6
fr-or	23	0.0	30	96.7	53	54.7
la-fr	23	4.3	27	40.7	50	24.0
max-fr	23	26.1	31	35.5	54	31.5
na-fr	23	17.4	30	6.7	53	11.3
pa-ex	22	27.3	28	0.0	50	12.0
pa-fr	23	4.3	30	86.7	53	50.9
pal-max	22	40.9	30	10.0	52	23.1
pal-pal	22	31.8	30	10.0	52	19.2
pa-so	22	63.6	30	0.0	52	26.9
premax-max	23	17.4	31	25.8	54	22.2
pt-ba	22	4.5	30	90.0	52	53.8
pt-pal	23	8.7	29	37.9	52	25.0
so-ex	23	95.7	29	0.0	52	42.3
zy-pa-ex	22	0.0	29	96.6	51	54.9

3.2.2 Cranial maturity and age class allocation

3.2.2.1 Suture index

The suture index (refer to section 2.3.2.2) with no missing values for any suture could be calculated for 76.1% (n = 51) of specimens (refer to Appendices 11 and 12). Of those, preliminary cranial maturity status (based on criteria outlined in table 2.9) had been assigned to 82.4% (n = 42) of specimens, of which 47.6% (n = 20) and 52.4% (n = 22) were classified as cranially immature and mature, respectively.

Median suture index differed significantly ($p < 0.001$) between specimens initially regarded as cranially immature and mature (Table 3.4). The lower limit of the interquartile range computed for mature specimens (8.0) was regarded as the cut-off point for cranial maturity given that interquartile ranges of the suture index determined for immature and mature individuals did not overlap. Compliance between preliminary cranial maturity status and cranial maturity status based on the suture index was achieved for 92.9% (n = 39) of skull specimens (Table 3.5).

Table 3.4. Median, interquartile range (I.Q.R.), total range, sample size (n) and Mann-Whitney U test results for the suture index of *Delphinus* sp. skull specimens from New Zealand waters according to the preliminary cranial maturity status. Note: U = test statistic; p = p-value; * = < 0.001. Only specimens with an exact suture index were included.**

Suture index	Immature (n = 20)	Mature (n = 22)	Mann-Whitney U	p
Median (I.Q.R.)	2.3 (1.0 - 5.1)	8.5 (8.0 - 9.5)	17.0	***
Range	0.0 - 9.5	7.0 - 10.0		

Table 3.5. Compliance, given as a percentage, between preliminary cranial maturity status and cranial maturity status based on the suture index for *Delphinus* sp. skull specimens from New Zealand waters. Note: The cut-off point for cranial maturity was set at the lower limit of the interquartile range obtained for mature specimens for the suture index.

Suture index	Cranially Immature	Cranially Mature	Percentage compliance
Score ≤ 7.5	19	2	**92.9**
Score ≥ 8	1	20	

3.2.2.2 Age at cranial maturity

An exact suture index could be computed for 21 individuals of known age and for a further 7 skull specimens with minimum ages. In total, 42.9% (n = 12) and 57.1% (n = 16) of those were males and females, respectively.

The suture index was positively correlated with age in both sexes (Kendall's tau b, male: correlation coefficient = 0.796, p = 0.002, n = 10; female: correlation coefficient = 0.768, p < 0.001, n = 13). The index obtained for all specimens of known age that had preliminarily been classified as cranially immature fell below those of mature specimens in all cases (Fig. 3.4). A maximum index of 10 (representative of advanced fusion of all 10 sutures investigated was only obtained in the oldest specimens > 33 years). A suture index of 8.0 and 9.0 were only recorded for individuals of ≥ 11 years. The suture index (7.0) of the female specimen WS04-34Dd (10 years) that had been preliminarily classified as cranially mature, fell between suture indices obtained for cranially immature and mature specimens of known age. The suture index of the male specimen WS05-06Dd, which was also 10 years of age, fell below scores obtained for individuals aged 6 to 8 years.

No inferences could be made about potential differences between the sexes in respect to pattern of suture closure with age, owing to small sample size and lack of both male

specimens with exact ages above 13 years and female specimens in the age range 4 to 7 years. However, on inspection of Fig. 3.4, no obvious differences were apparent and both sexes were pooled.

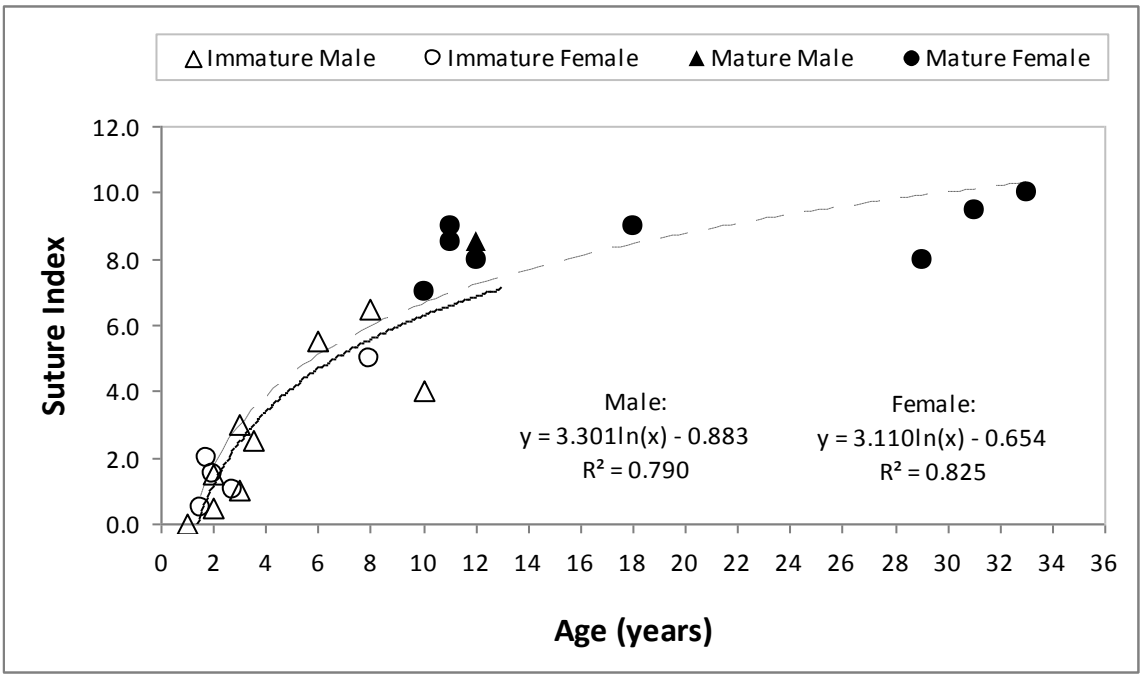

Figure 3.4. Suture index plotted against age (years) for *Delphinus* sp. skull specimens from New Zealand water, by sex and preliminary cranial maturity status. Note: Lines of best fit represent logarithmic lines for both the male (unbroken) and female (dashed) data set.

3.2.2.3 Age class allocation of specimens of unknown age

Median suture index differed significantly ($p < 0.001$) with age class (Table 3.6; Fig. 3.5). Dunn's Multiple Comparisons Post hoc tests revealed that the median suture index differed significantly between all three age classes, with specimens in older age classes having significantly (I *vs* II and II *vs* III: $p < 0.05$; I *vs* III: $p < 0.001$) higher values (Table 3.6).

Table 3.6. Suture index computed for *Delphinus* sp. skull specimens from New Zealand waters according to age class. Kruskal-Wallis test result is also shown. Note: I.Q.R. = interquartile range; W = test statistic; df = degrees of freedom; p = p-value; * = < 0.001; n = sample size; yrs = years.**

Suture index	Age class I 1- 3 yrs	Age class II 6 - 10 yrs	Age class III ≥ 11 yrs	Kruskal-Wallis W	df	p
Median (I.Q.R.)	1.3 (0.6 - 1.9)	5.5 (5.0 - 6.5)	8.8 (8.0 - 9.1)	22.392	2	***
Range	0.0 - 3.0	4.0 - 7.0	8.0 - 10.0			
n	10	5	12			

Figure 3.5. Suture index of *Delphinus* sp. skull specimens from New Zealand waters according to three age classes. Note: Horizontal lines represent the median, boxes the interquartile range and vertical lines the range; yrs = years; n = sample size.

Given that ranges of the suture index did not overlap between age classes (Table 3.6 and Fig. 3.5), the lower limit of the ranges of age class II (5.5) and III (8.0) were regarded as the cut-off point for those two age classes. Based on this criteria, individuals of unknown age (n = 30) were allocated to one of the three age classes (1 - 3 years, 6 - 10 years, and ≥ 11 years; Appendix 11). The specimen KS10-01Dd could not be allocated to an age class, as the suture index fell between the range of age class I and II. This finding was due to the fact that specimens with the age of 4 to 5 years were not available for the present study.

3.3 Validity of rostral fusion and total body length as cranial maturity indicators

Premaxilla-maxilla fusion of all individuals assessed as cranially mature (based on the suture index only) was ≥ ½ the length of the rostrum (Fig. 3.6). None of the cranially immature specimens displayed rostral fusion of ≥ 75%. All cranially immature specimens in which rostral fusion exceeded 50% of the length of the rostrum (n = 5), were approaching cranial maturity (based on age data and / or the suture index).

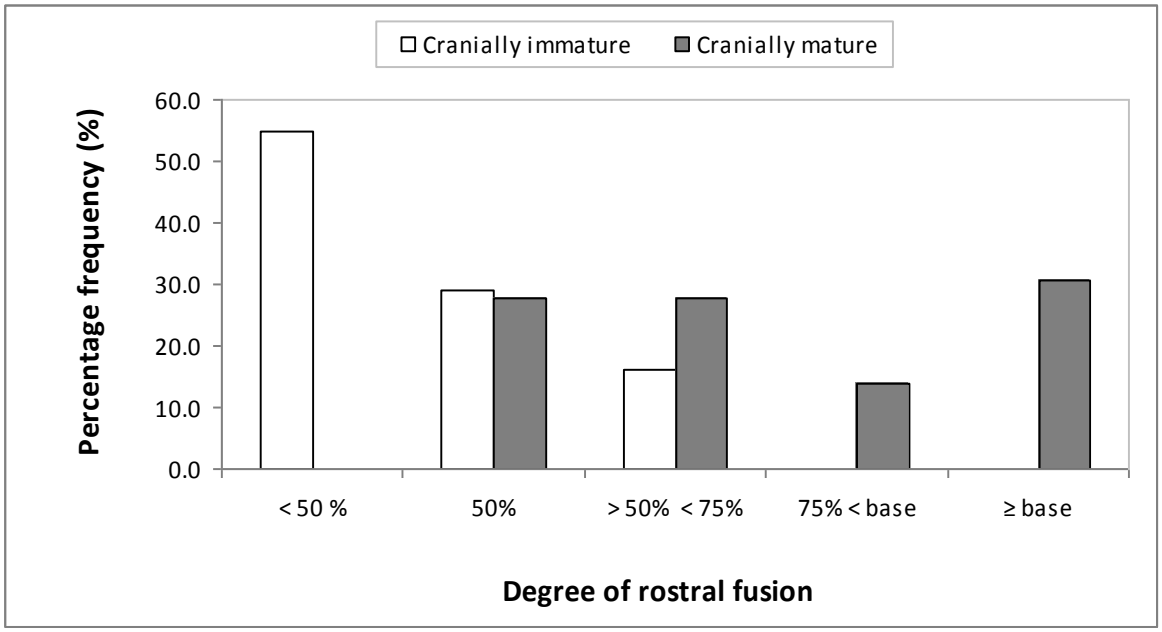

Figure 3.6. Percentage frequency of five different degrees of rostral fusion by cranial maturity status (based on suture index) for *Delphinus* sp. from New Zealand waters. Note: percentages represent extent of fusion over the length of the rostrum from the tip; base = base of rostrum.

Median TBL differed significantly with cranial maturity status (Kruskal-Wallis: $W = 28.110$, $df = 3$, $p < 0.001$). Dunn's Multiple Comparisons Post hoc test revealed that mature specimens had significantly larger median TBL than immatures of both sexes (Table 3.7). Median TBL did not differ significantly (> 0.05) between males and females. In total, 75.0% (n = 6) of cranially mature males, but only 47.6% (n = 10) of mature females had TBL ≥ the asymptote (asymptote: males: 204.0 cm, females: 199.9 cm). Overall, two cranially immature male specimens (WS05-06Dd: 10 years, suture index: 4.0 and KS09-13Dd: 8 years, suture index: 6.5) had TBL of 214.0 and 220.0 cm, respectively and thereby were clearly above the asymptote (Fig. 3.7).

Table 3.7. Median, interquartile range (I.Q.R.), and total range for total body length (TBL), of cranially immature (Im) and mature (Mat) male and female *Delphinus* sp. from New Zealand waters. Note: n = sample size.

TBL (cm)	Male (Im)	Female (Im)	Male (Mat)	Female (Mat)
Median	174.0	183.0	212.5	198.0
(I.Q.R.)	(167.0 - 182.0)	(177.4 - 189.0)	(205.5 - 220.3)	(195.0 - 206.0)
Range	133.0 - 220.0	159.0 - 189.5	190.0 - 241.0	187.0 - 212.0
n	13	12	8	21

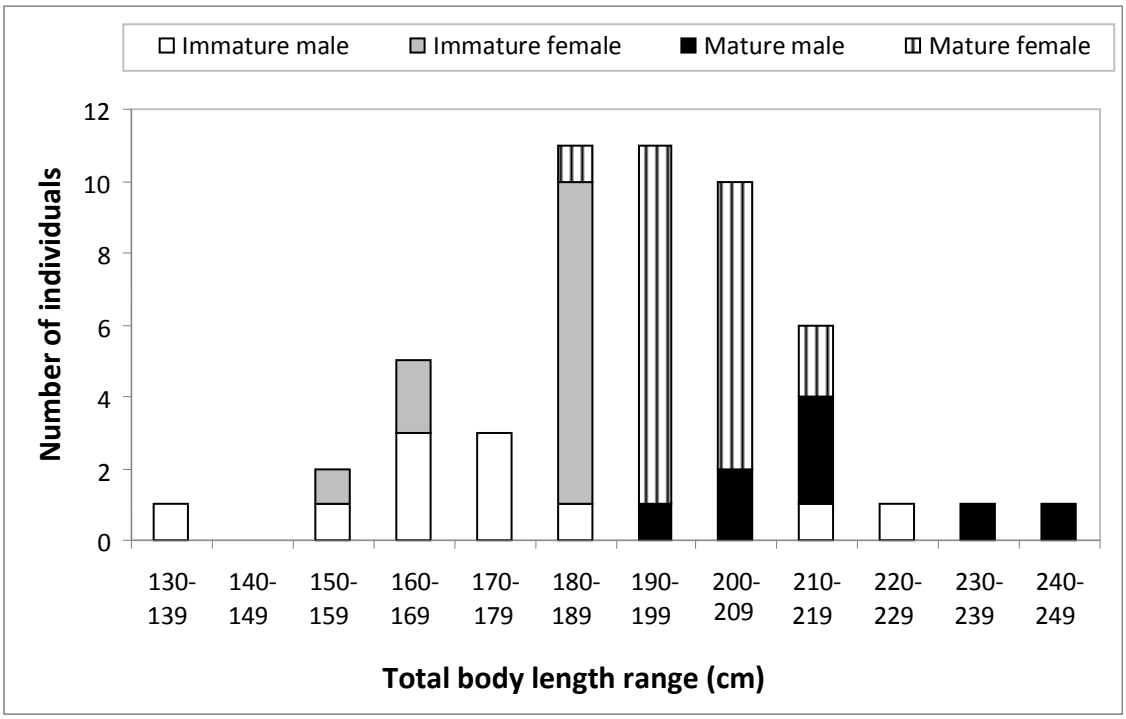

Figure 3.7. Total body length of cranially immature male (n = 13) and female (n = 12) as well as cranially mature male (n = 8) and female (n = 21) *Delphinus* sp. specimens from New Zealand waters for which crania have been assessed in the present study. Note: Cranial maturity was based on a suture index of ≥ 8.0.

3.4 Re-assessment of cranial maturity status of individual skull specimens

In total, two female specimens preliminarily classified as cranially mature (WS04-34Dd: 10 years, TBL = 189.0 cm; total score: 7.0; WS07-01Dd: 9 years, TBL = 189.5 cm, total score: 5.5 with scores missing for the fr-fr and fr-in sutures), were just below the cut-off point for cranial maturity (Appendix 12). As a precaution, both individuals were regarded as cranially immature. In total, two specimens preliminarily classified as cranially immature based on TBL data (WS97-17Dd: female, 190.0 cm and KS11-10Dd: male, 190.0 cm) were re-classified as cranially mature using the revised cranial maturity criteria (refer to section

2.3.2.5). This decision was based on the fact that the suture index of both individuals were among the highest scores (9.0 and 9.5, respectively) computed for all specimens assessed.

All individuals for which preliminary cranial maturity status had not been determined (n = 4), because biological data and rostral fusion had indicated contradictory cranial maturity status, were assessed as cranially immature (Appendix 12). Of these, three individuals were males with known ages (WS05-06Dd: 10 years, KS09-10Dd: 8.75 years, and KS09-13Dd: 8 years). The fourth specimen was a female (KS10-18Dd) with a TBL of 182.0 cm and a suture index of 5.5, in which rostrum fusion exceeded 50 % of the rostrum. In total, 66.7% (n = 6) of museum specimens with no additional biological data (MM000981, MM001550, MM001688, MM002221, MM002220, and MM002246) had reached the cut-off point for cranial maturity and were regarded as cranially mature (refer to Appendix 12).

3.5 Revised additional information

3.5.1 Maturity status and sex ratio

Based on the devised cranial maturity criteria, a total of 46.3% (n = 31) and 53.7% (n = 36) of skull specimens were regarded as cranially immature and mature, respectively (Appendices 11 and 12). Sex was known for 93.6% (n = 29) and 83.3% (n = 30) of immature and mature individuals, respectively. Sex ratio of immatures was approximately 1:1 (males: n = 16, females: n = 13), while that of mature specimens was almost 1:3 (males: n = 8, females: n = 22).

3.5.2 Carcass location

Stranding and by-catch location was known for all individuals except for two museum specimens (MM002220 and MM002221). Just over half of the sample size of mature males (62.5%, n = 5) and females (59.1%, n = 13) had been obtained from the Hauraki Gulf (HG). Likewise, sample size from cranially immatures of both sexes was larger from HG (males: n = 10 and females: n = 8) as compared to non-HG (males: n = 6 and females: n = 5) waters (Fig. 3.8). All immatures were stranded and by-caught individuals, while three mature females (WC06-10Dd: *Shona*, WC06-08Dd: *Kelly*, and WC98-30Dd: *Cassana*) had been captured off Napier, Hawkes Bay and held captive in Marineland, Napier for > 11 (*Cassana*) and > 30 (*Shona* and *Kelly*) years prior to their death.

3.5.3 Total body length and age

Exact TBL was available for 79.1% (n = 53) of the skull specimens. The maximum TBL recorded for cranially immature male and female *Delphinus* sp. were 220.0 and 189.0 cm, respectively. TBL of cranially mature males and females ranged from 190.0 to 241.0 cm (n = 8) and from 187.0 to 212.0 cm (n = 22), respectively.

Exact ages were estimated for a total of 18 cranially immature and 8 mature specimens. Minimum ages were known for a further 11 cranially mature individuals (Table 3.8; Appendix 10). Age of cranially immature and mature males ranged from 1 to 10 years (n = 10) and from > 11 to > 15 years (n = 4), respectively. In comparison, ages for immature and mature females ranged from 1.5 to 10 years (n = 8) and from 11 to over 33 years (n = 15), respectively. Both female specimens (WC08-06Dd: *Kelly* and WC06-10Dd: *Shona*) aged > 30 years had died in captivity. TBL and age range are, however, not representative of the

population because the data were only based on individuals for which skulls were included for analyses presented in the current study.

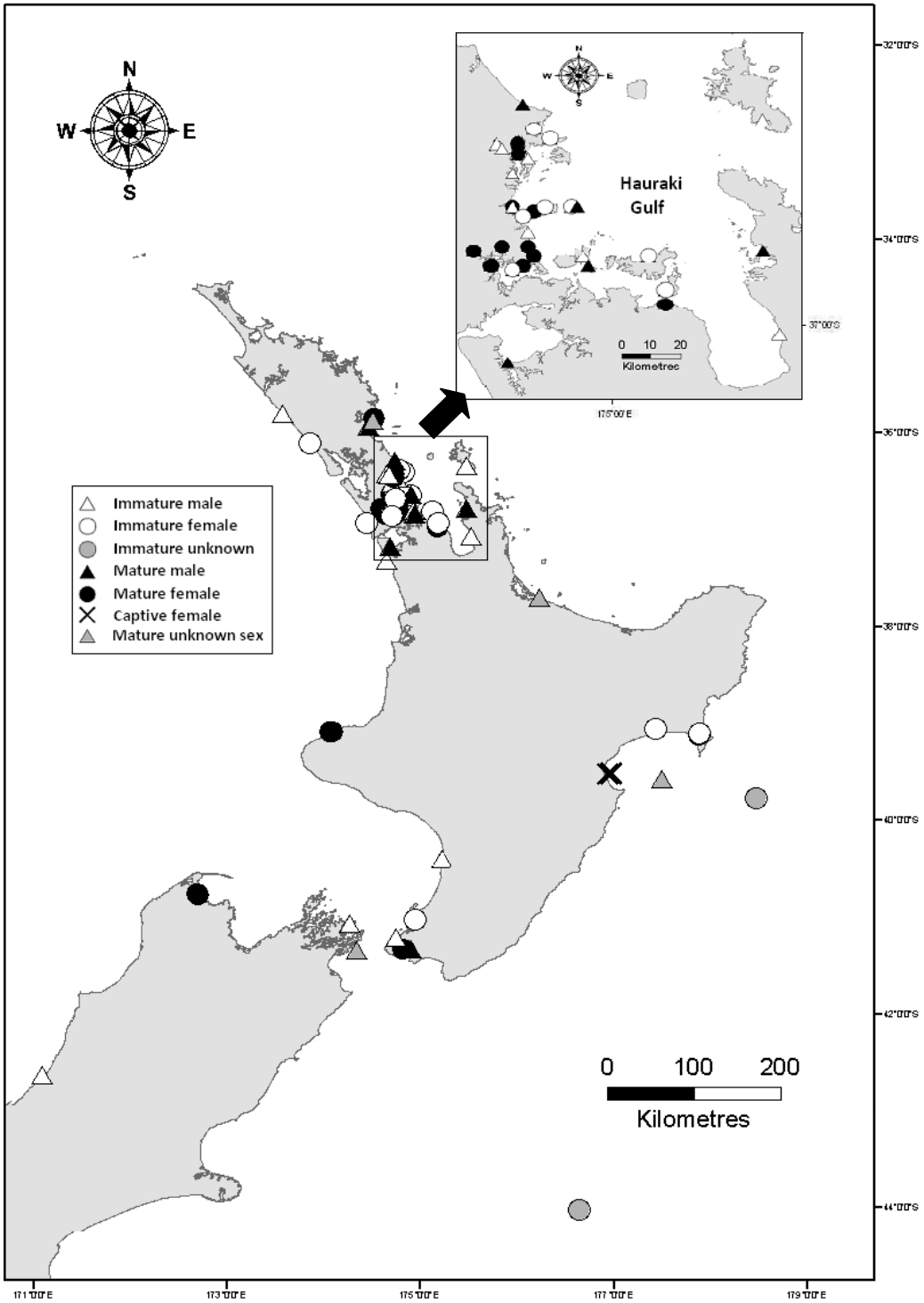

Figure 3.8. Stranding and by-catch location of *Delphinus* sp. skull specimens included for analyses in New Zealand waters. Note: Maturity status refers to cranial maturity status determined based on the suture index.

Table 3.8. Mean ± SD, range, and sample size for total body length (TBL), age, condylobasal length (CBL), rostrum length (RL), and rostrum length to zygomatic width (RL/ZW) ratio for cranially immature (Im) and mature (Mat) male and female *Delphinus* sp. from New Zealand waters. Note: n = sample size; yrs = years. Mean age is based on exact ages only, not on minimum estimates. CBL, RL, and RL/ZW ratio values are based on specimens with rostrum categories 1 and 2 only.

Character	Males (Im)	Females (Im)	Males (Mat)	Females (Mat)
TBL (cm)				
Mean ± SD	176.7 ± 23.8	179.9 ± 10.7	213.9 ± 16.0	199.9 ± 7.7
Range	133.0 - 220.0	159.0 - 189.0	190.0 - 241.0	187.0 - 212.0
n	13	12	8	21
Age (yrs)				
Mean ± SD	4.9 ± 3.4	5.9 ± 3.5	-	15.8 ± 7.0
Range	1.0 - 10.0	1.5 - 10.0	12.0 - > 15.0	11.0 - > 33.0
n	10	8	4	15
CBL (mm)				
Mean ± SD	417.4 ± 57.9	438.1 ± 12.1	463.6 ± 19.3	446.4 ± 17.2
Range	301.1 - 461.2	424.4 - 455.7	446.4 - 494.9	422.7 - 468.5
n	9	5	5	12
RL (mm)				
Mean ± SD	258.8 ± 45.3	272.8 ± 7.0	291.6 ± 17.9	279.0 ± 13.3
Range	165.5 - 292.6	265.8 - 283.0	276.1 - 321.8	261.3 - 298.1
n	9	5	5	14
RL/ZW				
Mean ± SD	1.49 ± 0.12	1.52 ± 0.04	1.50 ± 0.08	1.49 ± 0.06
Range	1.22 - 1.60	1.50 - 1.57	1.39 - 1.59	1.40 - 1.61
n	9	5	5	12

3.6 Metric skull measurements

Mean condylobasal length (CBL) and rostrum length (RL) did not differ significantly (ANOVA: CBL: F = 0.602, df = 2, p = 0.561; RL: F = 0.523, df = 2, p = 0.603) between cranially mature females with rostrum ratings category 1 to 3 (Appendix 13). Owing to small sample size, this difference could not be statistically evaluated in immature specimens and mature males. It was decided to include measurements of rostra ratings 2, due to the finding that the mean of both RL and CBL was slightly higher in cranially mature females with

ratings 2 as compared to females with fully intact rostra (Appendix 13). Measurements (CBL and RL) from specimens with rostra ratings 3 were excluded from all remaining analyses given that the mean value was below the mean obtained for individuals of both category 1 and 2 (Appendix 13).

Summary statistics for CBL, RL, and rostrum length to zygomatic width (RL/ZW) ratio, separately for both maturity status and sex are detailed in Table 3.8. In total, 55.9% (n = 33) of specimens of known sex had rostrum ratings of 1 and 2. Of those, one cranially mature female specimen (KS09-18Dd: TBL = 197.0 cm; > 10 years) had to be excluded owing to a major congenital deformity of the rostrum (refer to Appendix 14). Furthermore, CBL could not be determined for the cranially mature female KS08-03Dd, as the occipital region of the braincase was missing. Median CBL and RL did not differ significantly with maturity status (Kruskal-Wallis: CBL: W = 5.339, p = 0.149; RL: W = 3.412, p = 0.332) when comparing four different categories (immature males, immature females, mature males, and mature females) (Appendix 15).

Cranially immature animals could also not clearly be distinguished from mature individuals based on either of the following: CBL, RL, and RL/ZW ratio as a function of (1) TBL or (2) age (Figs. 3.9 and 3.10). CBL and RL in the range of mature specimens were already attained in all cranially immature individuals with TBL of ≥ 171.0 cm (n = 9) and age of ≥ 8 years (n = 4), indicating that both measures may not be definite indicators of cranial maturity. Due to lack of both age data and specimens with rating categories 1 and 2 between 3 and 8 years of age, it was unclear where CBL and RL in this age range fell below values obtained for cranially mature individuals. However, data on zygomatic width, and mandible length and height indicated that values in the range of mature specimens may already be attained at approximately 6 years of age (Fig. 3.11).

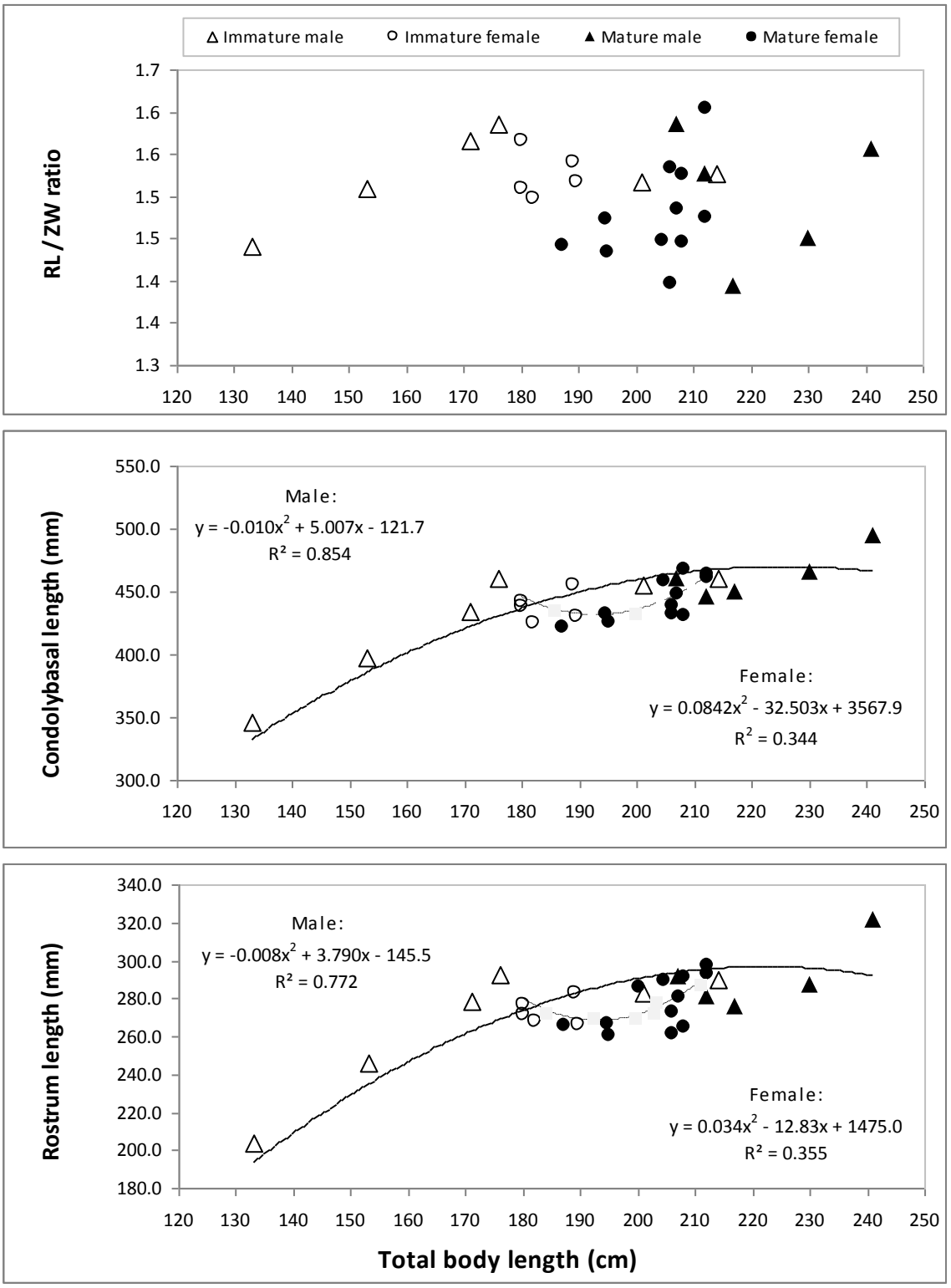

Figure 3.9. Relationship between total body length and rostrum length to zygomatic width (RL/ZW) ratio (top), condylobasal length in mm (middle) and rostrum length in mm (bottom) for cranially immature and mature male and female *Delphinus* sp. from New Zealand waters. Note: Curves represent polynomial lines fitted through the male (unbroken) and female (dashed) data set for both condylobasal length and rostrum length *versus* total body length.

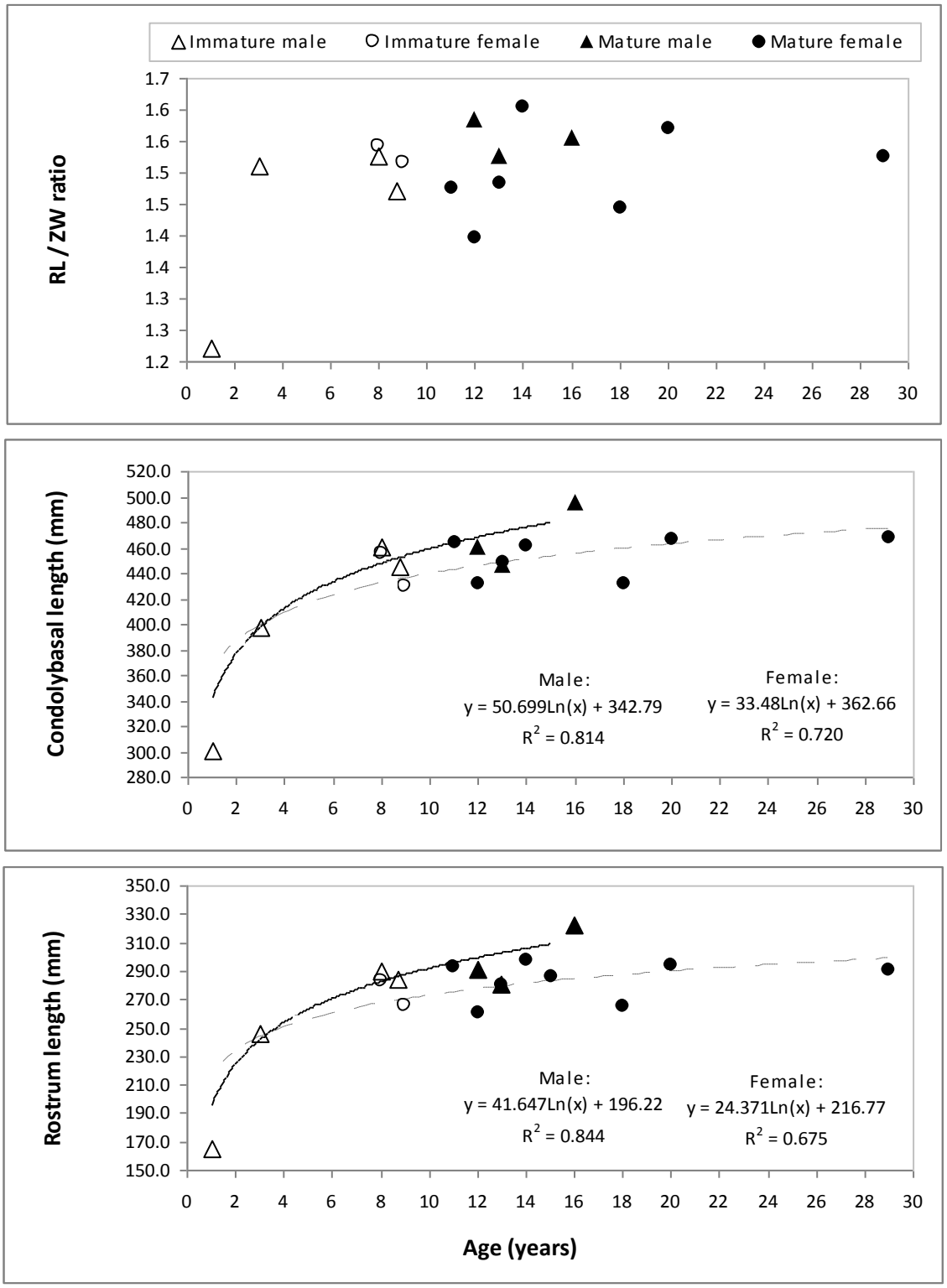

Figure 3.10. Relationship between age (years) and rostrum length to zygomatic width (RL/ZW) ratio (top), condylobasal length in mm (middle) and rostrum length in mm (bottom) for cranially immature and mature male and female *Delphinus* sp. from New Zealand waters. Note: Curves represent logarithmic lines fitted separately through the male (unbroken) and female (dashed) data set for both conylobasal length and rostrum length *versus* age.

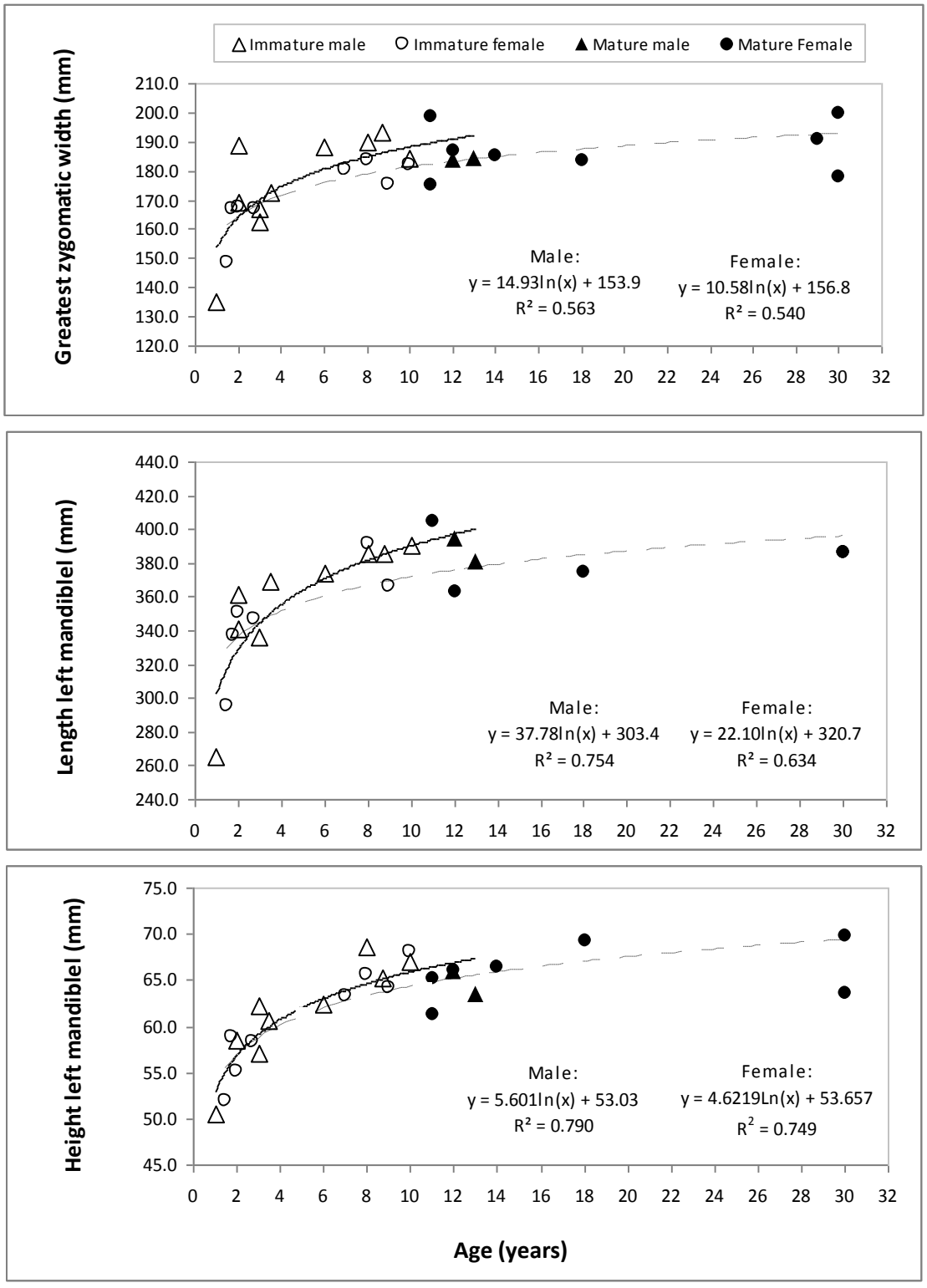

Figure 3.11. Relationship between age (years) and zygomatic width in mm (ZW) (top), left mandible length in mm (middle) and left mandible height in mm (bottom) for cranially immature and mature male and female *Delphinus* sp. from New Zealand waters. Note: Curves represent logarithmic lines fitted separately through the male (unbroken) and female (dashed) data sets for ZW, and mandible length and height *versus* age.

3.7. Relative skull weight

3.7.1 Measures of relative skull weight in relation to sex

In total, 34.3% (n = 23) of skull specimens were included for relative skull weight analyses (Appendix 16). Of those, 21.7% (n = 5), 65.2% (n = 15), and 13.1% (n = 3) were males, females, and specimens of unknown sex, respectively. As noted earlier, two of the females, *Shona*: WC06-10Dd and *Kelly*: WC08-06Dd, had been held in captivity for > 30 years. In total, only two male and two female specimens were cranially immature.

All male specimens had relatively heavier skulls at a given skull length and width compared to females (Fig. 3.12). A small sample size of immatures prevented statistical assessment of differences in skull weight with maturity status for a given sex. However, cranially immature male specimens fell within or above the range of mature males, while both immature female specimens had slightly lighter skulls than mature females when skull weight was plotted against skull length (condylobasal length) (refer to Fig. 3.12). Linear regression analyses revealed that skull weight was significantly ($p < 0.01$) and positively correlated with skull length in males. The same trend applied to female *Delphinus* sp. when both captive specimens were excluded ($p < 0.05$) (Table 3.9). Likewise, skull weight was only significantly ($p < 0.001$) correlated with skull width in females when captive specimens were excluded, owing to relative lighter skulls in the latter. Skull weight in females was still significantly correlated with both skull length ($p < 0.05$) and width ($p < 0.001$) when immature specimens were included. In contrast, correlation between skull weight and skull width was not significant ($p < 0.05$) in males. All individuals of unknown sex (n = 3) fell within the range of males.

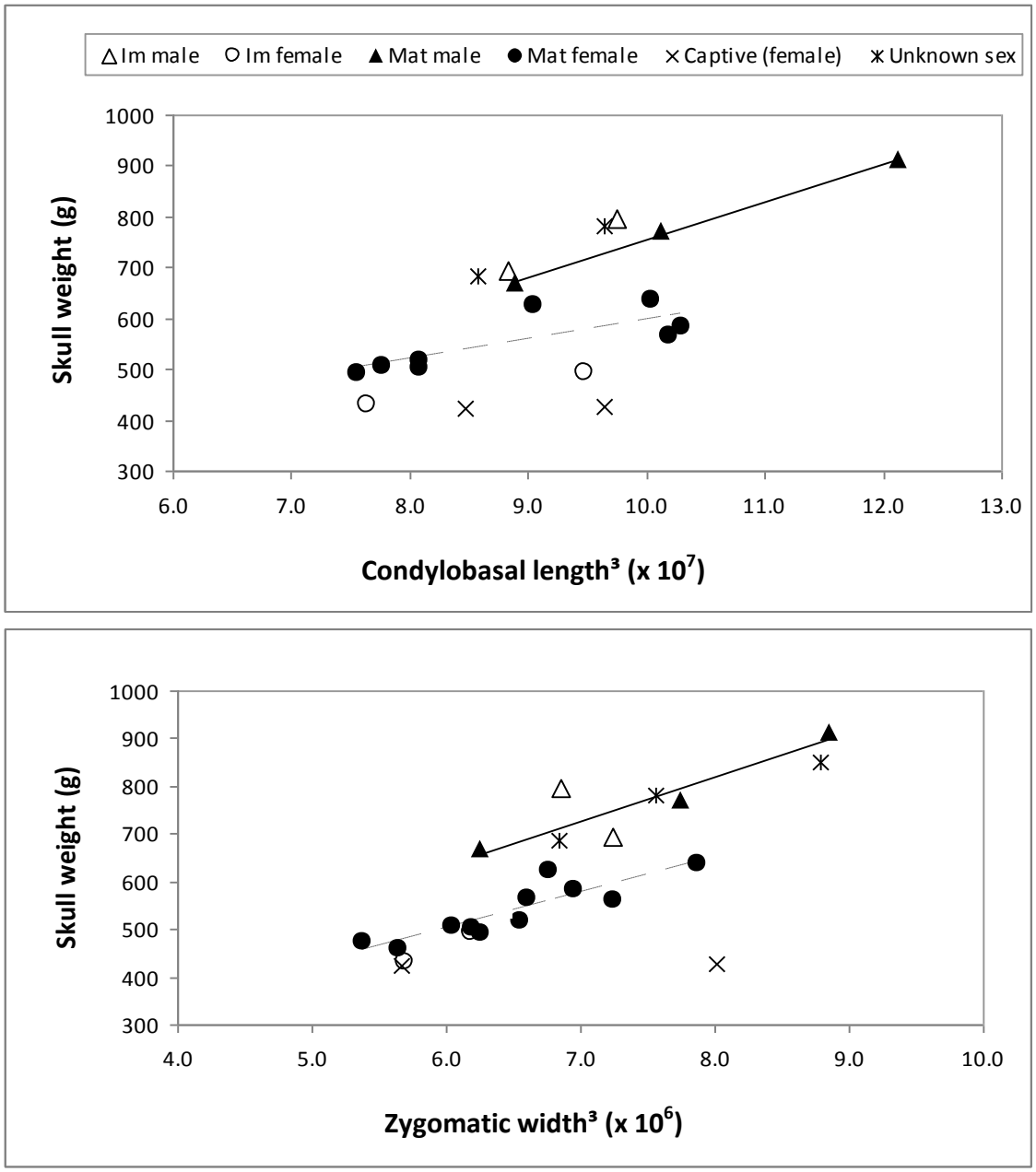

Figure 3.12. Relationship between skull weight (g) and skull length (condylobasal length³ in mm x 10^7) (top) and skull width (zygomatic width³ in mm x 10^6) (bottom) for *Delphinus* sp. from New Zealand waters of known maturity status, known and unknown sex, and of specimens held captive. Note: Im = cranially immature; Mat = cranially mature. Lines of best fit are fitted separately through the male (unbroken) and female (dashed) data sets.

Table 3.9. Linear regression results of skull weight (SW) as a factor of skull length (CBL^3) and zygomatic width (ZW^3) by sex for *Delphinus* sp. from New Zealand waters. Note: all = including both captive (n = 2) and cranially immature (n = 2) specimens; excl. cap. = excluding captive specimens; excl. Im = excluding cranially immature specimens; n = sample size; p = p-value; values in bold = < 0.05; ** = < 0.01; * = < 0.001.**

	SW *versus* CBL^3			SW *versus* ZW^3		
	n	**r^2**	**p**	**n**	**r^2**	**p**
Female (all)	12	0.262	0.089	15	0.259	0.053
Female (excl. cap.)	10	0.527	**0.018**	13	0.779	***
Female (excl. cap / Im)	8	0.642	**0.017**	11	0.769	***
Male	5	0.928	**	5	0.714	0.072

A significant ($p < 0.001$) difference in both SW/CBL^3 ratio and SW/ZW^3 was detected between sexes, with males having heavier skulls than females (Table 3.10). Captive specimens were excluded from statistical analyses, owing to small sample size (n = 2). As a precaution, immature females were also omitted from analyses, given that these specimens (n = 2) tended to have a slightly lower relative skull weight as a function of skull length compared to mature females (refer to Fig. 3.12).

Table 3.10. Mean ± SD, 95% confidence interval (CI), range and, sample size of skull weight to skull length³ (SW/CBL³) ratios (x 10^{-6}) and skull weight to zygomatic width³ (SW/ZW³) ratios (x 10^{-5}) obtained for captive female and stranded and by-caught male and female *Delphinus* sp. from New Zealand waters. Unpaired t-test results for comparison between female (excl. immature and captive specimens) and male specimens are also given. Note: n = sample size; t = test statistic; p = p-value; * = < 0.001.**

				Unpaired t-test	
SW/CBL³ ratio	**Captive**	**Male**	**Female**	**t**	**p**
Mean ± SD	4.71 ± 0.40	7.74 ± 0.28	6.29 ± 0.45	6.358	***
(95% CI)	-	(7.39 - 8.09)	(5.91 - 6.97)		
Range	4.42 - 4.99	7.52 - 8.18	5.56 - 6.92		
n	2	5	8		
SW/ ZW³ ratio					
Mean ± SD	6.40 ± 1.52	10.43 ± 0.79	8.33 ± 0.45	6.891	***
(95% CI)	-	(9.45 - 11.41)	(8.03 - 8.63)		
Range	5.32 - 7.47	9.57 - 11.63	7.75 - 9.26		
n	2	5	11		

Both SW/CBL³ and SW/ZW³ ratios of the three *Delphinus* sp. specimens of unknown sex fell within the 95% CI of the mean obtained for males (Table 3.11). Owing to a rating category 3, the SW/ZW³ ratio but not the SW/CBL³ ratio could be determined for specimen MM002221.

Table 3.11. Potential sex for *Delphinus* sp. specimens (n = 3) of unknown sex based on skull weight to skull length³ (SW/CBL³) ratios (x 10^{-6}) and skull weight to zygomatic width³ (SW/ZW³) ratios (x 10^{-5}) obtained.

Specimens	SW/CBL³	Potential sex	SW/ZW³	Potential sex
MM001688	8.11	M	10.37	M
MM001850	7.99	M	10.01	M
MM002221	-	-	9.69	M

1.7.2 Measures of relative skull weight in relation to total body length and age

TBL had been recorded for 80.0% (n = 4) of male and 93.3% (n = 14) of female specimens, but exact ages were only available for 60.0% (n = 3) and 46.7% (n = 7) of males and females, respectively Appendix 16). Neither TBL nor age data were known for specimens of unknown sex (n = 3) acquired from the Museum of New Zealand Te Papa Tongarewa.

Relative skull weight (SW/CBL^3 and SW/ZW^3) of both captive females was lighter than skulls from free-ranging females with similar or longer TBL (Fig. 3.13). Measures of relative skull weight and TBL were only positively correlated when sexes were pooled (both including and excluding captive specimens) but not for females only (Table 3.12; Fig. 3.13). However, correlation tended to be higher when captive females were excluded. Males could not be analyzed separately due to small sample size (n = 4). The mature female specimen KS09-14Dd (> 10 years) had a lower relative skull weight as compared with the male specimen KS08-10Dd (13 years) with the same TBL of 212.0 cm. A significant negative correlation between measures of relative skull weight and age was recorded for both sexes (pooled) when captive specimens were included. This relationship was absent when these two oldest (captive) individuals were excluded, though the majority of other individuals were < 20 years (87.5%, n = 7) (Table 3.12; Fig. 3.14).

Table 3.12. Pearson correlation analyses (r) between relative skull weight and total body length (TBL) as well as between relative skull weight and age for *Delphinus* sp. from New Zealand waters. Note: SW/CBL³ = skull weight to condylobasal length³ ratio; SW/ZW³ = skull weight to zygomatic width³ ratio; n = sample size; Incl. cap. = including captive specimens (n = 2); Excl. cap. = excluding captive specimens; p = p-value; values in bold = < 0.05; ** = < 0.01.

	SW/CBL³ *versus* TBL			SW/ZW³ *versus* TBL		
	n	**r**	**p**	**n**	**r**	**p**
Females incl. cap.	11	0.063	0.854	14	0.040	0.892
Females excl. cap.	9	0.392	0.297	12	0.465	0.128
Incl. cap.	15	0.546	**0.035**	18	0.543	**0.02**
Exl. cap.	13	0.684	**	16	0.681	**

	SW/CBL³ *versus* age			SW/ZW³ *versus* age		
	n	**r**	**p**	**n**	**r**	**p**
Incl. cap.	9	-0.733	**0.025**	10	-0.677	**0.032**
Excl. cap.	7	-0.450	0.312	8	-0.336	0.415

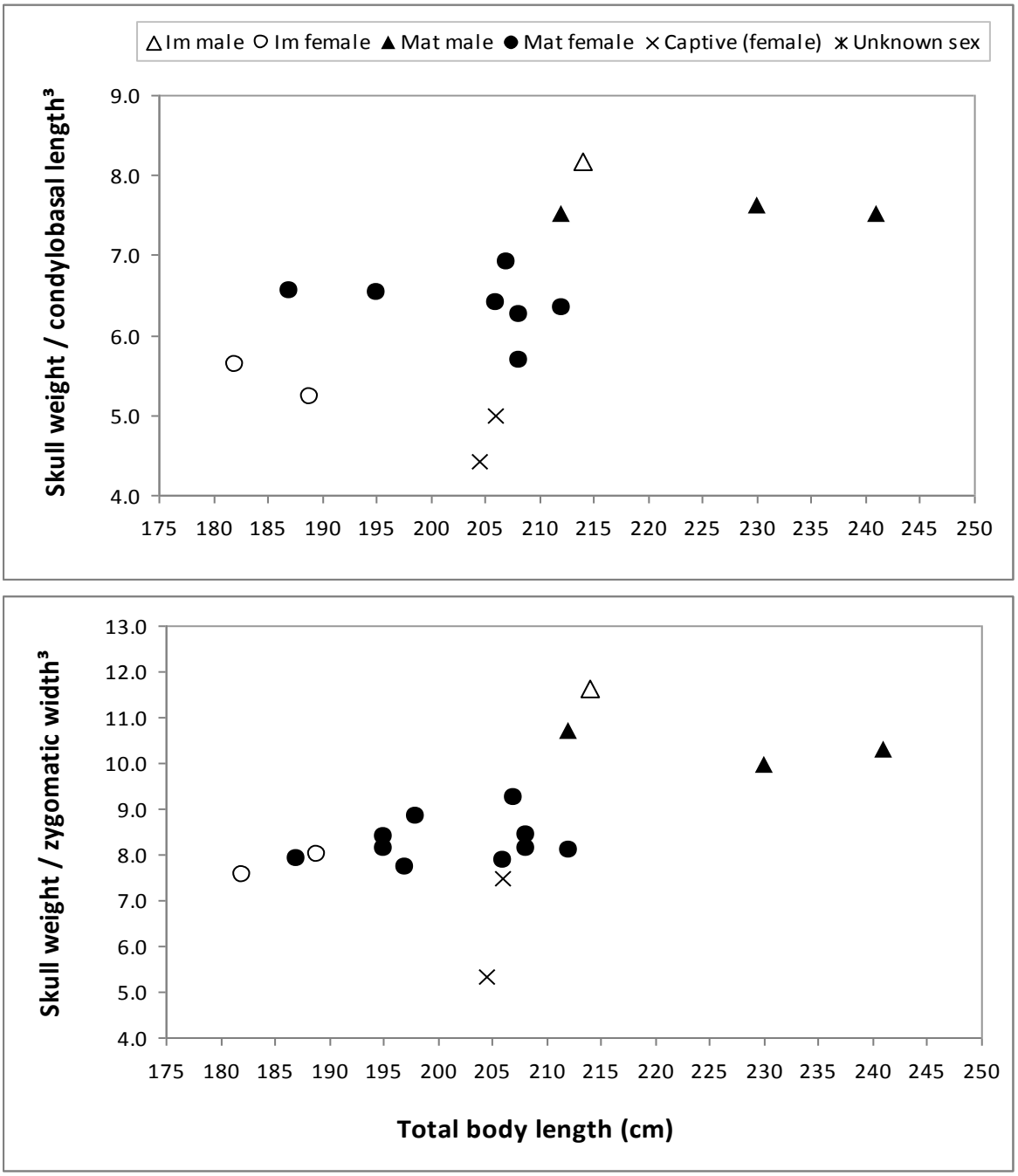

Figure 3.13. Relationship between skull weight to condylobasal length³ ratio (x 10^{-6}) and total body length (top) and between skull weight to zygomatic width³ ratio (x 10^{-5}) and total body length (bottom) for male and female *Delphinus* sp. from New Zealand waters and for specimens held captive.

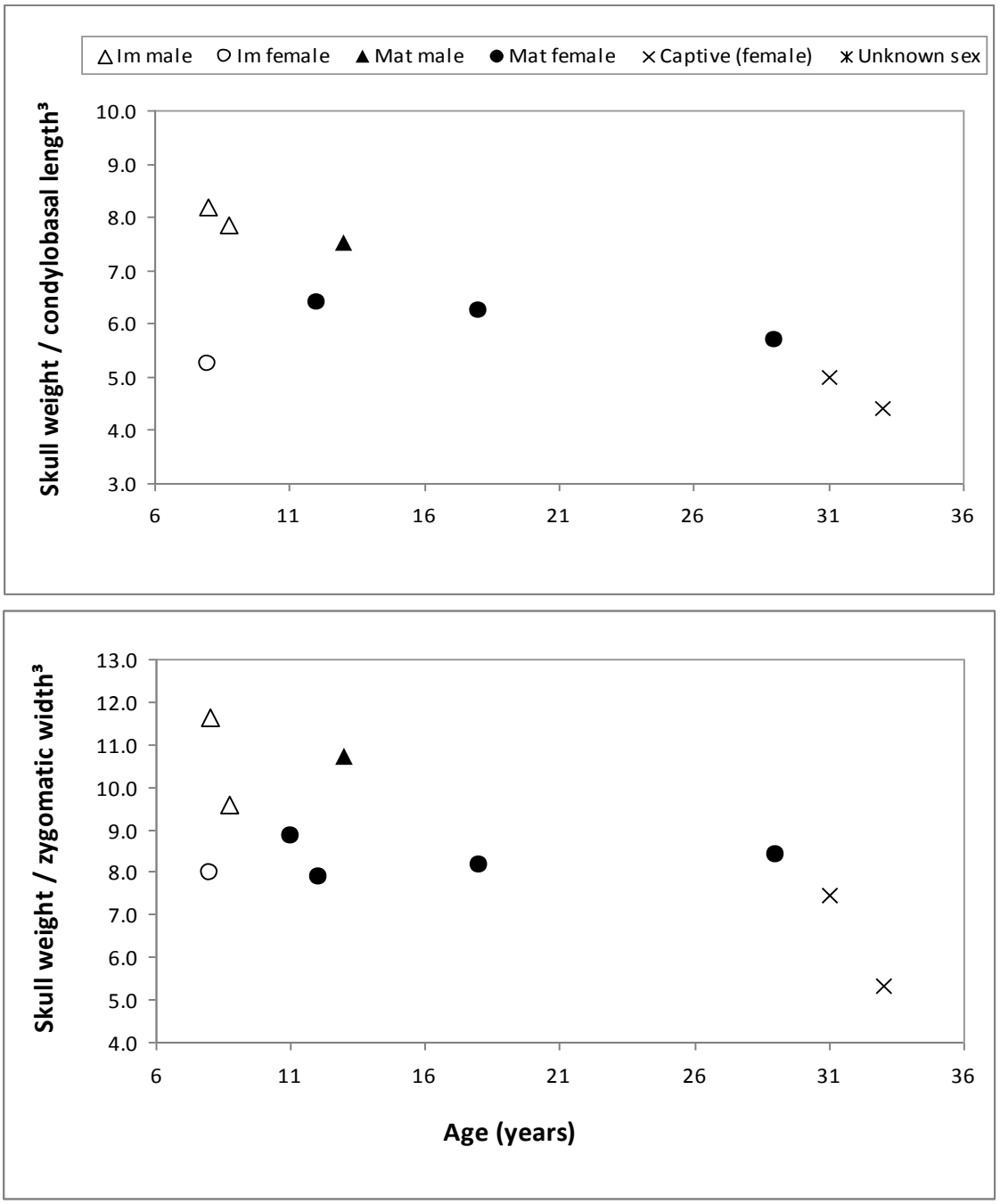

Figure 3.14. Relationship between skull weight to condylobasal length³ ratio (x 10^{-6}) and age (top) and between skull weight to zygomatic width³ ratio (x 10^{-5}) and age (bottom) for male and female *Delphinus* sp. from New Zealand waters and for specimens held captive.

3.8 Non-metric characters

In total, two characters, mesial fenestration in the basioccipital (MFBOCC) and mesial fenestration in the vomer (MFV), were excluded from analyses, owing to the complete lack of difference in trait expression between specimens (fenestrations in relation to both characters were absent in all samples). The remaining 23 non-metric characters were used to assess differences between cranially immature and mature specimens. The interalveolar septa (IAS) of both upper and lower as well as left and right sides of the jaw were identical in all specimens investigated. Consequently, one tooth row, the left maxillary, was chosen to represent the developmental status of the interalveolar septa for a given individual.

Symmetric trait expression was observed in six bilateral non-metric characters, including two that could be assigned to development status (Table 3.13). Asymmetric trait expression was recorded for two characters, contact between premaxilla and nasal (CPN) and advancement of the maxillae relative to the nuchal crest (MNC). Trait expressions for these characters were recorded significantly more often on the right side of the skull ($\chi^2o > 5$). Correspondingly, correlation between sides was lowest for those two characters (Table 3.13).

Table 3.13. Comparison of occurrence frequency of trait expression between sides of bilateral non-metric cranial characters. Note: -- = bilateral absence; +- = left presence and right absence; -+ = left absence and right presence; ++ = bilateral presence; χ^2o = difference between sides (Chi-Square significant at > 5 for 1 degree of freedom); ø = correlation between sides; values in bold = signficance. For character abbreviation refer to section 2.2.6.

Character	--	+ -	-+	++	n	χ^2o	ø
CPN	25	0	34	1	60	**34**	0.110
NFCOEX	5	1	1	61	68	0	0.819
LFV	10	2	2	44	58	0	0.800
PAELF	44	1	1	2	48	0	0.814
OF	22	1	0	21	44	1	0.956
WMF	57	2	1	9	69	0.3	0.833
MNC	24	1	15	28	68	**12.3**	0.596

A significant difference ($p < 0.05$) in non-metric trait expression frequency between cranially immature and mature specimens was detected in 30.4% (n = 7) out of 23 characters assessed (Table 3.14). However, misclassification indices of all characters (n = 4; COH, IAS, WMF, and MNC), in which trait expression could be clearly assigned to a developmental status (refer to Table 2.11), indicated that only interalveolar septa (IAS) was a relative reliable indicator of cranial maturity (refer to Table 3.15). Total misclassification of IAS was only 10.5% (n = 7). All misclassified individuals were specimens that had been classified as cranially immature based on the suture index. Misclassification of immatures was 22.6% (n = 7). Second lowest total misclassification rate of 27.3% (n = 18) was obtained for width of maxillae relative to the frontal bones (WMF) (Table 3.15). This was also attributed to immatures, as the misclassification index of mature specimens based on WMF was 0.0%. However, a total of 60.0% (n = 18) of immatures were misclassified, indicating that WMF was not a reliable indicator of cranial maturity (Table 3.15). Likewise, mature specimens could not be clearly determined based on any of the remaining characters (n = 3) for which Chi-Square / Fisher's Exact tests detected a significant ($p < 0.05$) difference in trait expression with maturity status (Table 3.16).

Table 3.14. Trait expression frequency of non-metric cranial characters in cranially immature (Im) and mature (Mat) *Delphinus* sp. skull specimens from New Zealand waters. Note: (L) and (R) = left and right side of the skull, respectively; ant = anterior; post = posterior; blw = below; abv = above; pres = present; abs = absent; premax = premaxilla; max = maxilla; piri = piriform; umb = umbrella shaped; squ = square shaped; nar = narrow; part = partial; n = sample size; numbers separated by semicolon = where first number = number of individuals with first trait expression and second number = number of individuals with alternative trait expression; χ^2 = Chi-Square statistic; df = degrees of freedom; FE = Fisher's Exact test, which was used when sample size in any cell was < 5; p = p-value; values in bold = p < 0.05; ** = < 0.01; * = < 0.001. For character abbreviation refer to section 2.2.6.**

Non-metric character	Trait expression	Total n	n per trait expression		Chi-Square	
			Im	Mat	χ^2 (df = 1)	p
PMIOF	ant; post	60	25; 6	16; 13	3.393	0.066
PLIOF	ant; post	59	2; 27	1; 29	FE	0.612
DPM	blw; abv	59	25; 5	23; 6	0.004	0.950
CPPT	pre; abs	66	1; 32	0; 33	FE	1
HMTPR	premax; max	48	4; 20	12; 12	FE	**0.031**
HV	blw; abv	63	6; 24	8; 25	0.010	0.919
CPN (L)	pre; abs	67	1; 32	1; 33	FE	1
CPN (R)	pre; abs	59	14; 14	20; 11	0.745	0.388
EAPLPR	ant; post	53	21; 4	23; 5	FE	1
SFM	piri; oval	64	29; 3	26; 6	FE	0.474
O	pre; abs	62	9; 22	14; 17	1.106	0.293
NFOCEX (L)	abs; ≥ 1	65	28; 4	31; 2	FE	0.427
GOCC	nar; wide	58	11; 17	23; 7	6.873	**
SB	umb; squ	54	25; 2	26; 1	FE	1
FBOCV	pres; abs	63	29; 2	23; 9	FE	**0.043**
PPEV	post; ant	64	15; 15	26; 8	3.769	0.052
VS	nar; wide	57	14; 13	16; 14	0.013	0.911
LFV (L)	pre; abs	65	24; 9	28; 4	FE	0.215
PIOSF	post; ant	61	23; 8	25; 5	0.312	0.576
PAELVF (L)	ant; post	59	2; 27	2; 28	FE	1
OF (L)	open; spine	58	14; 13	5; 26	6.817	**
IAS	part; fully	66	16; 14	0; 36	FE	***
WMF (L)	max; frontal	67	10; 21	0; 36	FE	***
MNC (L)	ant; at/post	65	26; 5	17; 17	6.865	**
MNC (R)	ant; at/post	65	18; 13	11; 23	3.360	0.067

Table 3.15. Efficiency of the developmental status of non-metric characters as cranial maturity indicator for *Delphinus* sp. skull specimens from New Zealand waters, as determined by percentage misclassification for specimens assessed as cranially immature and mature, and total misclassification (combined for immatures and matures). Note: L = left side of the skull; n = sample size. For character selection for the misclassification computation and character abbreviation refer to section 2.3.4 and 2.2.6, respectively.

Non-metric character	Percentage (%) misclassified					
	Immature		Mature		Total	
	n	%	n	%	n	%
IAS	31	22.6	36	0.0	67	10.5
WMF	30	60.0	36	0.0	66	27.3
COH	27	48.2	31	16.1	58	31.0
MNC (L)	31	16.1	34	50.0	65	33.9

Table 3.16. Frequency of trait expression of unilateral non-metric characters recorded on cranially immature and mature *Delphinus* sp. skull specimens from New Zealand waters for the purpose of evaluating efficiency of characters as cranial maturity indicators. Note: Numbers in parentheses represent sample size. Only characters for which a significantly difference ($p < 0.05$) in trait frequency expression was computed are listed. For complete list of characters assessed and associated χ^2-test results refer to Table 3.14. For character abbreviation refer to section 2.2.6.

Non-metric character and traits	Percentage frequency (%) per character trait	
	Immature	Mature
HMTPR		
Maxillae elevated	16.6 (4)	50.0 (12)
Premaxilla elevated	83.3 (20)	50.0 (12)
GOCC		
Narrow gap	39.3 (11)	76.7 (23)
Wide gap	60.7 (17)	23.3 (7)
FBOCV		
Present	93.5 (29)	71.9 (23)
Absent	6.5 (2)	29.0 (9)

3.9 Tooth condition

Tooth condition was only assessed on intact *Delphinus* sp. heads archived frozen at Massey University (n = 49). Of those specimens, 20.4% (n = 10) were excluded from analyses, because several teeth had been removed from the upper jaw or were missing due to bone damage (rating category 4). Following this, 20 cranially immature and 19 mature specimens were available for analyses. Ages were known for 64.1% (n = 25) of individuals, of which 52.0 (n = 13) and 48.0% (n = 12) were cranially immature and mature, respectively.

Cranially immature specimens (n = 20) had a significantly ($p < 0.001$) higher median percentage (88.4%) of normal teeth than mature specimens (12.8%, n = 19), while the latter had a significantly ($p < 0.01$) higher percentage of partly worn (52.0%) and broken (4.8%) rostral teeth (Table 3.17; Fig. 3.15). None of the immature specimens had teeth worn down to the gum line, while the maximum percentage of completely worn teeth in mature specimens was 11.0% with a median percentage of 5.3%. Although several mature specimens (n = 8) were missing between 1.1 - 17.3% of teeth, the median percentage was zero and there was no significant difference in percentage of missing teeth between maturity categories. Likewise, there was no significant difference in percentages of not erupted and partly erupted teeth between maturity categories (Table 3.17; Fig. 3.15).

Table 3.17. Percentage frequency of rostral teeth per tooth condition category (n = 7) separately for cranially immature and mature *Delphinus* sp. skull specimens from New Zealand waters. Mann-Whitney U test results for differences with maturity status are also given. Note: n = sample size; I.Q.R = interquartile range; p = p-value; ** = < 0.01; * = < 0.001; n/a = test could not be performed as sample size of immatures was zero.**

Tooth condition	Immature (n = 20)		Mature (n = 19)		Mann Whitney	
	Median (I.Q.R)	Range	Median (I.Q.R)	Range	U	p
Not erupted	0.0 (0.0 - 0.0)	0.0 - 9.1	0.0 (0.0 - 1.76)	0.0 - 38.3	159.5	0.391
Partly erupted	2.4 (1.2 - 3.4)	0.0 - 7.5	1.1 (0.0 - 2.4)	0.0 - 13.1	127.0	0.078
Normal	88.4 (51.3 - 96.5)	17.1 - 97.9	12.8 (5.5 - 30.3)	0.0 - 91.8	38.0	***
Partly worn	4.2 (0.0 - 43.4)	0.0 - 71.9	52.0 (41.9 - 58.5)	3.5 - 91.7	76.0	**
Worn to gum	0.0 (0.0 - 0.0)	0.0 - 0.0	5.3 (0.0 -11.0)	0.0 - 26.7	n/a	n/a
Broken	0.0 (0.0 - 5.5)	0.0 - 24.4	4.8 (2.4 - 16.6)	0.0 - 53.6	105.5	**
Missing	0.0 (0.0 - 0.0)	0.0 - 2.3	0.0 (0.0 - 2.6)	0.0 - 17.3	125.0	0.064

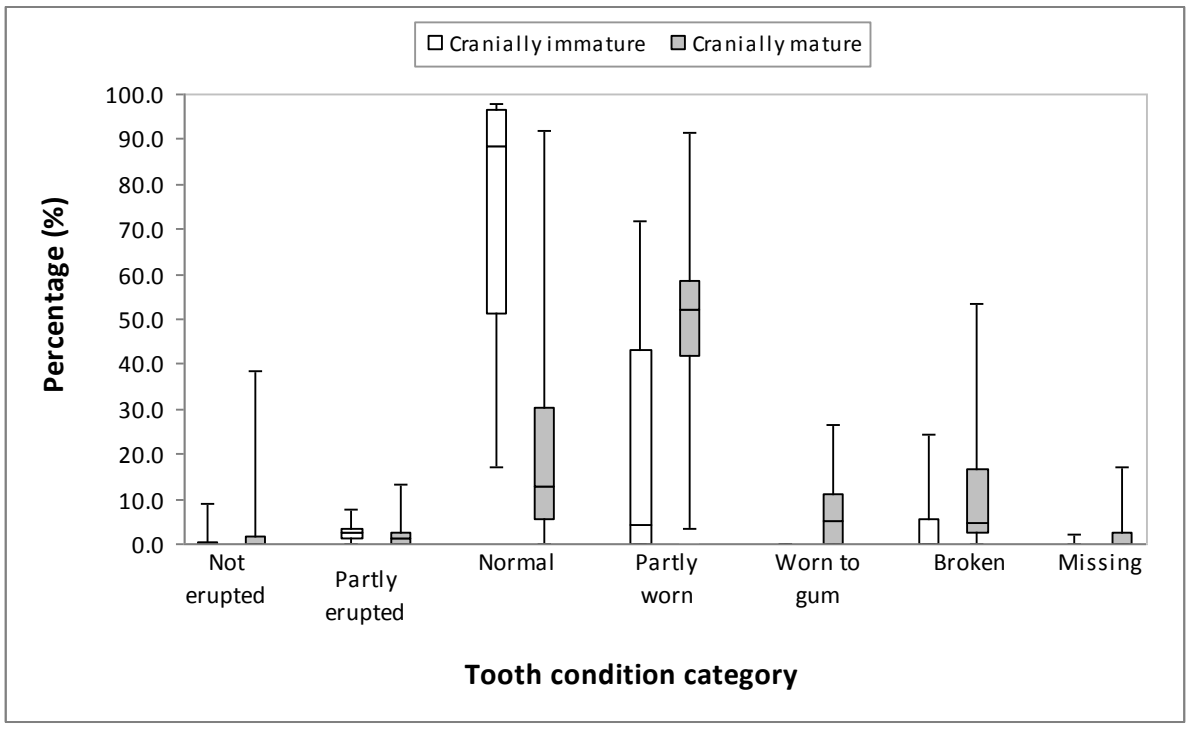

Figure 3.15. Rostral tooth condition of cranially immature (n = 20) and mature (n = 19) *Delphinus* sp. skull specimens from New Zealand waters according to seven categories and displayed as a percentage. Note: Horizontal lines represent the median, boxes the interquartile range, and vertical lines the range.

Kruskal-Wallis tests revealed that median percentage of rostral teeth in the five tooth condition categories (partly erupted, normal, partly worn, worn to gum line, and broken teeth) differed significantly ($p < 0.05$) between age classes (Table 3.18; Fig. 3.16). Dunn's Multiple Comparisons Post hoc test detected that age class I (1 - 3 years) specimens had a significantly ($p < 0.05$) higher median percentage (3.4%, n = 8) of partly erupted teeth as compared to age class III ($\geq$ 11 years) individuals (1.1%, n = 12). Furthermore, age class I specimens had a significantly ($p < 0.001$) higher percentage (96.1%) of normal teeth than age class III specimens (11.4%, n = 12). Although median percentage of normal teeth of age class II individuals (n = 5) was lower and higher compared to age class I and III specimens, respectively, these differences were not significant ($p > 0.05$). Median percentage of partly worn teeth of age class I specimens was significantly less compared to age class II ($p < 0.05$) and III ($p < 0.001$) individuals. Maximum percentage of partly worn teeth recorded for specimens aged 1 - 3 years was 6.8%, which did not overlap with age class II animals (minimum percentage: 17.9%). Although median percentage of partly worn teeth of age class III was slightly higher as compared to age class II, this difference was not significant ($p > 0.05$). None of the teeth of individuals in age class I and II (n = 13) were worn down to the gum line, and with a median percentage of 7.1% age class III specimens had a significantly ($p < 0.01$) higher percentage of completely worn down teeth than age class I and II specimens. Median percentage of broken teeth was (1) significantly ($p < 0.01$) higher in age class II specimens (6.4%, n = 5) as compared to age class I specimens (0%, n = 8); and (2) significantly ($p < 0.05$) higher in age class III (3.8%, n = 12) than in age class I specimens. Percentage of broken teeth did not differ significantly ($p > 0.05$) between age class II and III individuals.

Table 3.18. Percentage frequency of rostral teeth per tooth condition category (n = 7) of New Zealand *Delphinus* sp. skull specimens according to three age classes (1 - 3 years, 6 - 10 years and ≥ 11 years). Kruskal-Wallis test results for differences with age class are also given. Note: n = sample size; yrs = years; I.Q.R = interquartile range; p = p-value; value in bold = < 0.05; ** = < 0.01; * = < 0.001.**

Tooth condition	Age Class I (1 - 3 yrs) (n = 8)			Age Class II (6 - 10 yrs) (n = 5)			Age Class III (≥ 11 yrs) (n = 12)			Kruskal-Wallis	
	Median	(I.Q.R.)	Range	Median	(I.Q.R.)	Range	Median	(I.Q.R.)	Range	W	p
Not erupted	0.0	(0.0 - 0.0)	0.0 - 0.0	0.0	(0.0 - 0.0)	0.0 - 6.5	0.6	(0.0 - 2.4)	0.0 - 38.3	5.490	0.064
Partly erupted	3.4	(3.0 - 3.7)	1.2 - 5.9	1.1	(1.1 - 1.3)	0.0 - 2.4	1.1	(0.0 - 1.5)	0.0 - 5.6	7.817	**0.020**
Normal	96.1	(92.0 - 96.7)	88.2 - 97.9	31.2	(26.7 - 42.5)	17.1 - 74.4	11.4	(4.3 - 30.1)	1.2 - 46.9	17.387	***
Partly worn	0.0	(0.0 - 1.5)	0.0 - 6.8	51.7	(48.9 - 55.9)	17.9 - 68.3	55.5	(50.5 - 60.9)	37.0 - 91.7	16.246	***
Worn to gum	0.0	(0.0 - 0.0)	0.0 - 0.0	0.0	(0.0 - 0.0)	0.0 - 0.0	7.1	(0.0 - 16.3)	0.0 - 26.7	11.659	**
Broken	0.0	(0.0 - 2.5)	0.0 - 5.9	6.4	(5.4 - 12.2)	3.4 - 24.4	3.8	(2.3 - 11.4)	0.0 - 19.3	11.715	**
Missing	0.0	(0.0 - 0.0)	0.0 - 0.0	0.0	(0.0 - 0.0)	0.0 - 1.1	0.0	(0.0 - 0.3)	0.0 - 17.3	2.233	0.327

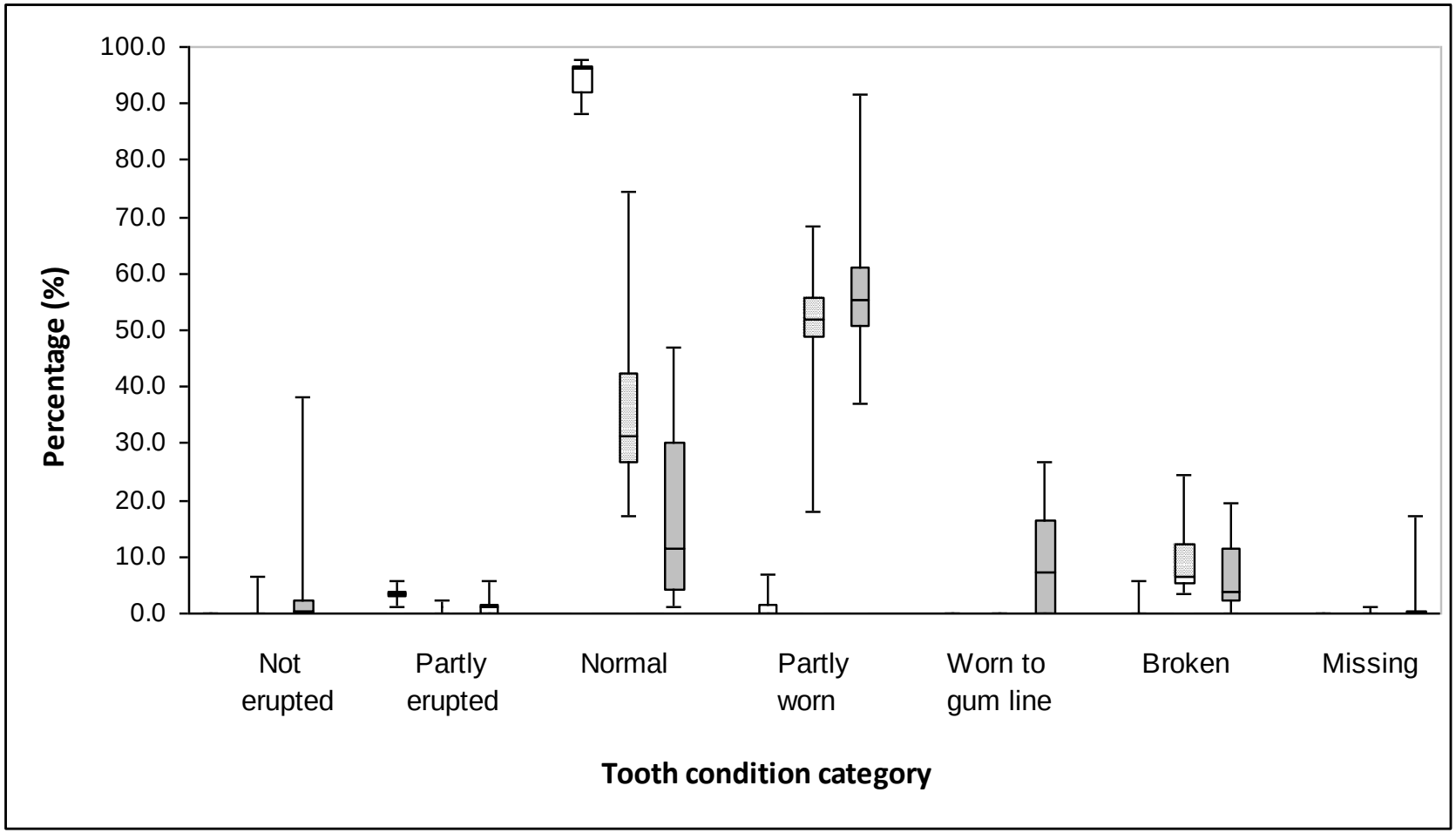

Figure 3.16. Rostral tooth condition of *Delphinus* sp. skull specimens from New Zealand waters according to three age classes (1 - 3 years: white boxes, n = 8; 6 - 10 years: dotted boxes, n = 5; ≥ 11 years: grey boxes, n = 12) and displayed as a percentage. Note: yrs = years. Horizontal lines represent the median, boxes the interquartile range, and vertical lines the range.

PART II: Sexual dimorphism, taxonomy, geographic variation, and precision of two data acquisition methods

3.10 Sexual dimorphism in cranially mature *Delphinus* sp.

3.10.1 Individual metric characters

No significant difference was detected in median rostral (Mann-Whitney U test: U = 32.0, p = 0.480) and mandibular (U = 214.0, p = 0.641) tooth socket counts between immature (rostral: 99 (range: 92 - 111), n = 9; mandibular: 100.5 (range: 92 - 107), n = 18) and mature (rostral: 101 (range: 92 – 108), n = 9; mandibular: 98 (range: 86 - 110), n = 26) specimens. Data for immature and mature individuals were therefore pooled for remaining analyses. Median rostral and mandibular tooth socket counts did not differ significantly (rostral: U = 32.0, p = 0.807; mandibular: U = 170.5, p = 0.505) between male (rostral: 99 (range: 92 - 111), n = 7; mandibular: 98.5 (range: 90 - 104), n = 14) and female (rostral: 100.5 (range: 95 - 106), n = 10; mandibular: 99.5 (range: 86 - 110), n = 28) *Delphinus* sp.

In total, 5 out of the 71 cranial metric characters recorded, were excluded from statistical analyses. Of those, WPR60, WPR1/2, and WPR3/4 were omitted, as fusion prevented determination of the reference points in the majority of specimens assessed. LANF (L) and (R) (revised in the present study) were excluded, given that these were the only characters that did not pass the normality test after a log-transformation. Absolute size differences between sexes, assessed using t-tests, were detected in TBL and in 22.7% (n = 15) of cranial characters (total number of cranial characters analysed, n = 66), with mature males having a significantly ($p < 0.05$) larger skull size than females (Appendix 17). Of those, 86.7% (n = 13) of cranial characters were width measurements. In total, 66.7% (n = 10) of cranial characters displaying sexual size dimorphism (SSD) could be allocated to a functional complex, 70.0% (n = 7) of

which were related to the feeding apparatus: Width of rostrum at base (WRB), width of rostrum at 60 mm (WR60) and ¾ length (WR3/4), maximum diameter of the left (MaxDLTF) and right temporal fossa (MaxDRTF), post orbital width (POOW), and height of the left mandible (HLM). The remaining three characters were related to the vision complex (preorbital (PROW) and least supraorbital width, LSOW) and braincase (greatest parietal width (GWPA)).

In sexual dimorphic cranial characters, percentage difference of mean character size ranged from 3.5 to 12.5% between males and females (Table 3.19). The character WR3/4 displayed the largest difference with 12.5%, followed by greatest width of the right maxilla (GWRM) and WRB, both of which differed with 6.3%. Mean CBL and rostrum length (RL) differed by 3.8% and 4.4%, respectively. These differences between the sexes were, however, statistically not significant ($p > 0.05$).

CBL and mandible length were significantly and positively correlated with length of both mandibles (Pearson correlation: right mandible: $r = 0.979$, $p < 0.001$, $n = 13$; left mandible: $r = 0.965$, $p < 0.001$, $n = 13$). Length of the right mandible (LRM) was employed as an alternative covariate, for ANCOVA within the current study (due to missing rostrum tips in some individuals) owing to the slightly higher correlation with CBL compared to the left mandible. Using ANCOVA, none of the cranial character differed significantly ($p > 0.05$) between the sexes when either CBL or LRM were employed as a covariate in order to correct for skull size, i.e. assess for sexual dimorphism in skull shape (Appendix 17).

Table 3.19. Percentage difference between mean cranial measurements obtained for male and female *Delphinus* sp. from New Zealand waters. Note: n = sample size; only characters that exhibited sexual size dimorphism (SSD) (refer to Appendix 17) are listed. For character abbreviation refer to section 2.2.4.

Cranial character	Mean character size (mm)				% Difference
	Male	n	Female	n	
WR3/4	45.0	5	39.9	14	12.5
GWRM	69.9	7	65.6	22	6.3
WRB	98.0	8	92.0	21	6.3
WR60	64.8	8	61.0	23	6.0
WBOCS	54.9	8	51.7	20	6.0
MaxDRTF	41.5	8	39.2	21	5.7
MaxDLTF	41.3	8	39.2	21	5.2
LLSQ	52.6	8	50.1	21	4.9
GWM	183.9	7	175.3	21	4.8
PROW	173.4	8	165.3	20	4.8
LSOW	169.6	8	161.7	22	4.8
GWLM	77.8	8	74.2	21	4.7
HLM	67.8	7	65.1	21	4.1
POOW	194.7	8	187.0	20	4.0
GWPA	153.1	8	147.8	20	3.5

3.10.2 Functional complexes

In both sexes, the coefficient of variation (CV), employed as a measure of individual variation, of all cranial characters that could be allocated to a functional complex of the skull (n = 40) was < 10.0 %, except for the width of the prenarial triangle at the base of the rostrum, which exceeded 10.0% in both sexes (males: 11.7%, females: 16.5%) (Fig.3.17). Overall, 72.5% (n = 29) and 75.0% (n = 30) of characters in the male and female data sets, respectively, had associated CVs of < 6%. The majority (81.8%, n = 9) of characters for which individual variation among males was greatest as indicated by CVs of > 6%, were related to the feeding apparatus (RL, width of rostrum at ½ length (WR1/2), WR3/4, height of

right mandible (HRM), and all measures related to the post-temporal fossae, except for the height measure on the left side). The other two characters with CVs of > 6 % were related to the breathing / sound producing complex (width of pterygoids (WPT) and width of the prenarial triangle at the base of the rostrum (WTB)). Likewise, the majority (80%, n = 8) of characters for which individual variation was greatest in the female data set, were related to the feeding complex (WR1/2, WR3/4, height and width measures related to the post-temporal fossae and the major diameter of the temporal fossae proper). The other two characters with associated CVs of > 6% were measures related to the braincase (distance from the nuchal crest to the top of the foramen magnum (HBCFM)) and to the breathing / sound producing complex: WTB.

Variability between functional complexes differed significantly (Kruskal-Wallis: W = 17.044, df = 2, p = 0.004). The vision apparatus was excluded from statistical analyses, owing to small sample size of characters (n = 4) corresponding to this functional complex. Dunn's Multiple Comparisons Post hoc test revealed that the feeding apparatus of both sexes (males: median = 6.0, range = 3.1 - 9.6, n = 23; females: median = 5.7, range = 3.4 - 9.9, n = 23) was significantly (males: $p < 0.01$; females: $p < 0.05$) more variable than the braincase of males alone (median = 3.3, range = 2.9 - 3.9, n = 6) (Fig. 3.18). The large range observed for the breathing / sound producing apparatus in both sexes was due to the high individual variability for one character (width of the prenarial triangle at the base of the rostrum (WTB)).

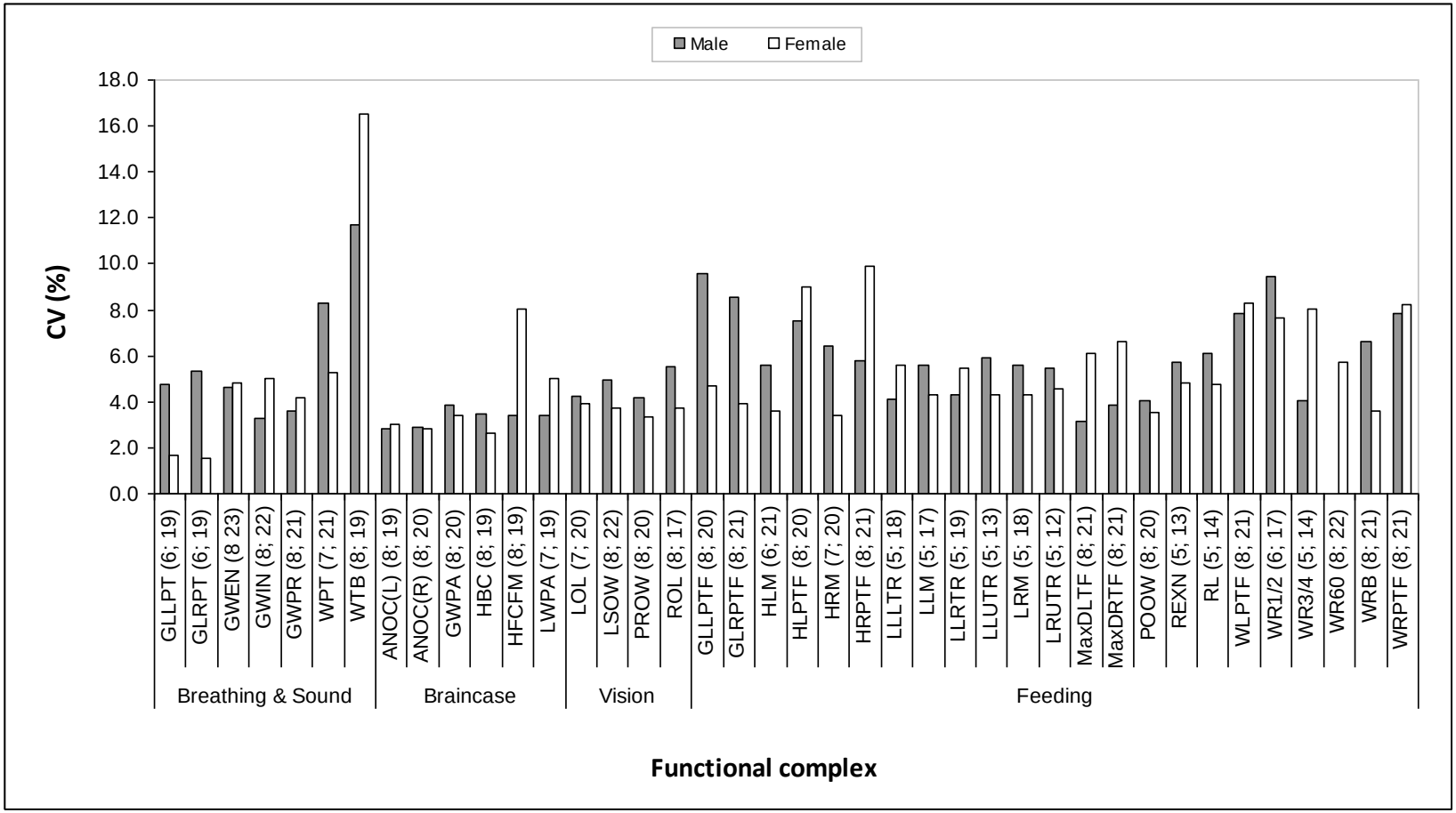

Figure 3.17. Coefficient of variation (CV) as a measure of individual variation, given as a percentage and separately for each sex for metric characters measured on cranially mature *Delphinus* sp. skulls from New Zealand waters. Note: Characters are grouped into the functional complexes of the delphinid skull and listed alphabetically, numbers in parentheses represent sample size, where the first and second number relates to males and females, respectively. For character abbreviation refer to section 2.2.4.

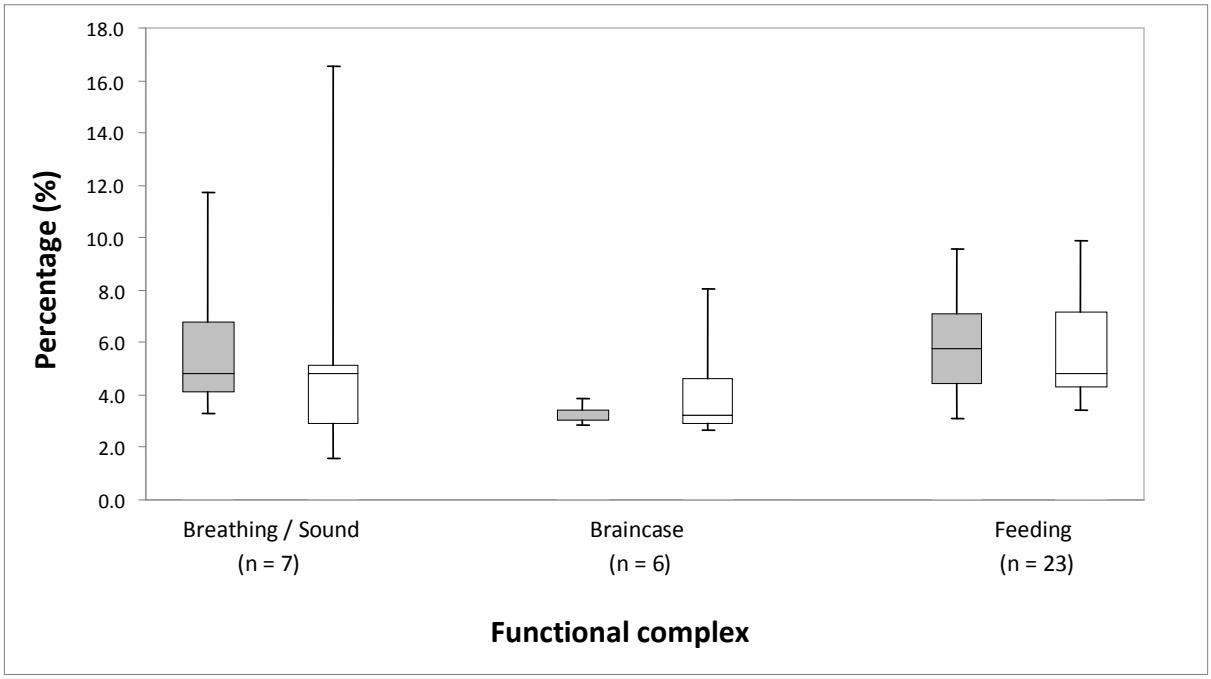

Figure 3.18. Variation, given as a percentage of three functional cranial complexes based on metric measurements taken on cranially mature *Delphinus* sp. skulls from New Zealand waters and displayed independently for each sex (male: grey boxes; female: white boxes). Note: Horizontal lines represent the median, boxes the interquartile range, and vertical lines the range.

3.10.3 Non-metric characters

All non-metric characters for which trait expression was independent of maturity status (n = 17) were also independent of sex, except for one character. Trait expression of 'the extension of the ascending process of the right maxilla relative to the nuchal crest' (MNC) differed significantly (Fisher's Exact test: $p < 0.001$) between the sexes (Appendix 18). In females, the top margin of the ascending process of the right maxilla was in line with or extended underneath the nuchal crest overhang in 81.8% (n = 27) of specimens (Fig. 3.19). In contrast, the top margin of the ascending process in the majority of males (82.6%, n = 19) lay ahead of the nuchal crest overhang.

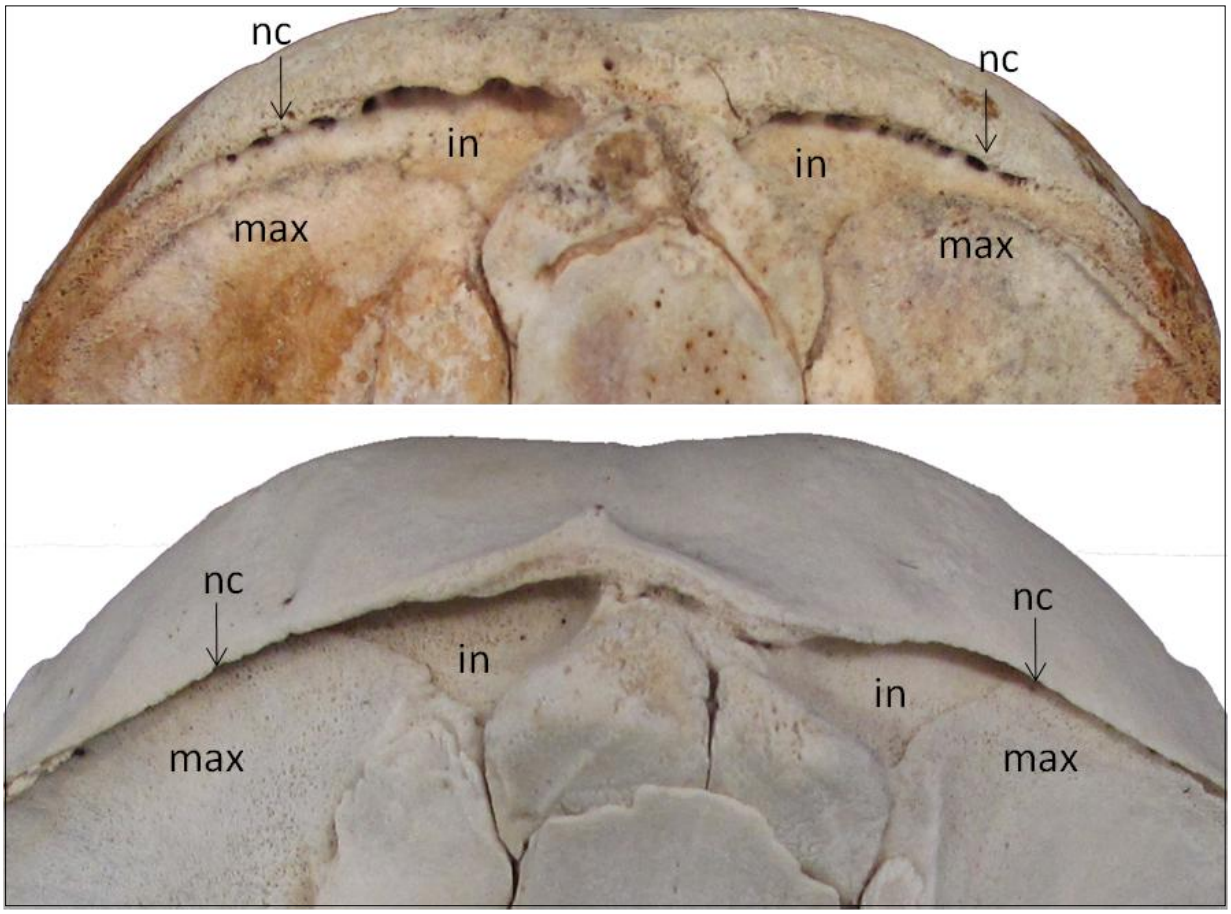

Figure 3.19. Examples of trait expression 1 (margin of the ascending process of the maxillae (max) lies ahead of the nuchal crest overhang (nc), top) and 2 (margin of the ascending process of max is in line with or extends underneath nc, bottom) in a cranially mature male (top) and female (bottom) *Delphinus* sp. specimen from New Zealand waters. Note: in = interparietal.

3.11 Taxonomy

3.11.1 Rostrum length to zygomatic width ratio and tooth socket counts in cranially immature and mature Delphinus *sp.*

Within this section only individuals with rostrum ratings 1 and 2 were used in the analyses, unless otherwise stated. Rostrum length to zygomatic width (RL/ZW) ratios of cranially mature New Zealand common dolphin specimens (combined for both sexes and including specimens of unknown sex, n = 4) ranged from 1.39 to 1.61 (n = 21) (Table 3.20; Figs. 3.20 and 3.21). Mean RL/ZW ratio of mature males was slightly higher than for females. Mean RL/ZW ratio, pooled for mature specimens, was 1.49 (Table 3.20). RL/ZW ratios represented a continuum, with the mode (47.6%, n = 10) recorded in the category 1.45 - 1.49 (Fig. 3.21). In total, 66.7%, (n = 14) of mature specimens had RL/ZW ratios of < 1.50 (Figs. 3.21).

Table 3.20. Mean ± SD and range of rostrum length to zygomatic width ratios (RL/ZW) obtained for cranially mature (top) and immature (bottom) *Delphinus* sp. from New Zealand waters. Results are shown both separately and pooled for each sex and rating category. Note: n = sample size; pooled = includes specimens of unknown sex. For (rating) category description refer to section 2.2.4.

Mature	Category 1			Category 2			Category 1 and 2		
Sex	Mean ± SD	Range	n	Mean ± SD	Range	n	Mean ± SD	Range	n
Male	1.51 ± 0.06	1.45 - 1.56	3	-	1.39 - 1.59	2	1.50 ± 0.08	1.39 - 1.59	5
Female	1.47 ± 0.05	1.40 - 1.57	6	1.51 ± 0.06	1.44 - 1.61	6	1.49 ± 0.06	1.40 - 1.61	12
Pooled	1.48 ± 0.05	1.40 - 1.57	13	1.50 ± 0.08	1.39 - 1.61	8	1.49 ± 0.06	1.39 - 1.61	21

Immature	Category 1			Category 2			Category 1 and 2		
Sex	Mean ± SD	Range	n	Mean ± SD	Range	n	Mean ± SD	Range	n
Male	1.55 ± 0.06	1.44 - 1.60	6	-	1.22 - 1.47	2	1.49 ± 0.12	1.22 - 1.60	8
Female	1.54 ± 0.03	1.51 - 1.57	3	-	1.50 - 1.52	2	1.52 ± 0.03	1.50 - 1.57	5
Pooled	1.53 ± 0.05	1.44 - 1.60	12	1.43 ± 0.14	1.22 - 1.52	4	1.50 ± 0.09	1.22 - 1.60	14

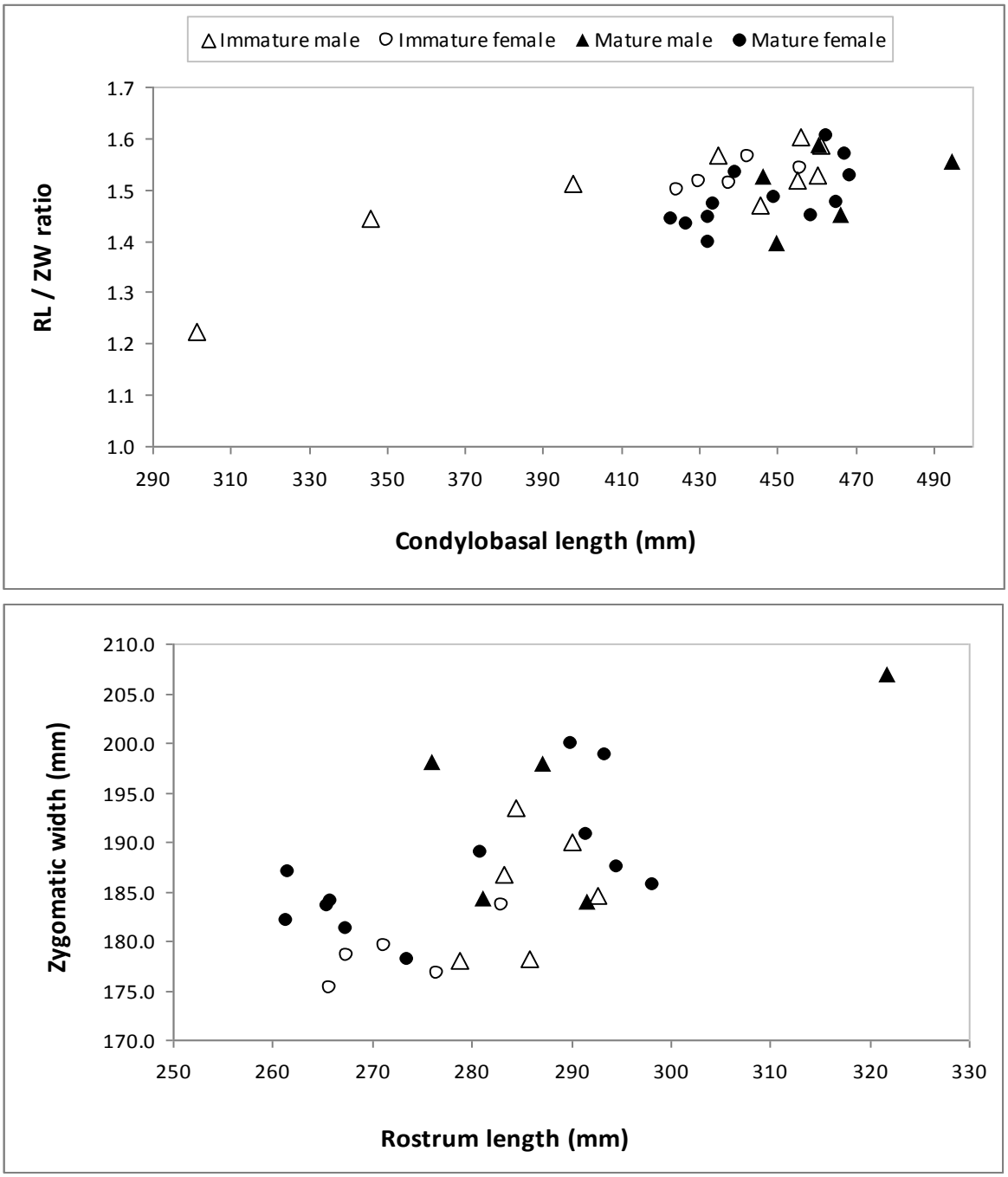

Table 3.20. Rostrum length to zygomatic width ratio (RL/ZW ratio) *versus* condylobasal length (mm) (top) and zygomatic width *versus* rostrum length (bottom) for cranially immature and mature male and female *Delphinus* sp. from New Zealand waters.

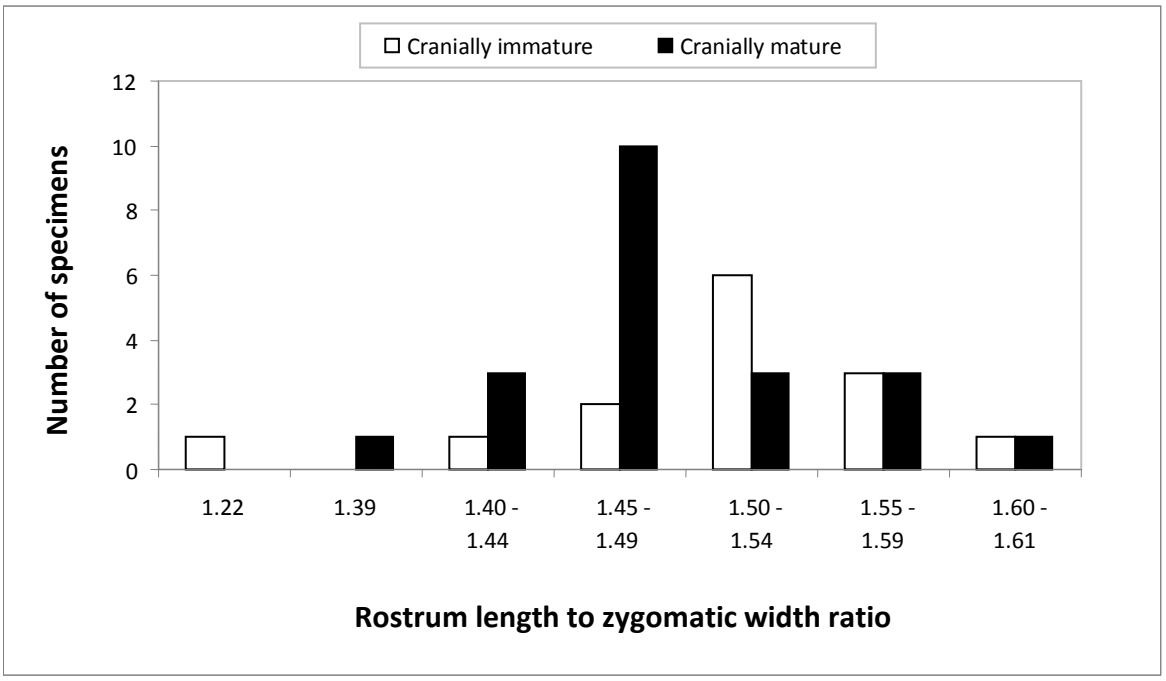

Figure 3.21. Number of cranially immature (white bars) and cranially mature (black bars) *Delphinus* sp. skull specimens from New Zealand waters against rostrum length to zygomatic width ratio categories.

RL/ZW ratios of immature common dolphin specimens ranged from 1.22 to 1.60 (Table 3.20 and Fig. 3.20). The mean RL/ZW ratio was 1.50 and thereby slightly higher than for mature specimens. Likewise, the mode (1.50 - 1.54) for immature specimens (42.9%, n = 6) was slightly higher than for mature individuals (Fig. 3.21).

In total, 37.5% (n = 3) and 9.1% (n = 2) of mature males and females had RL/ZW ratios ≥ 1.55 and ≥ 1.52, respectively. These are the values that mark the lower limit of *D. capensis* (for each sex) inhabiting Californian waters. Overall, 23.8% (n = 5) of mature specimens had a RL/ZW ratio within the range of *D. capensis*. RL/ZW ratios of mature specimens of unknown age with a rostrum category 1 (n = 5) ranged from 1.46 to 1.48 and were thereby all within the range of *D. delphis* (Appendix 19). RL/ZW ratios within the range of *D. capensis* were obtained for 40.0% of immatures (male: n = 5; female: n = 1). In addition, one male

specimen (WS05-06Dd), with a rating category 3, had a RL/ZW ratio within the range of the long-beaked form (Appendix 19).

Number of tooth sockets present at one side of the upper jaw ranged from 45 to 56 in males and from 47 to 55 in females (Table 3.21). Mean upper alveoli count for males and females was 50.5 ± 3.6 and 50.2 ± 2.2, respectively.

Table 3.21. Tooth socket count range from *Delphinus* sp. from New Zealand waters. Note: n = sample size; Max upper / lower: maximum count from left and right upper / lower jaw. Cranially immature and mature specimens were pooled.

Jaw	Male	n	Female	n	Unknown sex	n
Upper left	45 - 55	7	47 - 55	10	48 - 49	2
Upper right	45 - 56	9	48 - 53	10	-	
Lower left	45 - 53	14	43 - 55	29	48 - 53	3
Lower right	45 - 54	17	43 - 55	30	47 - 53	4
Max upper	47 - 56	7	48 - 55	10	-	
Max lower	45 - 54	14	43 - 55	28	48 - 53	3
Mean ± SD upper	50.5 ± 3.6	7	50.2 ± 2.2	10	-	
Mean ± SD lower	48.9 ± 2.2	14	49.8 ± 2.8	28	-	

3.11.2 Variation within New Zealand waters

No significant ($p > 0.05$) regional differences in mean RL/ZW ratios was detected between cranially mature individuals from Hauraki Gulf (HG) and non-Hauraki Gulf (non-HG) waters (Table 3.22). Statistical assessment of regional differences among HG and non-HG mature males could not be conducted, owing to small sample size of non-HG specimens (n = 3).

Table 3.22. Mean ± SD of rostrum length to zygomatic width (RL/ZW) ratios and unpaired t-test results obtained for cranially mature *Delphinus* sp. from Hauraki Gulf (HG) and non-Hauraki Gulf (non-HG) within New Zealand waters. Note: combined = both sexes pooled; n = sample size; t = test statistic; df = degrees of freedom; p = p-value. Male specimen could not be assessed independently due to small sample size of non-HG specimens (n = 3).

	RL/ZW ratio			Unpaired t-test		
	n	Mean ± SD	Range	t	df	p
HG Female	7	1.47 ± 0.05	1.40 - 1.57	1.184	10	0.264
Non-HG Female	5	1.51 ± 0.03	1.44 - 1.61			
HG combined	10	1.48 ± 0.07	1.39 - 1.59	0.608	18	0.551
Non-HG combined	10	1.50 ± 0.06	1.44 - 1.61			

3.11.3 Kalya Index

The Kalya Index could be estimated for 86.6% (n = 58) of specimens. Of those, 46.6% (n = 27) and 53.5% (n = 31) were cranially immature and mature individuals, respectively. The mean Kalya Index did not differ significantly (Unpaired t-test with Welch correction: t = 1.246, df = 46, p= 0.219) between immature (mean ± SD: 107.3 ± 3.0, n = 27) and mature (mean ± SD: 108.8 ± 5.8, n = 31) specimens, therefore data were pooled for analyses. The mean Kalya Index calculated for *Delphinus* sp. from New Zealand waters was 108.1 ± 5.3 (n = 58), ranging from 100.3 to 125.6. The two lowest values (100.3 and 100.9) were derived from immatures (Fig. 3.22). Overall, 81.0% (n = 47) of values were between 103.0 and 111.9. In total, 8 mature specimens (25.8%) had a Kalya Index that was higher than any value obtained for immatures (Fig. 3.22). The specimens with the highest indices were one individual of unknown sex (MM001688) from Tauranga and a female specimen (W08-17Dd: > 29 years) from New Plymouth. However, there was no significant difference (Unpaired t-test with Welch correction: t = 0.973, df = 41, p = 0.336) between HG (mean ± SD: 107.5 ± 3.7, n = 30) and non-HG (mean ± SD: 108.8 ± 5.8, n = 26) individuals.

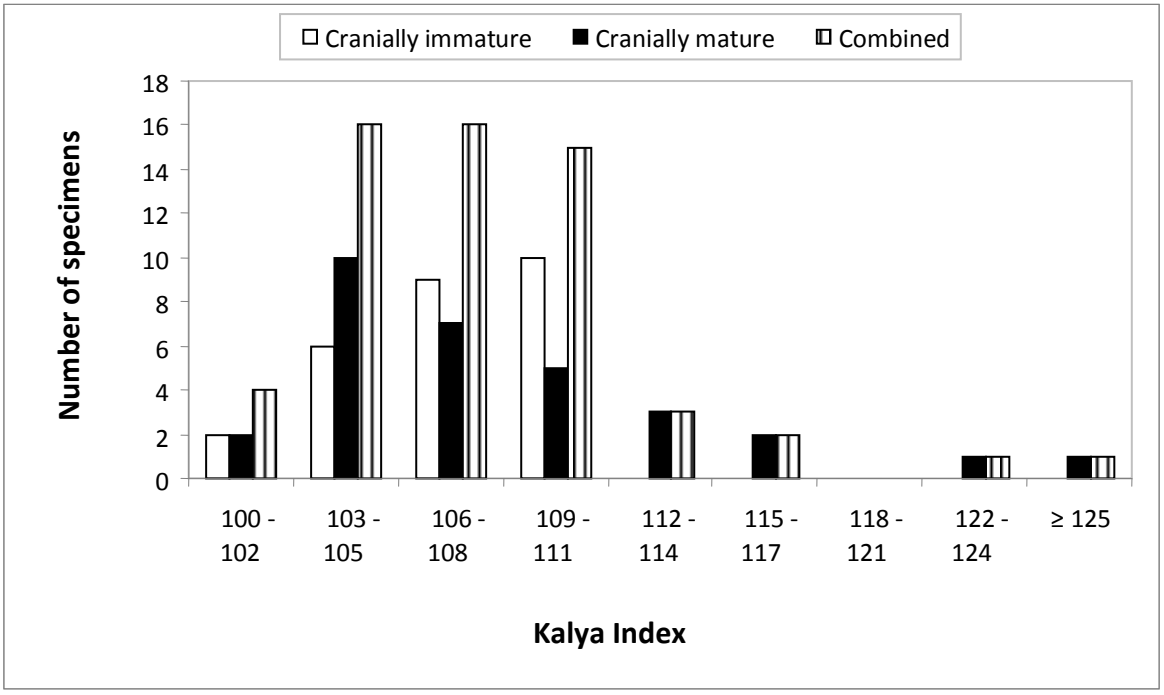

Figure 3.22. Frequency distribution (count) of the Kalya Index obtained for *Delphinus* sp. from New Zealand waters separately and combined for cranially immature and mature specimens.

3.12 Geographic variation

3.12.1 Metric data

No significant geographic difference ($p > 0.05$) was detected in skull size between HG and non-HG female *Delphinus* sp. from New Zealand waters based on two subsets of metric cranial characters (subset 1: excluding characters associated with length measures of the rostrum; subset 2: including characters associated with the length of the rostrum) using Multivariate Analysis of Variance (MANOVA) (refer to Table 3.23). Likewise, Multivariate Analysis of Covariance (MANCOVA) did not reveal significant ($p > 0.05$) regional differences in skull shape between HG and non-HG females based on subset 2. The male data set could not be tested for geographic variation owing to small sample size of non-HG specimens ($n = 3$).

Table 3.23. Multivariate Analysis of Variance (MANOVA) test results for geographic variation analyses between cranially mature females *Delphinus* sp. from Hauraki Gulf (HG) *versus* non-HG regions within New Zealand waters based on two subsets of metric cranial characters. Note: Subset 1 = excluding characters related to the length of the rostrum (CBL and RL) in order to maximize sample size; Subset 2 = including characters related to the length of the rostrum (CBL and RL); n = sample size; Wilk's λ = test statistic; df = degrees of freedom; p = p-value. Multivariate Analyses of Covariance (MANCOVA) could only be performed on subset 2, as CBL was employed as a covariate. For character abbreviation refer to section 2.2.4.

Subset	n		Cranial characters	MANOVA			
	HG	non-HG		Wilk's λ	F	df	p
1	10	5	ANOC(R), WRB, WR60, GWPR, GWEN, GLLPTF, LOL, MaxDLTF, WPT, PROW, ZW, LLLAC, HLM, and LLMF	0.125	0.539	1	0.804
2	7	5	CBL, RL, ANOC(R), WRB, WR60, GWPR, GWEN, GLLPTF, MaxDLTF, WPT, and ZW	0.023	4.272	1	0.361

Subset	n		Cranial characters	MANCOVA			
	HG	non-HG		Wilk's λ	F	df	p
2	7	5	RL, ANOC(R), WRB, WR60, GWPR, GWEN, GLLPTF, MaxDLTF, WPT, and ZW	0.024	4.554	1	0.349

3.12.2 Non-metric data

In total, trait expression of 15 non-metric characters was independent of maturity status and sex (refer to sections 3.8 and 3.10.3, respectively). Trait expression frequency in any of those characters did not differ significantly (χ^2, $p > 0.05$) between specimens from HG and non-HG waters when assessing females independently and when sexes were pooled (Appendix 20). In contrast, a significantly ($p < 0.05$) higher frequency (69.2%, n = 9) of a lack of contact between the premaxilla and nasal on the right side of the skull only, was detected in male

specimens from HG waters as compared to non-HG specimens from the same sex (25%, n = 3) (Appendix 20).

No significant ($p > 0.05$) differences in mean measure of divergence estimates were found between common dolphin specimens (pooled and separately for both sexes) from HG and non-HG waters (Table 3.24) based on the set of non-metric cranial characters listed in Appendix 21.

Table 3.24. Results for the Mean Measure of Divergence (MMD) computation for New Zealand *Delphinus* sp. skull specimens from Hauraki Gulf *versus* non-Hauraki Gulf waters pooled and separately for both sexes. Note: SD = standard deviation; p = p-value; MMD significant at p > 2.

	MMD	SD	p
Combined	0.037	0.252	0.145
Male	0.043	0.121	0.354
Female	0.076	0.135	0.567

3.13 Precision of two metric data acquisition methods

3.13.1 Measurement error

Mean percentage measurement error (ME) from repeats of manual (calliper) and digitized (microscribe) recordings for 33 metric cranial characters measured on 22 cranially mature *Delphinus* sp. skulls from New Zealand waters is displayed in Appendix 22. In all cases, variance associated with calliper readings was smaller (range: 0.1 to 0.7%) as compared to microscribe recordings (range: 1.1 to 10.7%), indicating a higher precision for the former. Characters with the lowest variance of 1.1% and 1.2% (n = 2) in the microscribe data set were WR60 and WR1/2, respectively. In total, approximately 54.6% (n = 18) of all cranial

characters recorded by digitization had associated MEs of < 5.0%. ME of 42.4% (n = 14) of characters ranged from 5.0 to < 10.0% and only one character (TRIN) had an associated ME of ≥ 10.0%.

A significant positive correlation was detected between mean character size and variance in the calliper data set (Pearson Correlation: r = 0.470, p = 0.006, n = 33), although this relationship was absent from the microscribe data set (r = 0.137, p = 0.446, n = 33) (Fig. 3.23). As noted earlier, characters ≤ 300 mm in length were recorded with digital callipers, while those > 300 mm in length were taken with manual callipers (with a precision of 0.1 mm).

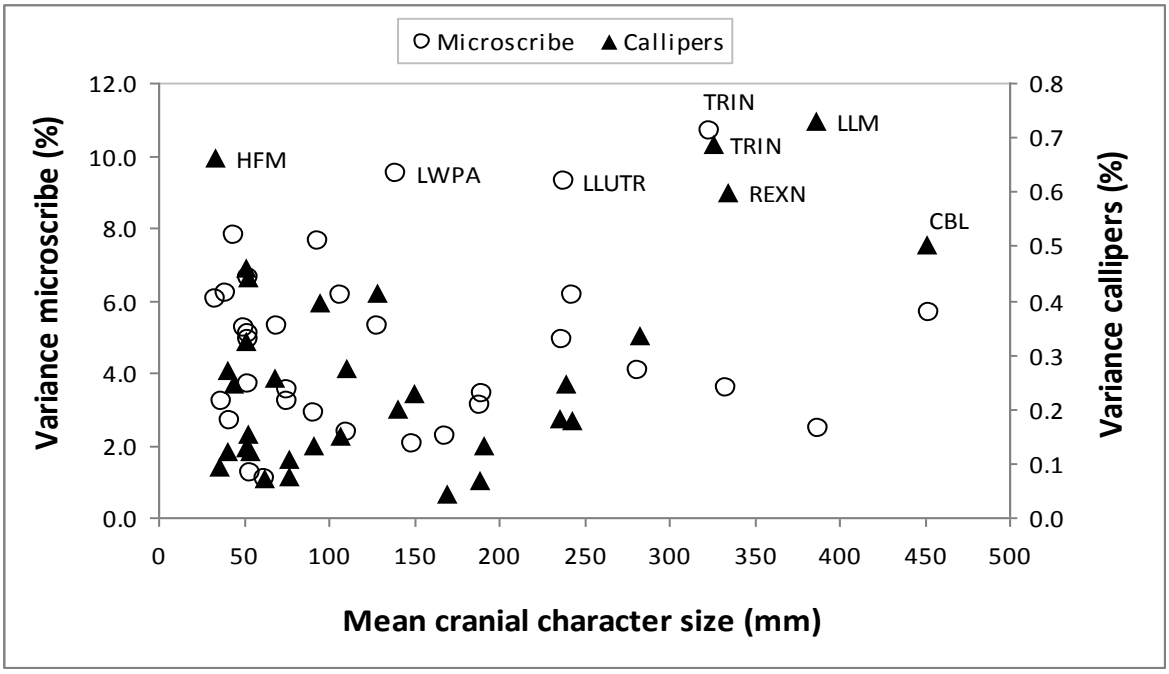

Figure 3.23. Variance, as a measure of measurement error (ME), plotted against mean cranial character size for two data acquisition methods (vernier callipers: triangles, microscribe: circles) based on cranial measurements (each recorded three times) on *Delphinus* sp. skulls from New Zealand waters. Note: Character abbreviations are given for the highest variances of both data sets. For abbreviation refer to section 2.2.4.

Mean absolute difference (MAD) and associated 95% CI between calliper and microscribe recordings for a given cranial character ranged from 0.2 (0.2 - 0.3) mm in PROW to 3.3 (2.5 - 4.2) mm in HFM (Fig. 3.24; Appendix 23). In total, 69.7% (23 out of 33) of characters displayed MADs with associated 95% CI below the significance threshold of > 1mm, a large majority of characters assessed. However, 30.3% (n = 10) of characters investigated had a significant level of measurement error between calliper and microscribe recordings. In 60.0% (n = 6) of those cases, the upper limit of the 95% CI of the mean ranged from 1.1 to 1.5 mm (LOL, LRLAC, LWPA, REXN, RL, and ROL). Whereas the upper limit of the 95% CI of the four characters with the highest MAD values ranged from 1.6 to 4.1 mm (CBL, TRIN, WFM, and HFM) (Appendix 23).

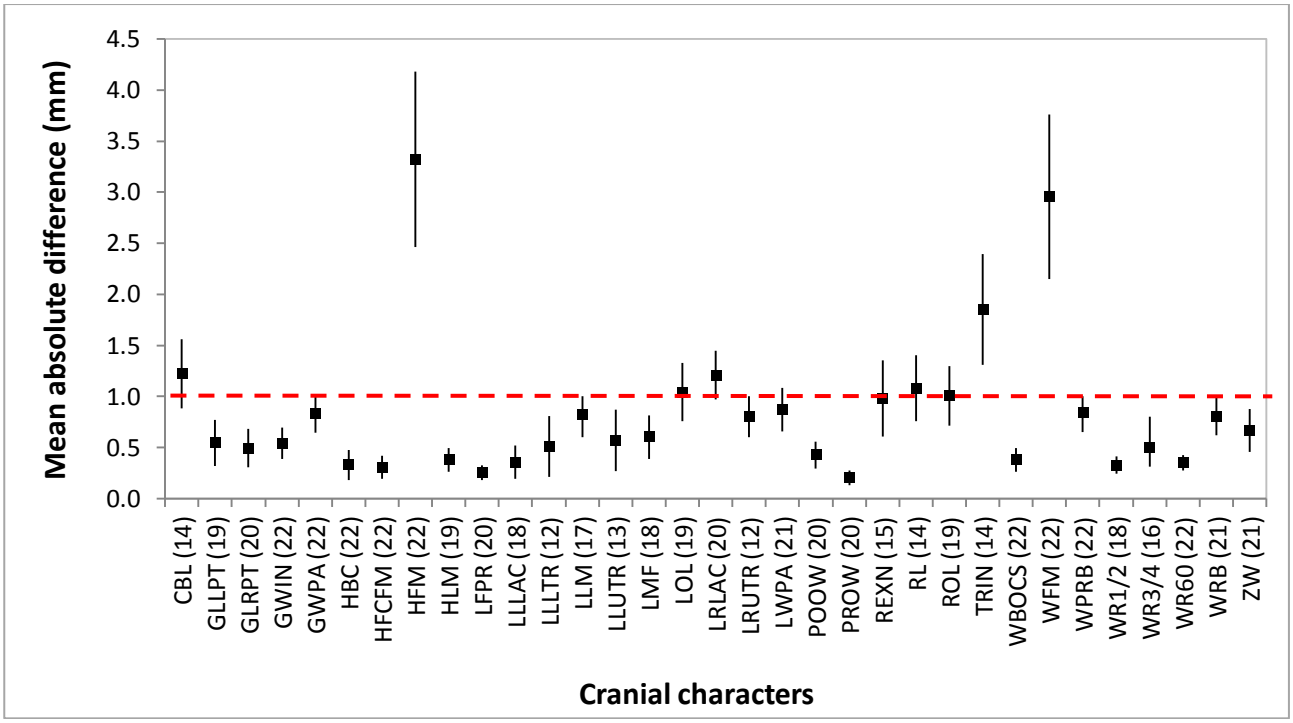

Figure 3.24. Measure of the mean absolute difference (in mm) for cranial characters recorded with vernier callipers and a microscribe on cranially mature *Delphinus* sp. skulls (n = 22) from New Zealand waters. Note: symbols represent the mean and vertical lines the 95% Confidence Interval (95%CI) of the mean, numbers in parentheses represent sample size, the horizontal line represent the significance threshold (at 1 mm). A significant level of measurement error was associated with all characters in which the 95% CI exceeded the 1 mm threshold. Specimens of known and unknown sex were included. For character abbreviation refer to section 2.2.4.

Relative error magnitude (REM) of the 33 characters assessed ranged from 0.1 to 9.4% (Appendix 23). In total, 75.8% (n = 25) of characters had an associated REM of ≤ 1.0%, deemed 'excellent' and six further characters (GWIN, LOL, LRLAC, ROL, WPRB, and WR3/4) displayed REM values between 1.0 and 3.9%, regarded as 'very good'. REM of the remaining two characters (WFM and HFM) was very high with 8.4 and 9.4%, respectively, and both were considered 'moderate' with HFM being close to 'poor'.

3.13.2 Measurement error in relation to taxonomy and sexual dimorphism

Absolute differences between callipers and microscribe recordings of rostrum length (n = 20) and zygomatic width (n = 20) for a given individual ranged from 0.1 to 1.4 mm and 0.1 to 0.9 mm, respectively (Appendix 24). In total, 70.0% (n = 14) of RL and 100% (n = 20) of ZW measurements differed by < 1 mm. For 75.0% (n =15) of individuals the differences in RL and ZW had no effect on the RL/ZW ratio calculated, while the ratio for 25.0 % (n = 5) differed by 0.01. However, this difference did not affect the allocation of individual skulls to short-or long-beaked forms.

Identical unpaired t-test outcomes (significant or non-significant results) between the calliper and microscribe data sets were obtained for all cranial characters (n = 33) tested for sexual dimorphism between mature male and female common dolphins (Appendix 25).

CHAPTER 4

Discussion

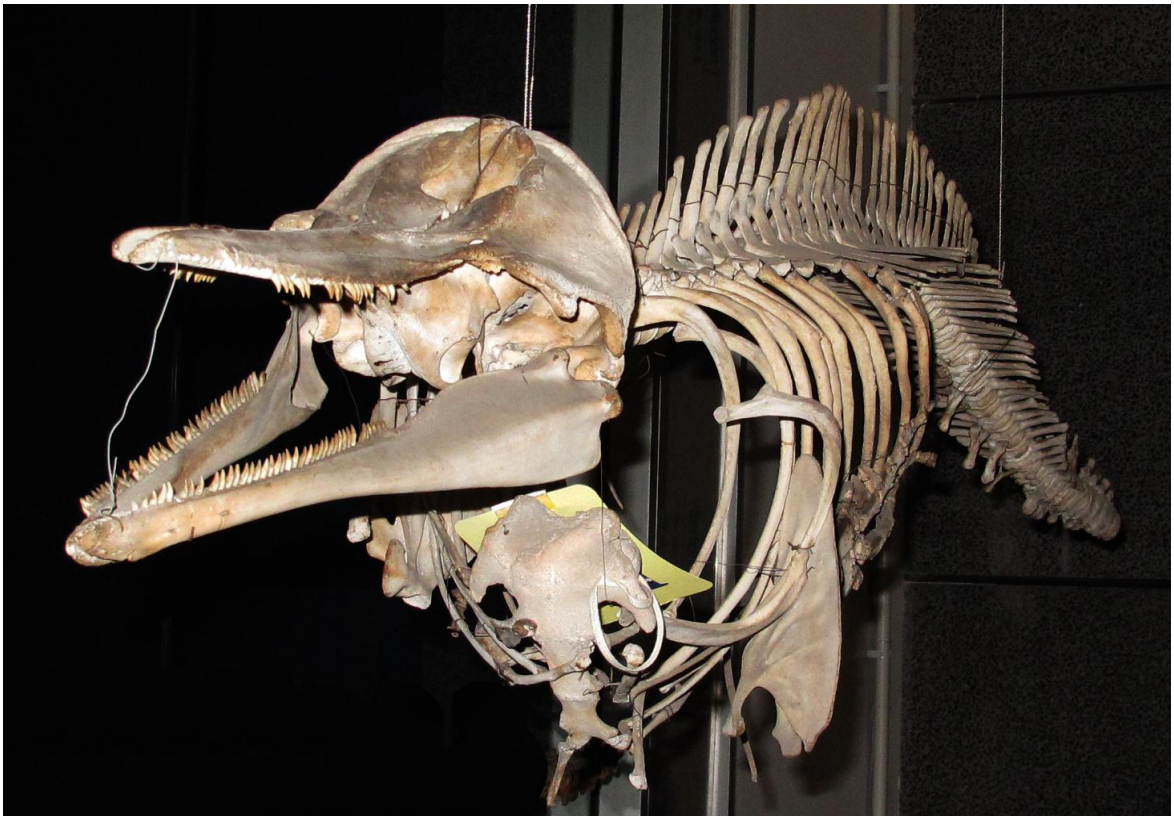

Plate 4.1. Skeleton of a *Delphinus* sp. specimen from New Zealand waters displayed at the Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand. Photograph taken with the courtesy of the Museum of New Zealand Te Papa Tongarewa.

4.1 General remarks

In the present study, Part I aimed at (1) investigating the maturation process of the skull, (2) determining a cut-off point for cranial maturity; (3) allocating specimens of unknown age and maturity status to an age class; and (4) assessing the validity of several cranial elements as cranial maturity indicators in *Delphinus* sp. from New Zealand waters. Degree of sexual cranial dimorphism, taxonomic status, and geographic variation in cranial features of the New Zealand common dolphin were further investigated in Part II. In addition, precision between metric measures obtained through two data acquisition methods (callipers and a microscribe) were assessed. Major findings of both parts are discussed herein.

PART I: Cranial maturity indicators and skull growth

The maturation process of the common dolphin skull was investigated through suture closure, and a suture index was computed to determine a cut-off point for cranial maturity. Furthermore, different degrees of rostral fusion, as well as total body length (TBL), condylobasal length (CBL), trait expression of non-metric characters, and tooth condition were assessed for their use as indicators of cranial maturity.

4.2 Pattern of suture fusion

The first objective of Part I in this study was to investigate the cranial maturation process of 16 cranial sutures in *Delphinus* sp. from New Zealand waters (cranially immature: n = 31, cranially mature: n = 36). Although the odontocete skull displays directional, bilateral asymmetry characterized by a larger right side of the skull (Rommel, 1990), all bilateral

sutures assessed (n = 14) in the present study displayed a symmetric degree of suture fusion. This finding is in accordance with previous skull morphometric studies conducted on odontocetes (e.g. González, 2002; Chen et al., 2011). In the study herein, degree of fusion was correlated with age in all sutures assessed, except for the supraoccipital-exoccipital (so-ex) suture. However, pattern of suture fusion of the remaining 15 sutures was not uniform. Sutures located on the occipital region of the braincase were the earliest to fuse (i.e. so-ex, parietal-supraoccipital (pa-so), and parietal-exoccipital (pa-ex)). Concurring, previous studies reported that the braincase is the earliest functional complex to display suture fusion (e.g. Perrin, 1975; González, 2002; Chen et al., 2011). However, complete fusion of the so-ex suture was only recorded in Argentinean *D. delphis* specimens > 5 years (González, 2002), as compared to the observation that complete obliteration of this suture was already attained in New Zealand specimens of 1 year of age. The finding of the present study is, however, in accordance with the pattern of fusion reported for Risso's dolphins, *Grampus griseus*, from Taiwanese waters, in which this suture was also amongst the earliest to fuse (Chen et al., 2011).

Partial obliteration of the frontal-orbitosphenoid (fr-or) and zygomatic-parietal-exoccipital (zy-pa-ex) sutures was only recorded in specimens aged ≥ 18 years, and complete obliteration was never observed. This is consistent with patterns of fusion observed in other odontocetes such as *Stenella* sp., in which fused suture lines related to the squamosal and orbitosphenoid were only reported in some older individuals (Perrin, 1975). Likewise, Chen et al. (2011) observed that sutures on the lateral sides of the braincase of Risso's dolphins only showed signs of fusion in some of the mature specimens investigated.

Misclassification of cranial maturity status based on individual sutures was > 50% in 37.5% (n = 6) of cranial sutures assessed, and degree of fusion of those sutures was, therefore, not indicative of maturity status. These findings concur with Perrin (1975) and González (2002),

who also demonstrated that only a small proportion of all cranial sutures investigated displayed a consistent pattern of fusion with maturity status and age (i.e 34.4%, n = 11, (González, 2002). In the present study, the frontal-frontal (fr-fr) and frontal-interparietal (fr-in) suture provided the lowest total percentage misclassification (10.4% and 10.6%, respectively). This finding is consistent with Chen et al. (2011), who identified that the fr-in suture was the best indicator for assessing sexual maturity in Risso's dolphins. Tavares et al. (2010) included degree of fusion of the nasal bones, the exoccipital bone, pterygoids, and the zygomatic process of squamosal for cranial maturity status determination of common dolphin specimens from the southern West Atlantic (Brazil, Uruguay, and Argentina). With the third lowest total percentage misclassification (11.3%, n = 6), degree of fusion of the nasal bones was also deemed a relatively good indicator of cranial maturity in the present study. One of both nasal bones was loose in the female common dolphin *Shona* (WC06-10Dd), one of the captive held specimens that was over 31 years of age. The loose nasal bone may be related to osteoporosis in old animals (Butti et al., 2007; Pope et al., 1989). However, in contrast, both nasal bones of the oldest (also captive) specimen, *Kelly* (WC08-16Dd) were fully fused. Tavares et al. (2010) did not specify which suture related to the exoccipital bones was assessed for cranial maturity status determination. In the current study, 27.3% (n = 6) of cranially immatures were misclassified based on the pa-ex suture and all, except one immature specimen, displayed an advanced degree of fusion of the so-ex suture and were therefore misclassified as cranially mature (n = 21). Likewise, in the current study, a total of 37.9% (n = 11) cranially mature specimens were misclassified as cranially immature based on the degree of suture closure of the pterygoid bones.

As noted previously, lowest total percentage misclassification in the present study was obtained for sutures located at the vertex of the skull (fr-fr, fr-in, and na-fr) (refer to Fig. 1.3). Important muscle groups related to the nasal complex attached at the vertex region (Mead,

1975). González (2002) suggested that relative late fusion of sutures related to the breathing complex could indicate extended growth of this functional complex. Fusion of these sutures was of intermediate status in the present study. However, this observation could be an artefact of small sample size.

4.3 Cranial maturity determination

The second objective of Part I was to determine a cut-off point between cranially immature and mature specimens based on a suture index and to estimate age at cranial maturity of *Delphinus* sp. from New Zealand waters. In total, 62.5% (n = 10) of cranial sutures (fr-fr, fr-in, lacrimal-frontal (la-fr), maxilla-frontal (max-fr), na-fr, parietal-exoccipital (pa-ex), palatine-maxilla (pal-max), palatine-palatine (pal-pal), premaxilla-maxilla (premax-max), and pterygoid-palatine (pt-pal) suture) were deemed appropriate for deciphering cranially immature from mature specimens and were therefore included for the suture index computation. All cranial sutures included by González (2002) for estimation of the suture index were also deemed appropriate in the current study, except for the so-ex suture. Fusion of this suture was not correlated with age in the present study, owing to early suture closure. Early suture fusion of the so-ex is generally recorded in mammals (Bärmann & Sánchez-Villagra 2012).

In the study herein, the suture index calculated suggested that cranial maturity in *Delphinus* sp. from New Zealand waters is attained at approximately 11 years (pooled for both sexes). This finding complies with estimated age (11 years) at cranial maturity in the short-beaked common dolphin, *D. delphis*, from Argentinean waters (González, 2002). In contrast, Japanese *D. Delphis* and *D. capensis* attain cranial maturity much earlier at approximately 5 and 4 years, respectively, based on the degree of rostral fusion (Amaha,

1994). However, ages determined by Amaha (1994) had not been verified by an ageing expert (S. Murphy, pers. comm.). A more recent life history study conducted on 39 *D. delphis* females from Japanese waters determined that the youngest individuals, aged 4 and 6 years (n = 3), did not show a single *corpora albicantia* (Takahashi et al., 2006). This finding suggests that these females were sexually immature or at the onset of sexual maturity. The authors determined, that 89.7% (n = 35) of sexually mature individuals were > 9 years of age. Given that growth continues in odontocetes after attainment of sexual maturity (Chivers, 2002), findings by Takahashi et al. (2006) may indicate that cranial maturity might be attained at a later age in the Japanese *D. delphis* population.

Age at cranial maturity estimated in the present study can not currently be compared to age at physical maturity (APM) of New Zealand *Delphinus* sp. given that such data are not yet available. It should be noted that the cut-off point for cranial maturity of the current study might be set very conservatively, due to small sample size. Nonetheless, cranial maturity attainment at approximately 11 years in male *Delphinus* sp. from New Zealand waters coincides with APM of *D. delphis* in Irish waters, where males reach asymptotic lengths at approximately 11 years (Murphy & Rogan, 2006).

Apart from one individual (KS10-01Dd), all additional specimens of unknown age (n = 29) were allocated to one of the three age classes (1 - 3 years, 6 - 10 years, and ≥ 11 years) based on their suture index (age class I: 0.0 - 3.5; age class II; 4.0 - 7.5; age class III: 8.0 - 10) (third objective of Part I). The suture index (3.5) of KS10-01Dd fell between the limits of age class I and II, which was a result of the lack of specimens aged 4 and 5 years.

4.4 Cranial maturity indicators

The final objective of Part I was to assess the validity of different degrees of rostral fusion, TBL, skull weight, and cranial elements as indicators of cranial maturity in *Delphinus* sp. from New Zealand waters.

4.4.1 Rostral fusion

Length of rostral fusion of all specimens regarded as cranially mature (based on the suture index) was ≥ 50% of the length of the rostrum (from the tip to the base), indicating that all specimens with rostral fusion of < 50% have not yet attained cranial maturity and should be regarded as cranially immature. The finding that premaxilla-maxilla fusion along the rostrum exceeded 50% in 16.1% (n = 5) of specimens assessed as cranially immature highlights that this criterion was not a reliable indicator of cranial maturity for common dolphins in the present study. None of the specimens assessed as cranially immature displayed fusion of ≥ 75% of the rostrum, indicating that *Delphinus* sp. specimens from New Zealand waters with rostral fusion of ≥ 75% can be regarded as cranially mature. This suggests that the extent of rostral fusion at cranial maturity in New Zealand specimens is less when compared to Japanese *D. delphis* (Amaha, 1994). The author determined that 'rostral fusion up to the base of the rostrum' indicates cranial maturity in the short-beaked form inhabiting Japanese waters. However, Amaha (1994) noted that both the rate and extent of premaxilla-maxilla fusion can differ between *Delphinus* sp. populations, which might account for the difference between her finding and the result reported herein. Amaha (1994) documented a maximum skull length (CBL) of 457.3 mm for the Japanese short-beaked common dolphin, as opposed to a maximum CBL of 494.9 mm obtained for New Zealand specimens in the present study. Such difference could indicate that New Zealand specimens attain a larger skull size. Differences in

skull size might influence degree and extent of rostral fusion, which would require scientific investigation.

4.4.2 Total body length

TBL of physically mature *D. delphis* varies greatly between geographic populations (Evans, 1975). Possible factors that influence geographic variation of body size in mammals include, but are not limited to, habitat, temperature (Bergmann's rule), quality and quantity of prey, resource competition, population density, and by-catch rates (Rosenzweig, 1968; Perrin, 1984; Yom-Tov et al., 1986; Lawton, 1989). Particularly large TBLs for *D. delphis* have been recorded from eastern North Atlantic waters, where males and females reach lengths of up to 250.0 and 230.0 cm, respectively (Silva & Sequeira, 2003; Murphy et al., 2006). An early record of physically mature short-beaked common dolphins from European waters even provides evidence for maximum TBL of 270.0 and 250.0 cm for males and females, respectively (Fraser, 1953), although it is not known if the species was identified correctly. The Black Sea common dolphin, *D.d. ponticus*, is among the smallest, with maximum TBL values of 219.0 and 200.0 cm and mean TBL values of 180.0 and 170.0 cm documented for males and females, respectively (Amaha, 1994; Perrin, 1984). Cranially mature male (n = 8) and female (n = 21) specimens included herein had maximum TBL of 241.0 and 212.0 cm, respectively. To date, a maximum TBL of 244.0 and 233.0 cm has been recorded for male and female New Zealand common dolphins, respectively (Stockin et al., 2011). *Delphinus* sp. from New Zealand waters thereby display relatively large body sizes. Mean TBL of cranially mature male and female New Zealand *Delphinus* sp. in the present study, as determined from the suture index and additional biological data, was 213.9 and 199.9 cm, respectively. Mean TBL of cranially mature males was thereby slightly higher compared to the asymptote

estimate (204.0 cm) derived for the same population (Stockin et al., 2011). This discrepancy is most likely due to the extremely small sample size of mature males available in the present study (n = 8), in addition to the presence of one particularly large male specimen (WS07-02Dd: TBL = 241.0 cm). Mean TBL of cranially mature female *Delphinus* sp. from New Zealand waters on the other hand, matched exactly with the asymptotic value (199.9 cm) estimated for New Zealand females by Stockin et al (2011). However, only 47.6% (n = 10) of cranially mature females in the present study had a TBL greater than or equal to the asymptote derived by Stockin et al. (2011). This finding could be an artefact of small sample size in both studies. Conversely, the discrepancy could suggest that cranial maturity is attained before physical maturity. In the spotted dolphin (formally spotted porpoise, *Stenella attenuata*) cranial maturity has been reported to occur before physical maturity (Perrin, 1975). In contrast, both cranial and physical maturity are attained at approximately the same age in the striped dolphin, *S. coeruleoalba*, inhabiting the western Mediterranean (Calzada et al., 1997). However, the authors noted that this finding should be interpreted with caution due to small sample size. Mean TBL of cranially mature specimens of both sexes was comparable to mean TBL estimated for both sexually mature male (213.5 cm, n = 14) and female (202.2 cm, n = 40) New Zealand *Delphinus* sp. (Stockin et al., 2011). The above findings, therefore, suggest that mean TBL of cranially mature individuals is comparable to estimated asymptotic body lengths and mean TBL of sexually mature New Zealand specimens.

4.4.3 Condylobasal length

CBL is commonly included in marine mammal skull morphometric studies as a criterion, among others, to decipher immature from mature specimens (e.g. Amano & Miyazaki, 1992; Brunner et al., 2004; Murphy et al., 2006; Westgate, 2007). In the eastern North Atlantic,

CBLs of mature male and female *D. delphis* were ≥ 420 mm and ≥ 400 mm, respectively (Murphy et al., 2006). However, these values could not be adapted for the present study as the CBL of specimens from both sexes that were classified as cranially immature with rostrum ratings 1 to 3 (male: n = 14; female: n = 10), based on suture index and age data (if available), exceeded those values (males: 64.3%, n = 9; females: 60.0%, n = 6). In total, 40.0% (n = 6) of those cranially immature specimens had rostral lengths of > 450 mm.

Herein, CBLs in the range of cranially mature specimens (males: 446.4 - 494.9 mm; females: 422.7 - 468.5 mm) were already attained by individuals of at least 8 years of age, and with a TBL of < 180 cm, indicating that CBL is not a good cranial maturity indicator for common dolphins in this region. However, an extremely small sample size, lack of very young specimens, and presence of cranially immature specimens that were close to the attainment of cranial maturity, most likely prevented the determination of an adequate cut-off point between cranially immature and mature specimens in the present study. Based on these findings and limitations, it is suggested that CBL should not be included as a criterion for cranial maturity assessment of *Delphinus* sp. from New Zealand waters, until a larger sample size becomes available.

4.4.4 Relative skull weight

Potential differences in relative skull weight (skull weight as a measure of condylobasal length (CBL) and zygomatic width (ZW)) between cranially immature and mature specimens could not be investigated in the present study, owing to small sample size of the former.

Concurring with de Buffrénil et al. (1985), who reported that common dolphin males tended to have a higher skeletal weight than females above a certain age (although the authors did not

specify what age), a significantly higher relative skull weight of males as compared to females was detected in the present study. However, de Buffrénil et al. (1985) were unable to assess sexual dimorphism in relative skeletal weight statistically due to small sample size of mature males (n = 2). Likewise, only five male specimens were included in the study herein. Relative skull weight of one male specimen (WS07-02Dd) from the current study was extremely high as compared to the remaining male specimens analyzed. Since bone density tends to be negatively correlated with age in mammals (Butti et al., 2007; Pope et al., 1989), it is unlikely that age accounted for the observed difference, as the specimen with the heaviest skull was the oldest male (> 15 years) in the data set. However, with a TBL of 241.0 cm and a CBL of 494.9 mm this male represented an extremely large common dolphin and the largest specimen in the data set. A high relative skull weight of WS07-02Dd might, therefore, represent an extreme value as a result of large body size.

An interesting finding of the present study was, that the captive female specimens *Shona* (WC06-10Dd) and *Kelly* (WC06-08Dd) had lower relative skull weights as compared to stranded and by-caught females with similar TBL. However, owing to small sample size, the difference between free-ranging and captive specimens could not be evaluated statistically. Butti et al. (2007) who analysed bone density of the humerus of the Mediterranean bottlenose dolphin, *Tursiops truncatus*, reported no significant difference between free-ranging and captive specimens in this osteological feature. Lower relative skull weight of both captive dolphins from the present study could be age-related. A negative correlation between bone density and age has been demonstrated for both aquatic and terrestrial mammalian species (Butti et al., 2007; Pope et al., 1989). *Shona* and *Kelly* had reached ages of > 31 and > 33 years, respectively. Unfortunately, only one free-ranging female specimen of similar old age (29 years) was available in the present study, which had a slightly higher relative skull weight as compared to both captive individuals. Another factor that might be at least partly

related to the lower relative weight of Kelly's skull could be the individual's health status. Analyses on the reproductive organs and teeth of Kelly have revealed abnormalities in her ovaries (Massey University, unpubl. data) and hypo-mineralization in the dentine (Murphy et al., in review).

While the limited sample size of the present study prevents any clear conclusion to be drawn regarding variation in relative skull weight of *Delphinus* sp. from New Zealand waters, it appears that males tend to have higher relative skulls weights. In addition, other factors such as age and an individual's health status are likely to influence relative skull weight.

4.4.5 Non-metric characters

In the present study, none of the non-metric characters assessed, were definite indicators of cranial maturity in New Zealand *Delphinus* sp. specimens. Lowest misclassification of non-metric characters, which were assessed for their validity as cranial maturity indicators, was obtained for the developmental status of interalveolar septa in the left maxillary tooth row (IAS). IAS has been employed as one criterion for cranial maturity determination in a previous study conducted on the common dolphin in the western South Atlantic (Tavares et al., 2010). The authors differentiated three developmental stages where fully developed septa were regarded as an indication for maturity. However, while IAS were fully developed in all mature specimens in the present study (misclassfication of 0.0%), 22.6% (n = 7) of cranially immature individuals also displayed fully developed septa and were misclassified as cranially mature. Given that the suture index computed in the present study suggests that cranial maturity is attained at approximately 11 years of age, it is not surprising that the IAS of specimens in the present study were fully developed before the onset of cranial maturity. Two

of the misclassified immature individuals were 10 years of age (WS05-06Dd: male; WS04-34Dd: female).

The significantly lower frequency (16%, n = 5) of an undivided orbital fissure in cranially mature specimens as compared to immature individuals (54%, n = 15) is in accordance with Mead & Fordyce (2009). The authors reported that the undivided orbital fissures, present in immatures, become separated by a bony protrusion as the animal ages (refer to Appendix 8). The non-metric character width of the maxillae relative to the frontal bones (WMF), devised in the present study, was not a reliable indicator of cranial maturity, as 60% (n = 18) of cranially immature specimens were misclassified. Of those, one male specimen (WS09-19Dd: TBL = 174.0 cm) of known age (6 years), had also attained a zygomatic width and mandible length in the range of cranially mature specimens. Unfortunately, the lack of age data in the present study prevented determination of the age at which the maxillae exceed the width of the frontal bones.

4.4.6 Tooth condition

As expected, cranially immature specimens had a significantly higher percentage (88.4%) of normal (fully intact) teeth as compared to mature specimens (12.9%), while the latter had a significantly higher percentage of partly worn (52.0%), and broken (4.8%) teeth. Degree of tooth wear has been employed as an aging technique in several terrestrial mammals (Morris, 1972). Owing to individual variation in tooth wear and inter-observer bias, precision of this method is, however, limited and errors unavoidable (Robinson, 1979). In the present study, high individual variation in the degree of tooth wear of common dolphins was documented among individuals of the age classes II and III. Nevertheless, findings suggest that tooth condition could, to some degree, be used as cranial maturity and age class indicator. The

youngest specimen included herein with known age was a 1-year-old calf with fully developed rostral teeth. However, given that specimens of less than 1 year of age were not included in the present study, ages when tooth eruption commences and when teeth are fully erupted were not established. Based on findings presented here, dolphins with ≤ 6.8% of partly worn rostral teeth are most probably between 1 and 3 years (age class I) and cranially immature. Presence of fully worn teeth provided evidence for cranial maturity, as no immature specimens possessed teeth that were worn down to the gum line. Specimens with fully worn teeth were thereby ≥ 11 years of age. Lack of significant difference in median percentage of broken teeth between age class II and age class III individuals was most probably an artefact of very small sample size, in conjunction with high individual variation within these two age classes. However, all individuals (n = 5) with the presence of ≤ 6.8% of partly worn rostral teeth, but with no teeth worn down to the gum line were in the age range 6 to 10 years and cranially immature.

PART II: Sexual dimorphism, taxonomy, geographic variation, and precision of two data acquisition methods

Presence of cranial sexual dimorphism and geographic variation was investigated through both metric and non-metric characters in cranially mature skull specimens only. Taxonomic status was assessed independently for both cranially immature and mature specimens. In addition, precision between linear calliper measurement and microscribe recordings were compared.

4.5 Sexual dimorphism

4.5.1 Metric characters

The first and second objectives of Part II in the study herein were to assess (1) the degree of cranial sexual dimorphism in cranially mature *Delphinus* sp. specimens from New Zealand waters; and (2) whether dimorphic features were related to a certain functional complex of the skull. Several factors including, but not limited to, mating system, diet, and habitat may lead to the development of sexual dimorphic features (Selander, 1966; Trivers, 1972). Overall, significant differences in absolute size between sexes were found in TBL and in 22.7% (n = 15) of skull characters investigated. Degree of sexual dimorphism has been demonstrated to vary greatly between geographic populations of odontocetes (Amano & Mayazaki, 1996; Amaha, 1994; Wang, 2000; Bell et al., 2002; Murphy, 2006).

Amaha (1994) reported that the number of sexual size dimorphic skull characters in common dolphin specimens from New Zealand waters was higher as compared to populations from the eastern and western North Atlantic, Peru, and the Black Sea. The majority of specimens (71%, n = 24) from the eastern North Atlantic population were obtained from French waters with the remaining specimens being British and Irish. In contrast to Amaha's (1994) findings, New Zealand specimens within the present study exhibited a smaller degree of sexual size dimorphism (SSD) as compared to specimens from English and Welsh waters assessed by Murphy (2006), when only taking cranial characters into account that had been included in both studies. The major difference between Murphy's (2006) findings and results presented herein was the lack of SSD in all measurements related to the length of the rostrum (RL), CBL, distance from tip of rostrum to external (REXN) and internal nares (TRIN), and length of upper tooth rows (LLUTR, LLLTR) were not significant in the present study. Amaha (1994) reported that sexually size dimorphic characters can differ between geographic

populations of common dolphins. However, in the present study, lack of significant SSD in characters aforementioned, was likely an artefact of small sample size, given that only few mature specimens (male: n = 5, female: n = 16) with rostrum ratings 1 and 2 were available. Amaha (1994) detected SSD in length measurements related to the rostrum in New Zealand specimens included in her study. However, given that sample size of Amaha's (1994) study was also small (males: n = 8; females: n = 6), results of both studies might not be representative of the New Zealand *Delphinus* sp. population and should be regarded with caution.

In the present study, the majority (86.7%, n = 13) of cranial characters displaying significant SSD, were width measures. This finding is in accordance with Bell et al. (2002), who reported that width measures were more discriminating than length measures for assessing sexual dimorphism in southern Australian *D. delphis*. Absence of sexual shape dimorphism in cranial character in the present study was most likely an artefact of small sample size, given that it has been documented in New Zealand specimens assessed by Amaha (1994) and also in other geographic *D. delphis* populations (Murphy, 2006; Samaii, et al., 2005).

The majority (63.6%, n = 7) of cranial sexual size dimorphic features that could be allocated to a functional complex herein, were related to the feeding apparatus. The remaining characters were associated with the vision apparatus (n = 2) and braincase (n = 1). Significant SSD in cranial characters related to the feeding apparatus and overall size of the skull were previously recorded in *Delphinus* sp. (Amaha, 1994; Heyning & Perrin, 1994; Murphy, 2006; Samaai et al., 2005) and several other delphinids, including the spinner dolphin, *Stenella longirostris* (Douglas et al., 1986), bottlenose dolphin (Turner & Worthy, 2003), and Fraser's dolphin, *Lagenodelphis hosei* (Perrin et al., 2003). Differences in rostral dimensions are thought to predominantly reflect differences in foraging ecology (Perrin, 1975). Male New Zealand *Delphinus* sp. had wider rostra as well as wider zygomatic and postorbital widths

compared to females. Absolute diameter of the temporal fossae was also larger in males. The major jaw muscle, the temporal muscle, passes through the temporal fossa and into the coronoid process of the mandible (Rommel, 1990). A larger diameter of the temporal fossa is thereby indicative of a stronger jaw musculature (Perrin, 1975). Length of left squamosal and height of left mandible were larger in males in the current study, which further indicated greater jaw strength. This was also previously noted in common dolphins in the eastern North Atlantic (Murphy, 2006).

Overall, differences in the feeding complex could be related to differences in feeding ecology between the sexes in this species (Purdie, 1994; Murphy, 2006). Stomach content analyses conducted on stranded (n = 76) and by-caught (n = 58) Irish common dolphins revealed that the proportion of cephalopods consumed was slightly higher in males compared to females (Brophy et al., 2005). Furthermore, similar analyses on *D. delphis* in the Bay of Biscay, France, revealed a weak correlation between prey and predator size (Meynier et al., 2008a). A small sample size (females: n = 24, males: n = 13) prevented Meynier et al. (2008b) and Stockin (2008) from investigating whether differences between the sexes existed when conducting the first stomach content analyses of New Zealand *Delphinus* sp. Stomach content and stable isotope analyses currently underway (Massey University, unpubl. data) might provide further insights as to whether dietary differences between males and females or specimens from different regions within New Zealand waters exist. Wider and more robust rostra could, however, also be an indication of aggressive intraspecific interactions (e.g. during mating) (Purdie, 1994; Murphy, 2006; Westgate, 2007). Structural differences between the sexes might, therefore, not necessarily be entirely based on function, but could potentially also incorporate an element of sexual selection

In both sexes, the majority of characters for which individual variation was greatest (Coefficient of Variation (CV): > 6%), were related to the feeding complex. Perrin et al.

(1999) recorded significant differences in rostral dimensions between *S. longirostris* belonging to a shallow water and deep water form. The author hypothesized that a more robust feeding apparatus could be favourable when pursuing large, demersal prey in shallow waters. In contrast, a more delicate feeding structure might be advantageous for catching smaller, fast moving pelagic prey (Perrin, 1975). In accordance, cranial morphometric analyses conducted on inshore and offshore *T. truncatus* populations in Californian waters also revealed that greatest differentiation occurred in osteological features related to feeding with the former population displaying a more robust rostrum and larger temporal fossa (Perrin et al., 2011). As noted previously (section 1.3.2.2), microsatellite data was suggestive of a putative coastal and offshore *Delphinus* sp. population in New Zealand waters. Future investigations in respect to potential morphological differences in the feeding apparatus between these two putative populations could therefore be of interest.

In the study herein, the height measurement of the post-temporal fossae displayed a greater individual variation in females as compared to males, while the converse was observed for the length measure of the post-temporal fossae. Several feeding strategies have been documented in New Zealand *Delphinus* sp. in New Zealand waters (Neumann & Orams, 2003; Burgess, 2006). It remains to be investigated, whether present findings represent actual differences in morphology, potentially related to differences in foraging strategies, or whether they are an artefact of small sample size of cranially mature males (n = 8). The feeding apparatus and the braincase were the most and least variable functional complex, respectively, which concurs with Perrin (1975), who obtained similar results for *Stenella* sp. Herein, only one character related to the braincase, distance from the top of the braincase to the tip of the dorsal notch of the formen magnum (HFCFM), displayed a CV of > 6% in females only. Given that the CV related to actual braincase height (HBC) was low in both sexes, high variation associated with HFCFM in females resulted from differences in the height of the foramen magnum, namely

due to the presence / absence, height of a distinct dorsal notch (refer to Appendix 5). Functional significance of this feature is unknown.

In conclusion, as anticipated, SSD was detected in cranial measurements obtained from cranially mature male and female *Delphinus* sp. skull specimens from New Zealand waters, the majority of which were related to the feeding apparatus. The finding that fewer characters than expected displayed SSD was most likely an artefact of small sample size.

4.5.2 Non-metric characters

Significant sexual dimorphism in non-metric characters was only detected in the position of the top margin of the ascending process of the right maxilla relative to the nuchal crest. In mature males, this margin lay ahead of the crest in the majority of specimens (82.6%, n = 19) investigated, while the ascending process extended to or underneath the overhang in the majority (81.8%, n = 26) of mature females. This finding was likely, at least, partly related to the length of the nuchal crest overhang, which develops through the process of supraoccipital telescoping during ontogeny (Miller, 1923). The length of the overhang was not measured in the present study, due to the difficulty of determining a common point of reference and the irregularity of the crest's margin. However, the overhang appeared more developed (elongated) in females, especially on the right side of the skull. Difference in appearance of the nuchal crest was also noted by Amaha (1994), who reported that the overhang in male Japanese *D. delphis* had an 'eroded' appearance as compared to females.

In odontocetes, several muscle groups related to the nasal passage attach at the vertex as well as at the ascending process of the maxillae and frontal bones that lie anterior to the nuchal crest (Mead, 1975; Huggenberger et al., 2009). A less developed nuchal crest might thereby provide a larger attachment side for these muscles, e.g. for the most superficial muscle related

to the nasal passage, the *pars posteroexternus*, which inserts at the lateral margin of the nuchal crest (Mead, 1975). A potential hypothesis could, therefore, be that male common dolphin specimens from New Zealand waters might tend to have a more developed nasal passage musculature. In odontocetes, muscles related to the nasal passage play an important role in both respiration and sound production (Mead, 1975; Huggenberger et al., 2009). Findings of the present study may thereby suggest the possibility of potential differences in vocalization between male and female New Zealand *Delphinus* sp.

A further important muscle related to the nasal passage is the nasal plug muscle, which originates at the prenarial triangle (Mead & Fordyce, 2009) (refer to Fig. 1.1). In the study herein, in both sexes, highest individual variation in metric measurements was documented for the width of the prenarial triangle at the base of the rostrum. The nasal plug muscle is connected to the nasal plugs, which seal the paired external nares, thereby preventing water entering the respiratory tract while the animal is submerged (Mead, 1975; Huggenberger et al., 2009). Upon surfacing, the nasal plug muscle withdraws the nasal plugs from the external nares towards the rostrum, enabling the dolphin to exhale (Mead, 1975; Huggenberger et al., 2009). In addition, this muscle plays an important role in the complex movement of the nasal plugs in relation to sound generation (Mead, 1975). Huggenberger et al. (2009) hypothesized that variation in facial structure might facilitate 'accoustic individuality' in odontocetes. Such may potentially be the case in *Delphinus* sp. from New Zealand waters, given the high variability in the width of the prenarial triangle documented in specimens included in the study herein. This hypothesis, however, requires further investigation.

4.6 Taxonomy and geographic variation

4.6.1 Species identification

The primary objectives of the present study were to investigate the taxonomic status of the New Zealand common dolphin and to assess potential population segregation within New Zealand waters. RL/ZW ratios calculated for cranially mature specimens ranged from 1.39 to 1.61. Both minimum and maximum values of the study herein had been obtained from specimens with a rostrum rating of 2. Owing to the fact that approximately 2 - 3 mm of the tip of the rostra were missing from specimens with rating category 2, RL/ZW ratios of those individuals represent a slight underestimate by approximately 0.01.

The finding that the mean RL/ZW ratio of cranially immature specimens (1.50) was comparable to the mean ratio determined for cranially mature individual (1.49) can be explained by a small sample size, as well as sampling biases. For example, only a limited number of very young specimens were available in the present study and three individuals were close to attaining cranial maturity. Interestingly, 40.0% (n = 6) of cranially immature individuals had RL/ZW ratios in the range of *D. capensis* inhabiting Californian waters. The slightly higher mean RL/ZW ratio obtained for immature as compared to mature individuals in the study herein might, therefore, also reflect sampling bias due to the presence of a higher proportion of longer-beaked immature individuals.

Mean RL/ZW ratio of cranially mature New Zealand *Delphinus* sp. reported herein, fell between the mean ratios recorded for *D. delphis* and *D. capensis* from Californian waters (Heyning & Perrin, 1994) and other geographic populations of these two species (Appendix 26). In addition, mean CBL, RL, ZW, and rostral tooth socket counts obtained for New Zealand specimens were of intermediate status (refer to Appendix 26). Results presented herein are, therefore, in concordance with findings from Amaha (1994), who reported that

specimens pooled from New Zealand and Australia were morphologically of 'intermediate status' between both recognized species. Amaha (1994) had obtained a mean RL/ZW ratio of 1.5 for New Zealand / Australian specimens. However, her sample was also limited in size (n = 23), containing only 15 New Zealand specimens. Mean RL/ZW ratio published for *D.c. tropicalis* (1.85) (Jefferson & Van Waerebeek, 2002) was outside the ratio range of *Delphinus* sp. from New Zealand waters (refer to Appendix 26).

Mean RL/ZW ratio of New Zealand specimens from the present study matched most closely with specimens from southern Australia (1.52) (Bell et al., 2002). This is consistent with genetic analyses, which revealed only low levels of differentiation between specimens from these two regions (Amaral et al., 2012) located in close geographic proximity (refer to Fig. 1.8). Both a slightly lower mean RL/ZW ratio and a smaller range of this ratio (mean: 1.49, range: 1.39 - 1.61) were obtained in the current study as compared to *D. delphis* specimens pooled from southern and south-eastern Australian, and Tasmanian waters (mean: 1.52, range: 1.36 - 1.73) (Bell et al., 2002). However, Bell et al (2002) detected two different forms, an inshore and offshore form. In addition, more recent studies have identified genetic differentiation between southern Australian and Tasmanian *D. delphis* (Bilgmann et al., 2008). Furthermore, at least three putative *D. delphis* populations were distinguished off the coastline of New South Wales (Möller et al., 2011). These findings might partly account for the large RL/ZW ratio range published by Bell et al. (2002) for specimens pooled from the aforementioned regions. Mean and maximum values obtained for RL were larger in New Zealand specimens, while lower minimum values have been published for common dolphins from southern Australian waters (Bell et al., 2002). The slightly higher mean rostral tooth count obtained for New Zealand specimens (refer to Appendix 26) can thereby be explained by the presence of some individuals with shorter rostra in southern Australian waters.

Overall, TBL values recorded for male New Zealand common dolphins (190 - 241 cm) tended to overlap to a larger degree with values published for *D. capensis* (202 - 235 cm) than values documented for *D. delphis*, and maximum TBL in the present study exceeded that of *D. capensis* (Appendix 26). Furthermore, two cranially immature male specimens (KS09-13Dd: 8 years, TBL = 214 cm; WS05-06Dd: 10 years, TBL = 220 cm) had TBLs greater than the asymptote reported by Stockin et al. (2011). Given that one cranially mature male (WS07-02Dd: > 15 years) included in the study herein had obtained a TBL of 241 cm, it is possible that the two aforementioned specimens could attain similar body sizes at physical maturity. Both New Zealand male and female common dolphins also displayed comparatively longer mean CBL and RL as well as a wider ZW than other geographic populations of *D. delphis*, except for the English / Welsh population, for which a comparable mean zygomatic width had been recorded (Appendix 26). These findings suggest that New Zealand *Delphinus* sp. tend to have larger skull and body size as compared to *D. delphis* from California and other regions. While this might reflect a true difference between geographic populations, higher values obtained in the current study might partly be due to the fact that extreme care was taken to only include cranially mature specimens. However, the larger TBL and ZW recorded for specimens from New Zealand are comparable to the eastern North Atlantic population (refer to Appendix 26). Larger body size exhibited by geographic populations of cetaceans inhabiting cooler waters might at least be partially explained by Bergmann's rule, as has previously been proposed (Ross & Cockcroft, 1990; Bell et al., 2002; Murphy et al., 2006; Amaral et al., 2012). Bergmann's rule states that: "Races of warm-blooded animals from cooler climates tend to be larger than races of the same species from warmer climates" (Mayr, 1956). Bergmann (1847) hypothesized that large body size in ectotherms inhabiting higher latitudes represents an adaptation to cold temperature, as the surface area to volume ratio, and thereby heat loss, decreases as body size increases.

Contrasting genetic results had been obtained for the physically mature female WS04-28Dd. Microsatellite data indicated a short-beaked phylogeny, while mtDNA data were suggestive of a long-beaked phylogeny (Stockin et al., in press). An important finding in the present study was the fact that the RL/ZW ratio obtained for this cranially mature female specimen was only 1.45 (rating category 3), indicating a short-beaked phylogeny. Even if the rostrum had been 10 cm longer, this allocation would not have changed. Morphometric data are thereby in support of the microsatellite data. The contradictory results obtained by aspects of the molecular analyses (i.e. mtDNA) further highlight the continued importance of morphometrics to complement genetic data when assessing species status (Reeves et al., 2004). No genetic information was available for specimens in the current study with RL/ZW ratios within the range of the long-beaked form (refer to Appendix 19 for specimen codes).

The Kalya Index of all skull specimens, except two individuals, was within the range reported by Miramontes Sequeiros (2010) for two *D. delphis* populations from the North Atlantic and North Pacific. The unsexed museum specimen (MM001688) from Tauranga, Bay of Plenty (refer to Fig. 1.9), with the highest index value of 125.6, had a RL/ZW ratio of only 1.46 (rating category 1). This specimen was thereby clearly within the range of the short-beaked form. The Kayla Index is currently being determined for the long-beaked form (Miramontes Sequeiros, 2010).

Concluding, results of the present study suggest that the New Zealand common dolphin is of 'intermediate status' between the short-beaked or long-beaked form, not fitting the exact description of either of both of those currently recognized species. This finding complies with privious morphometric (Amaha,1994) and molecular (Stockin et al., in press) research conducted on the New Zealand population. While current evidence does not support the existence of *D. capensis* in New Zealand waters, morphometrical findings of the present study, which are summarized below, suggested that, for the time being, the New Zealand

common dolphin should be regarded as a larger form of *D. delphis*. Once further genetic, morphometric, and ecological data become available, the taxonomy of the *Delphinus* genus might hopefully be resolved globally. The findings supporting the proposal to preliminarily classify the New Zealand common dolphin as a large form of *D. delphis* are as follows:

1. The range of RL/ZW ratios obtained for cranially mature New Zealand specimens presented a continuum with the mode found within the upper range of *D. delphis* from Californian waters (Heyning & Perrin, 1994)

2. In total, 37.5% (n = 3) and 9.1% (n = 2) of RL/ZW ratios obtained for cranially mature male and female New Zealand specimens, respectively, fell within the lower range of the long-beaked form (Heyning & Perrin, 1994)

3. The large TBL of New Zealand *Delphinus* sp. was comparable to TBL of *D. delphis* inhabiting the eastern North Atlantic, which also displays morphometric signs of being an intermediate form and is currently classified as a larger form of *D. delphis* (Murphy et al., 2006)

4. Mean CBL, RL, and tooth socket counts obtained for both sexes from New Zealand waters were larger than mean values published for other geographic populations of *D. delphis* (Heyning & Perrin, 1994; Murphy, 2004; Murphy et al., 2006; Westgate, 2007)

4.6.2 Geographic cranial variation

As already noted in section 1.3.1.2, the *Delphinus* genus may in fact belong to a single, large, morphologically highly variable species complex and beak length might relate to habitat

adaptation rather than taxonomy (Natoli et al, 2006; Pinela et al., 2010; Amaral et al., 2012). Genetic analyses provided evidence that geographic populations of the long-beaked form have evolved independently (Natoli et al., 2006). Such finding thereby contests the longestablished monophyly hypothesis of the long-beaked lineage that diverged early on from the short-beaked lineage, and subsequently dispersed into its current geographic ranges. Genetic results further suggested that long-beaked individuals from Mauritania, West Africa, are more closely related to the short-beaked form inhabiting the North Atlantic than the long-beaked form from other regions (Natoli et al., 2006). In addition, a morphometric study conducted on 72 common dolphin skulls from waters off the Mauritanian coast revealed high variation in cranial features and an overlap in RL/ZW ratio with both *D. delphis* and *D. capensis* (Pinela et al., 2011). RL/ZW ratios followed a cline and could not be separated. The authors, therefore, proposed that rather than the existence of two populations or species, only a single highly variable population comprised of both morphotypes, the short-beaked and long-beaked common dolphin is present in Mauritanian waters. Concurring, van Bree and Purves (1972) had previously highlighted the possibility that individuals with short and long rostrum might be present in a population to varying degrees. Natoli et al. (2006) hypothesized that habitat adaptation and resource polymorphism rather than taxonomy might be the underlying factors driving differences in rostrum length of the common dolphin.

Niche segregation due to differences in diet, can result in the separation of a population into niche groups (Smith, 1966). If different 'phenotypic extremes' are favoured in such niche groups, polymorphism (two or more phenotypes) might evolve within a population (Mayr, 1970; Moser & Cross, 1975). In accordance, stable isotope analyses on 72 *Delphinus* sp. skull specimens from Mauritanian waters revealed that $\delta^{15}N$ was correlated with rostral length, indicating that longer beaked individuals either fed on a higher trophic level or further offshore (Pinela et al., 2010). Habitat specialization and polymorphism can represent the first

steps in the process of speciation in populations that are not isolated geographically (sympatric populations) (Moser & Cross, 1975; Rice & Salt, 1988). Differences in foraging ecology within a common dolphin population might thereby drive local speciation (Bell et al., 2002; Natoli et al., 2006; Bilgmann et al., 2008; Pinela et al., 2010).

Common belief was that speciation might commence if the presence of different morphotypes becomes stable and reproductive isolation occurs (Sutherland, 1987). However, more recent molecular evidence suggests that reproductive isolation is not a prerequisite in the process of speciation, but that divergence can occur if gene exchange is restricted to some genes only (Nosil, 2004; Hey, 2006). In support of this hypothesis, some level of genetic differentiation in *D. delphis* from Australian waters has recently been detected based on both mtDNA and microsatellite data (Bilgmann et al., 2008; Möller et al., 2011). *D. delphis* is a highly mobile and wide-ranging delphinid (Evans, 1994) and only low levels of divergence have been demonstrated for geographic *D. delphis* populations within a given ocean basin, for example the North Atlantic (Mirimin et al., 2009; Amaral et al., 2012). Given this fact, low to moderate genetic differentiation between southern Australian and eastern South Tasmanian individuals, which are living in close geographic proximity (1500 km), was unexpected (Bilgmann et al., 2008). The authors noted that, while simple isolation by distance was unlikely to explain the observed genetic differentiation, it could not be ruled out completely, due to the fact that sampling of individuals in between those two areas was incomplete. Levels of differentiation were absent within approximately 600 km of the coastline off central South Australia (Bilgmann et al., 2008). The authors hypothesized that differences in sea surface temperature (SST) and local topography between southern Australian and eastern South Tasmanian waters could have influenced the distribution of prey. *D. delphis* may have adapted to local prey and only follow their movement pattern, which might thereby drive population structure of the common dolphin in a given geographic region (Amaral et al.,

2012). The diet of *D. delphis* inhabiting waters off South Australia is predominantly comprised of sardines, *Sardinops sagax*, and anchovies, *Engraulis australis* (Kemper & Gibbs, 2001), while individuals in Tasmanian waters most likely consume jack mackerel, *Trachurus declivis*, and redbait, *Emmelichthys nitidius* (Furlani et al., 2007). Likewise, fine scale genetic structure has recently been demonstrated for *D. delphis* off New South Wales, eastern South Australia, differentiating at least three genetic populations within several hundreds of kilometres – though it should be noted that a number of animals were biopsied from the same schools, and only 16 individuals were sampled from one of the putative populations (Möller et al., 2011). The authors reported that the pattern of differentiation coincided with variation in oceanographic features (East Australian Current) and hypothesized that the three putative *D. delphis* populations had most likely adapted to the three distinct water masses identified in that region characterized by differences in temperature and fish larvae assemblages. Recent genetic analyses also highlighted the importance of oceanographic features such as chlorophyll and SST in shaping genetic structure of *D. delphis* on a medium geographic scale (Amaral et al., 2012).

A high level of genetic diversity, comparable to *D. delphis* inhabiting Australian and eastern North Atlantic waters, has been demonstrated for New Zealand *Delphinus* sp. (Amaral et al., 2012; Stockin et al., in press). The authors reported that significant F_{IS} values (inbreeding coefficient) were obtained for those respective populations, which may relate to potential sub-structure within these regions. As already outlined earlier (refer to section 1.3.2.2), mtDNA suggested potential population segregation between Hauraki Gulf (HG) and non-HG *Delphinus* sp., while microsatellite data only indicated a separation between a putative coastal and offshore population (Stockin et al., in press). These findings suggest restricted gene flow may exist between females but not males from the HG and other regions (Stockin et al., in press). Field-data provide strong evidence that the HG is important for nursery groups of the

common dolphin year round, and side-fidelity of at least some individuals within HG waters has been suggested (Stockin et al., 2008a). In the present study, no regional differences were detected between HG (n = 10) and non-HG females (n = 5) based on metric data. However, an extremely small sample size prevents any firm conclusions to be drawn. Likewise, no significant regional differences between HG and non-HG specimens (pooled and separately for both sexes) were detected based on non-metric data. A significant difference in trait frequency expression was obtained for one non-metric character 'contact between premaxilla and nasal' (CPN) in the male data set. Given that the p-value was close to 0.05 (p = 0.047), the significance was likely due to chance (Brasili, et al., 1999, Sjøvold, 1984) or an artefact of small sample size (n = 25) rather than representing a true difference between HG (n = 13) and non-HG (n = 12) male specimens. Conversely, given mobility of the common dolphin (Evans, 1994) and the fact that regional allocation based on stranded specimens is not necessarily accurate due to carcass drift, it may be that some males from the present study regarded as HG specimens based on stranding location could represent individuals from the putative coastal population, or *vice versa*.

Pelagic and neretic water forms have been reported for the spinner dolphin (Perrin et al., 1999) and bottlenose dolphin (Wang et al., 2000). Morphometrical evidence has also been suggestive of the presence of a nearshore and offshore form of *D. delphis* in southern Australian waters (Bell et al., 2002). The authors noted that pelagic water specimens tended to have 'umbrella shaped' braincases, while individuals from neretic water appeared to predominantly display 'square shaped' crania (Bell, 2001). Anthropometric studies have demonstrated a correlation between climate and head shape (Beals et al., 1984; Bharati et al., 2001). Beals et al. (1984) reported that 30.0 - 40.0% of the variance in mean head shape between geographic populations could be explained by thermoregulation. The authors stated that the head shape of humans exposed to a cold climate provided a smaller surface area

compared to the head shape of humans inhabiting warmer climatic regions. Concurring, Bell (2001) hypothesized that that the 'umbrella shaped' crania characteristic for offshore water *D. delphis* specimens in southern Australian waters could represent an environmental adaptation to minimize heat loss in colder offshore waters. In the present study, the braincase of only three specimens was classified as 'square shaped' and 20.9% (n = 14) of individuals could not be clearly allocated to either of the two head shapes and were therefore not considered for analyses. However, skulls of individuals sampled from the putative 'offshore' population by Stockin et al. (in press) were not available for the present study and it is unclear if any specimens included herein, originated from deep water regions. Morphometric examination in relation to cranial shape differences between potential coastal and offshore specimens in New Zealand waters warrants, therefore, further investigation. However, given that delphinids are well insulated endotherms, it may well be that the shape of the braincase is not related to water temperature.

P-values for both non-metric characters (projection of the mesethmoid between the premaxillae (DPM) and contact between premaxillae (CPPT), which have been determined as most effective discriminators between Black Sea, western North Atlantic and eastern Tropical Pacific common dolphin populations by Perrin et al. (1994), were well above the α significant level ($p \leq 0.05$) in the current data set. However, samples in the present study were not derived from geographically isolated regions. Likewise, estimates of mean measure of divergence (MMD) (separately and pooled for both sexes) between HG and non-HG specimens were not significant. Nevertheless, the MMD value computed for females (0.076) was slightly higher as compared to males (0.043) which might suggest that, although not significant, females tend to show slightly more regional dissimilarities in non-metric character traits than males. This interpretation would be in accordance with mtDNA data presented by Stockin et al. (in press). Overall, small sample size in the current study

prevented firm conclusions being drawn regarding potential presence or absence of regional differences of both male and female *Delphinus* sp. from New Zealand waters.

In conclusion, evidence suggested that marine productivity and SST influence genetic structure in the common dolphin on both a small and medium geographic scale (Bilgmann et al. 2008; Möller et al., 2011; Amaral et al., 2012). High genetic diversity identified for the New Zealand population and the fact that genetic evidence is suggestive of a potential population segregation in this region (Amaral et al., 2012; Stockin et al., in press), highlights the importance of continued morphometric and genetic investigation in relation to population structure of *Delphinus* sp. in New Zealand waters. This is particularly important, given the relatively recent proposal based on mtDNA results that the southern Australian and eastern South Tasmanian *D. delphis* populations should be regarded as separate management units (Bilgmann et al., 2008).

4.7 Precision of two metric data acquisition methods

The final objective of the present study was to assess and compare measurement error (ME) associated with linear measurement obtained through two different data acquisition methods (callipers and microscribe digitization) by means of three different precision estimates, namely: variance of repeated measures, mean absolute difference (MAD), and relative error magnitude (REM). For all cranial characters (n = 33) recorded, variability of repeated measures (n = 3) was lower in the calliper data set (variance: callipers = 0.1 - 0.7%; microscribe = 1.1 - 10.7%). This result contrasts with that of Chen et al. (2008), who recorded linear measurements on dental casts and reported a lower ME for microscribe digitization compared to calliper measurements. However, the authors noted that ME was significantly higher in inexperienced observers. A higher ME obtained for repeated measures

of the microscribe data set in the present study could therefore partly be related to observer inexperience.

In the present study, a significant positive correlation between variance of repeated measures and mean character size was detected in the calliper data set. A significant dependence of variance on mean character size has previously been reported (Palmeirim, 1998; Muñoz-Muñoz & Perpiñan, 2010). However, it is more likely that the higher variances obtained for the largest characters in the current study was related to methodology rather than representing a true correlation with character size, as this relationship was absent from the microscribe data set. As noted earlier (section 2.2.4), measurements of ≤ 300 mm had been recorded with digital callipers, while standard manual vernier callipers had been used for measurements > 300 mm in length. Higher variances were obtained for all characters > 300 mm in length. However, variance of one character, distance of tip of rostrum to margin of internal nares (TRIN), which exceeded 300 mm in length, was higher in both the calliper and microscribe data sets. This indicates that the higher variance was most likely related to this character and not methodology. The relative difficulty of determining the point of reference at the internal nares most likely accounts for this observation.

Mean absolute difference (MAD) and associated 95% CI of 69.9% (n = 23) of calliper and microscribe recordings were below the 1 mm threshold, indicating high precision between both data acquisition methods for the majority of characters. In total, 10 characters (CBL, RL, height (HFM) and width (WFM) of the foramen magnum, left and right orbit length (LOL and ROL), length of the right lacrimal (LRLAC), least width of the parietal (LWPA), and the distance from the tip of the rostrum to the external (REXN) and internal nares (TRIN)), exceeded the MAD threshold of 1 mm. Of those, lower precision obtained for CBL, RL, REXN, and TRIN was at least partly due to the fact that landmarks for those characters were not placed in exactly the same location. The reference point of the tip of the rostrum (anterior

most tip of premaxillae) had been marked on paper for calliper recordings, given that the tip of the rostrum did not fall in a straight line with the second reference point in either of those four characters (refer to section 2.2.4). With the microscribe, landmarks of all characters were directly digitized on the skull. As a result, those characters (CBL, RL, REXN, and TRIN) could not be taken in an exact straight line, thus causing some error. The skull orientation outlined by Yamada et al. (2006), in which the rostrum is arranged horizontally for measurement purposes, was not applied in the present study. It therefore remains unknown, whether MAD would slightly differ when employing a different skull setup.

The remaining characters that exceeded the 1 mm threshold were HFM, WFM, LRLAC, LOL, ROL, and LWPA. All of these could also more accurately be recorded with the callipers, as points of reference for those characters were difficult to (1) determine by eye; and / or (2) place into a straight line during the digitization process. This was particularly the case in measurements related to the foramen magnum (HFM and WFM), due to the irregularity of the margins. A higher ME of repeated measures had also been obtained for HFM in the calliper data set. Statistically significant inter-observer differences for the cranial character orbit length has been reported by Jefferson and Van Waerebeek (2004), when conducting morphometric measurements on humpback dolphin (*Sousa* sp.) skull specimens, indicating the difficulty of determining exact points of reference for this character. However, only one observer was recording measurements in the study herein to reduce observer error bias. Higher ME associated with certain characters where landmarks are less easily locatable has been noted previously (Muñoz-Muñoz & Perpiñan, 2010).

In 75.0% (n = 15) of specimens, discrepancy between RL measures (≥ 1.3 mm) did not have an effect on the RL/ZW ratio calculated. The ratio in the remaining five specimens differed by 0.01, suggesting that the RL/ZW ratio is relatively robust to minor measurement error in RL and ZW values. This finding indicated that ratios determined by different methods were

comparable. All test outcomes (statistically significant or not significant) derived for individual cranial characters in respect to sexual dimorphism were identical, providing further strong evidence of high precision between both data acquisition methods. However, none of the characters which exceeded the 1 mm MAD threshold were found significant in the calliper set.

In conclusion, as anticipated, a high precision between calliper and microscribe recordings were obtained for all characters where reference points (1) could be unambiguously detected by eye; and (2) fell into a straight line when directly recorded on the skull, indicating that both data acquisition methods are equally valid for such measurements. In contrast, results presented herein suggest that callipers may provide higher accuracy when recording CBL, RL, REXN, TRIN, HFM, WFM, LWPA, and lacrimal and orbit lengths.

4.8 Limitations of the present study

Due to limitations listed hereafter, results presented in this thesis should be regarded as preliminary.

4.8.1 Total sample size

Owing to the reliance on infrequently stranded and by-caught individuals, an extended timeframe is required to obtain a large enough skull sample size to conduct morphometric studies on delphinids in the first instance. As a result cetacean researchers are rarely able to work with very large sample sizes. Even if total number of skulls appears large enough to carry out morphometric investigations, small sample size of certain age-sex classes might limit or prevent statistical analyses. To illustrate, in the present study, only 8 cranially mature

male crania were available, despite a total sample size of 67 common dolphin skulls. Furthermore, certain age classes were not represented or sample size was limited. This was partly due to the fact that skulls from immature specimens were collected opportunistically under the NZCDP, as the primary focus had been only to assess taxonomic status of New Zealand *Delphinus* sp. based on cranially mature specimens (K.A. Stockin, pers. comm.). Furthermore, age data were only available for a limited number of specimens available for the present study (37.3%, n = 25). Lack of biological data for several (n = 9) of museum specimens also limited the total sample size. Sample size for tooth condition analyses was limited to specimens stored at Massey University, as teeth of cleaned museum specimens had, of course, fallen out. In several specimens, teeth had been extracted for ageing purposes prior to commencing the recording of tooth condition, which further decreased the number of specimens that could be included for analyses.

4.8.2 Bone damage

Even if skulls are retrieved from carcasses, bone damage might render the osteological material useless for morphometric analyses. For example, one skull specimen retrieved by Massey University had been obtained from an individual that had live-stranded and due to poor health condition had to be euthanized by gunshot. The skull of this individual was completely shattered and therefore unusable.

Cranial components were missing in some skulls and, as a result, the full set of metric measurements could not always be recorded. Skeletal material available for analyses in the present study had been collected / prepared by several different people whose primary focus had not necessarily been to retrieve skulls for morphometric purposes. To illustrate, the braincase of several (27.8%, n = 5) cleaned museum specimens had been removed in order to

extract the brain. In some common dolphin crania archived frozen at Massey University, the occipital condyles had been cut off during necropsies. There were also several skulls for which mandibles had not been collected. A further issue is the fact that skulls obtained from beach-cast dolphins might have several broken bones. Depending on the location, the carcass might not be found for several weeks and osteological features could get broken more easily when bones become exposed as the flesh decomposes. One highly decomposed skull available in the study herein had several broken bones, including the mandibles. Particularly more fragile components, such as the tip of the rostrum, are prone to abrasion. Minor damage to rostra tips is a frequent issue encountered with common dolphin skulls (Purdie, 1994; Westgate, 2007). In addition, the skull cleaning / preparation process in the present study inflicted minor damage to some specimens, despite the fact that great effort was undertaken to limit this. In several cases, tooth sockets had been completely removed during the extraction of teeth for aging purposes, which prevented alveoli counts to be conducted on affected jaw bones (mainly left mandible).

Remaining flesh on several skulls (both cleaned museum specimens and crania prepared at Massey University) prevented scoring of some sutures and measurements to be taken. Most of the specimens with attached flesh at the vertex region were the very first specimens that had been cleaned as part of this study. Following the removal of all superficial flesh, skulls had initially been placed into the horse manure (*Equus* sp.) boxes with the dorsal side facing up. However, the top layer of manure dried out more quickly and, as a result, the decomposition process of the flesh around the vertex (the highest point of the skull) was restricted. After retrieval of the first specimens, the following skulls were placed into the boxes with the ventral side facing up, which facilitated a better decompostion of the flesh at the vertex region.

4.8.3 Methodology and observer bias

Although every effort was undertaken to record cranial metric measurements with the highest accuracy possible, it was most likely unavoidable to prevent small measurement error in characters for which one (RL, REXN, and TRIN) or both (CBL) points of references were transferred and recorded from paper (refer to section 2.2.4). In addition, exact points of reference were more difficult to determine for some characters, such as orbit and lacrimal length, REXN, and TRIN.

It has been demonstrated that ME of inexperienced observers, is statistically higher as compared to experienced observers when landmarks are repeatedly digitized with a microscribe (Chen et al., 2008). While effort was undertaken to digitize all landmarks as accurately as possible in the present study, it is most likely that small errors have been introduced as a result of observer inexperience, given that the author did not have experience in digitization prior to commencing this study. However, all landmarks were only recorded by the author to reduce inter-observer bias, which consequently could not be evaluated.

4.8.4 Statistical analyses

Statistical analyses were predominantly limited by sample size. Assessing differences in relative skull weight between immature and mature specimens and between individuals from HG and non-HG regions statistically was not possible given that sample size of fully intact immature and non-HG skull specimens was too small. Likewise, growth rates for metric cranial characters could not be calculated due to limited number of specimens with age data available for a given sex. Furthermore, geographic variation analyses of both metric and non-metric characters were compromised by small sample sizes and the male data set had to be

excluded from metric geographic variation analyses. Missing values, due to incomplete skulls and remaining flesh, further reduced sample size for multivariate analyses based on metric data. Small sample size prevented application of the parametric Chi-Square test in the majority of non-metric characters tested independently for differences between regions and computation of the MMD was compromised by small sample size. Finally, several limitations associated with the MMD computation should be considered. Firstly, it has been demonstrated that the value of the MMD is highly dependent on the characters selected (Harris & Sjøvold, 2004). Consequently, MMDs computed based on a different set of non-metric characters are not comparable (Harris & Sjøvold, 2004). The authors further advised that MMD computations should ideally only be based on characters that differ significantly between the sampled populations. In the present study, no non-metric characters individually tested by Chi-Square tests displayed a significant difference between samples and therefore, non significant MMD values were expected.

4.9 Future research

4.9.1 Skull preparation

In the study herein, the horse manure decomposition method was trialled for cleaning common dolphins skulls stored frozen as entire heads at Massey University. This decision was predominantly based on the inexpensive nature of this method and the fact that no maceration unit was available at Massey University. However, for future skull cleaning and preparation, it is recommended to consider exploring alternative methods (e.g. set up of a small maceration unit, which may only comprise one or two large sized aquariums). One of the drawbacks related to the horse manure decomposition method is the fact that the decomposition process is relatively slow (minimum of 8 weeks). In addition, it is a relatively

labour intensive method (e.g. collection and disposal of heavy bags of horse manure) and it is difficult to completely remove fibre from small crevices and foramina after recovering skulls from the manure boxes. Conversely, the cold water maceration method is much faster and skulls do not require additional cleaning afterwards (A. van Helden, pers. comm.). The trial of dermestid beetles is not recommended, given that the beetles do not favour fatty marine mammal flesh (A. van Helden, pers. comm.).

4.9.2 Cranial maturity

The cranial maturity cut-off point for New Zealand *Delphinus* sp. determined herein, based on the suture index computation, should be re-assessed and, if necessary, adjusted, as sample size increases and further age data for skull specimens become available. Of particular interest would be to investigate whether females attain cranial maturity at an earlier age as has been determined (11 years) based on the limited sample size available for the current study.

4.9.3 Bone density analyses

Actual bone density analyses of entire skulls or certain cranial parts (e.g. rostrum) might be of interest to further investigate potential differences between the sexes. In addition, investigations of a possible correlation between toxicity levels and bone density in the New Zealand common dolphin could be of value for conservation efforts regarding this genus. It has been demonstrated that the risk of osteoporosis in humans with urinary cadmium levels exceeding 3 nmol / mmol is twice as high as compared to individuals with lower cadmimum levels (Alfven et al., 2000). A study on heavy metals in different tissues in *Delphinus* sp.

from New Zealand has reported a maximum cadmium concentration of 52 mg/kg kidney wet weight (Stockin et al., 2007). The authors stated that maximum concentration in liver tissue was higher than compared to values reported for Australian specimens.

A further point for future research might be the assessment of variation in bone density with water depth (Gray et al., 2007). The authors found evidence from bone density analyses based on cross sections of ribs of archaeocetes, extant fresh water and marine mammals that '*high bone density is an aquatic specialization that provides static buoyancy control (ballast) for animals living in shallow water, while low bone density is associated with dynamic buoyancy control for animals living in deep water'* (Gray et al., 2007). Concurring, Bell et al., (2002) reported that common dolphin skull specimens from shallower waters appeared more robust.

4.9.4 Tooth condition

Future analyses of the dentition of common dolphins could incorporate teeth from both upper and lower jaws, especially given that tooth condition is now routinely recorded prior to tooth extraction under revised Massey protocols (as of 2010). An increased sample size of mature specimens could enable an assessment of tooth wear between mature males and females. Findings may provide further evidence for potential differences in foraging ecology between the sexes.

4.9.5 Sexual dimorphism

Most importantly, future morphometric studies conducted on the New Zealand common dolphin should determine whether sexual dimorphism exists in cranial measurements related

to the length of the rostrum. In addition, investigations related to potential differences in vocalisation patterns between and among males and females might prove valuable. Futhermore, given the time constraints of the present study, future morphometric work should also be conducted on the coronoid process of the mandible and the tympanoperiotic to determine whether differences exist between the sexes.

4.9.6 Taxonomy

It is highly recommended that RL/ZW ratios and tooth counts continue to be recorded for all skull specimens recovered from New Zealand waters to investigate whether individuals with values in the upper range of the long-beaked form are present within this population.

4.9.7 Geographic variation

Geographic differences between HG and non-HG female specimens based on metric data should be re-assessed given that sample size was extremely small. In addition, a MANOVA would need to be conducted for males, as a small sample size prevented such analysis in the present study. Of particular interest would be to include the cranial measurement WR3/4, which has been determined as a good discriminator between geographic common dolphin populations (Murphy et al., 2006; Westgate, 2007). Owing to small sample size this character had to be omitted from the analyses in the present study.

4.10 Summary

The purpose of this research was to provide further information regarding cranial maturity, sexual dimorphism, taxonomic status, and regional variation of *Delphinus* sp. from New Zealand waters. In addition, precision between two data acquisition methods was assessed. Major findings of the study are summarized below:

1. The frontal-frontal and frontal-interparietal sutures provided the lowest percentage misclassification (10.4% and 10.6%, respectively) for cranial maturity status assessment based on individual cranial sutures.

2. Based on the suture index computation, *Delphinus* sp. from New Zealand waters attain cranial maturity at approximately 11 years of age.

3. Specimens could be allocated to one of three age classes (1 - 3 years, 6 - 10 years, and ≥ 11 years) based on the suture index calculated.

4. All specimens with rostral fusion of < 50% were cranially immature, while all individuals with rostral fusion of ≥ 75% were cranially mature. Neither TBL nor CBL were reliable indicators of cranial maturity in examined specimens.

5. Specimens with ≤ 6.8% of partly worn rostral teeth are most probably between 1 - 3 years of age and cranially immature, while presence of teeth worn down to the gum line provided evidence for cranial maturity.

6. Sexual size dimorphism was detected in TBL and in 22.7% (n = 15) of cranial characters, with males displaying larger sizes. In total, 86.7% (n = 13) of those cranial characters were width measures. The majority (70.0%, n = 7) of characters that could be allocated to a functional complex were related to the feeding apparatus. Sexual dimorphism was recorded for the non-metric cranial character MNC, with males

displaying a higher frequency (82.6, n = 19) of a less advanced maxilla relative to the nuchal crest on the right side of the skull as compared to females (18.2%, n = 6).

7. Morphometric data did not provide evidence for the existence of the long-beaked form in New Zealand waters. RL/ZW ratio, CBL, RL, ZW, and TBL from cranially mature specimens overlapped with values published for *D. delphis* and *D. capensis* inhabiting Californian waters (Heyning & Perrin, 1994). Based on the finding that mean values of the above measurement were higher than mean values published for geographic populations of *D. delphis*, it is suggested that common dolphins from New Zealand waters should currently be regarded as a large form of *D. delphis*.

8. High precision, based on the MAD computation, between callipers and microscribe recordings, was obtained for 69.7 % (n = 23) of cranial characters assessed. This finding indicates that both data acquisition methods were equally valid for the majority of metric characters recorded. Callipers provided higher accuracy for characters in which reference points (1) were not easily detectable by eye (HFM, WFM, LWPA, and lacrimal and orbit lengths); or (2) could not be recorded in a straight line (relative to the midline of the skull) when directly placed on the cranium (CBL, RL, REXN, and TRIN).

4.11 Conservation significance of the findings

The primary objective of the study was to provide further information of relevance for the conservation of New Zealand *Delphinus* sp. As previously noted, current morphometric data do not provide evidence for the presence of the long-beaked form in New Zealand waters or support for population segregation between Hauraki Gulf and non Hauraki Gulf waters.

However, the present study was limited by very small sample size and both aspects warrant, therefore, further investigation. Such continued assessment is of critical importance, given that molecular data have been suggestive of potential population segregation of the common dolphin in New Zealand waters (Stockin et al., in press).

The New Zealand common dolphin is currently listed as 'not threatened' (Baker et al., 2010) with a national species-specific action plan for this genus in New Zealand waters still lacking (Suisted & Neale, 2004). According to the New Zealand Threat Classification, the listing of a native, resident species in any category other than 'data deficient' requires evaluation. As noted by Stockin (2008), the panel argued that the 'not threatened' status was the most appropriate, as common dolphins are frequently sighted in certain regions. However, given that continued scientific uncertainty exists regarding actual abundance and density estimates, taxonomy, and potential population segregation, the listing of *Delphinus* sp. as 'not threatened' is not based on a scientific evaluation (Stockin & Orams 2009; Stockin et al., in press). A potential population decline in the absence of critical baseline data cannot be determined and necessary guidelines for conservation and management not implemented (Stockin, 2008; Bearzi, 2003). This is of particular concern, given that several anthropogenic impacts including by-catch, net entanglement (Stockin et al., 2009), tourism (Stockin et al., 2008b), and pollution (Stockin et al., 2007) have been identified for this species in New Zealand waters. Postmortem analyses of *Delphinus* sp. stranded between 1998 and 2008 in New Zealand water's revealed that 41.2% (n = 35) of individuals, for which cause of death could be determined, were regarded as human induced (Stockin et al., 2009). The authors further reported that 28.2% (n = 24) displayed evidence of net entanglement. Such fishery induced mortality even represented an underestimate, as animals killed in commercial fisheries (n = 115) were not included in the analyses (Stockin & Orams, 2009; Stockin et al., 2009). These findings could be of conservation concern, especially given the fact that fishery

related impacts were among the factors driving the dramatic decline of the Mediterranean common dolphin population, which is listed as 'threatened' since 2003 (Bearzi, 2003; Bearzi et al., 2003; Piroddi et al., 2011). Lack of large-scale studies assessing abundance and distribution prevented detection of a population decline at an early stage (Bearzi et al., 2003). Such a fundamental error should be prevented by all means in New Zealand. One important action would be to relist *Delphinus* sp. as 'data deficient', highlighting the necessity to extend collection of scientific baseline data for adequate threat evaluation (Stockin & Orams, 2009). Currently, 13 cetacean species are regarded as 'data deficient' in New Zealand (Baker et al., 2010). As opposed to the common dolphin, four of those species, the pygmy right whale, *Caperea marginata*, southern bottlenose whale, *Hyperoodon planifrons*, pygmy sperm whale, *Kogia breviceps*, and hourglass dolphin, *Lagenorhynchus cruciger*, do not have any known threats (Baker et al., 2010) or an extensive tourism industry dependent upon them.

Concluding, for the aforementioned reasons, it appears scientifically incorrect and risky from a conservation point of view that the common dolphin is listed as 'not threatened' rather than 'data deficient' in New Zealand waters (Stockin & Orams, 2009). It is, therefore, strongly suggested that *Delphinus* sp. research be extended to enable the sustained collection of further baseline data necessary to evaluate threat status and thereby prevent an undetected potential population decline as a result of cumulative anthropogenic impacts. Adequate threat status assessment of the New Zealand common dolphin is of particular importance, given that (1) morphologically, specimens are of intermediate status between both recognized species; and (2) genetic analyses are suggestive of a putative population segregation within New Zealand waters (Stockin et al., in press

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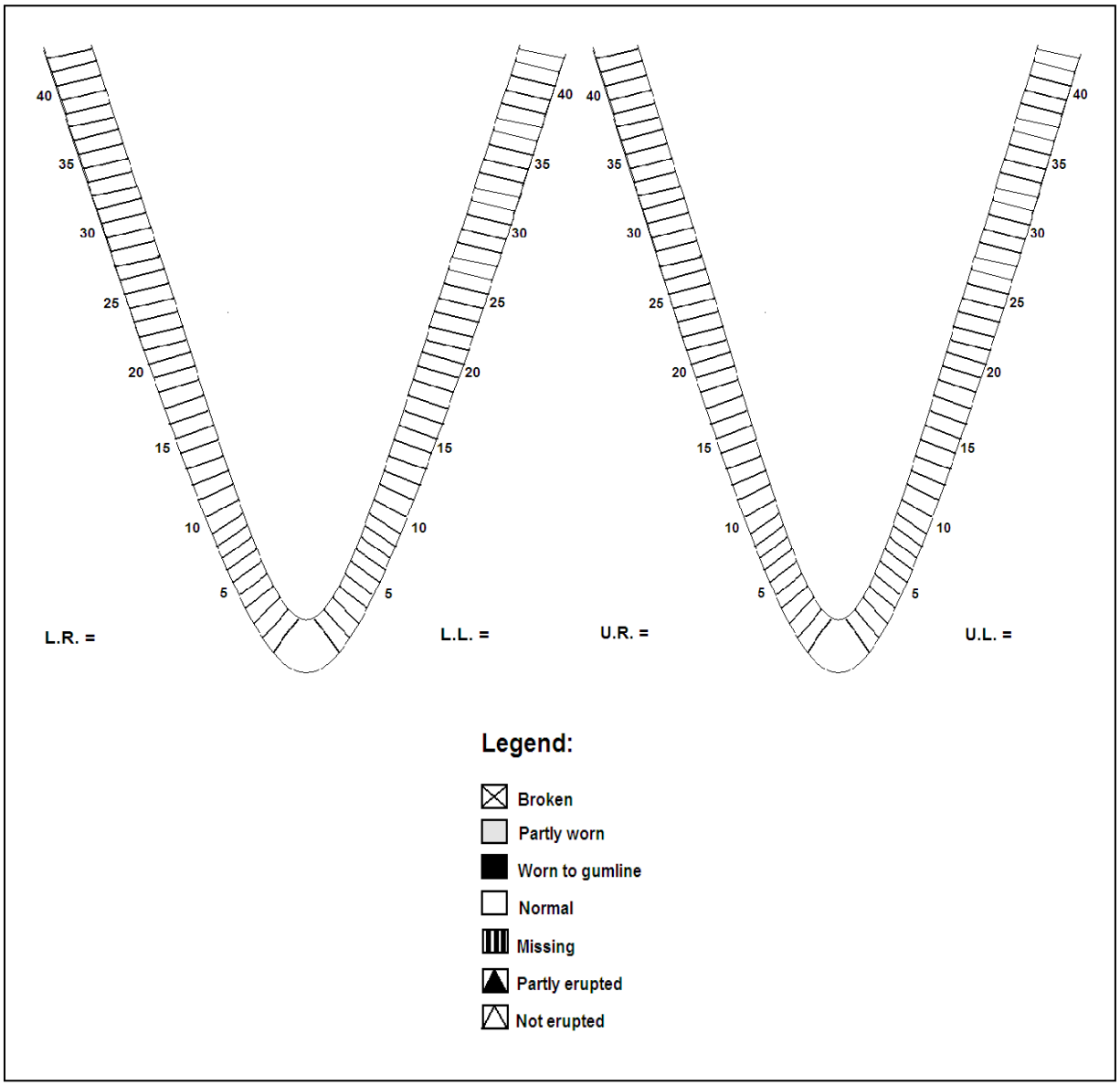
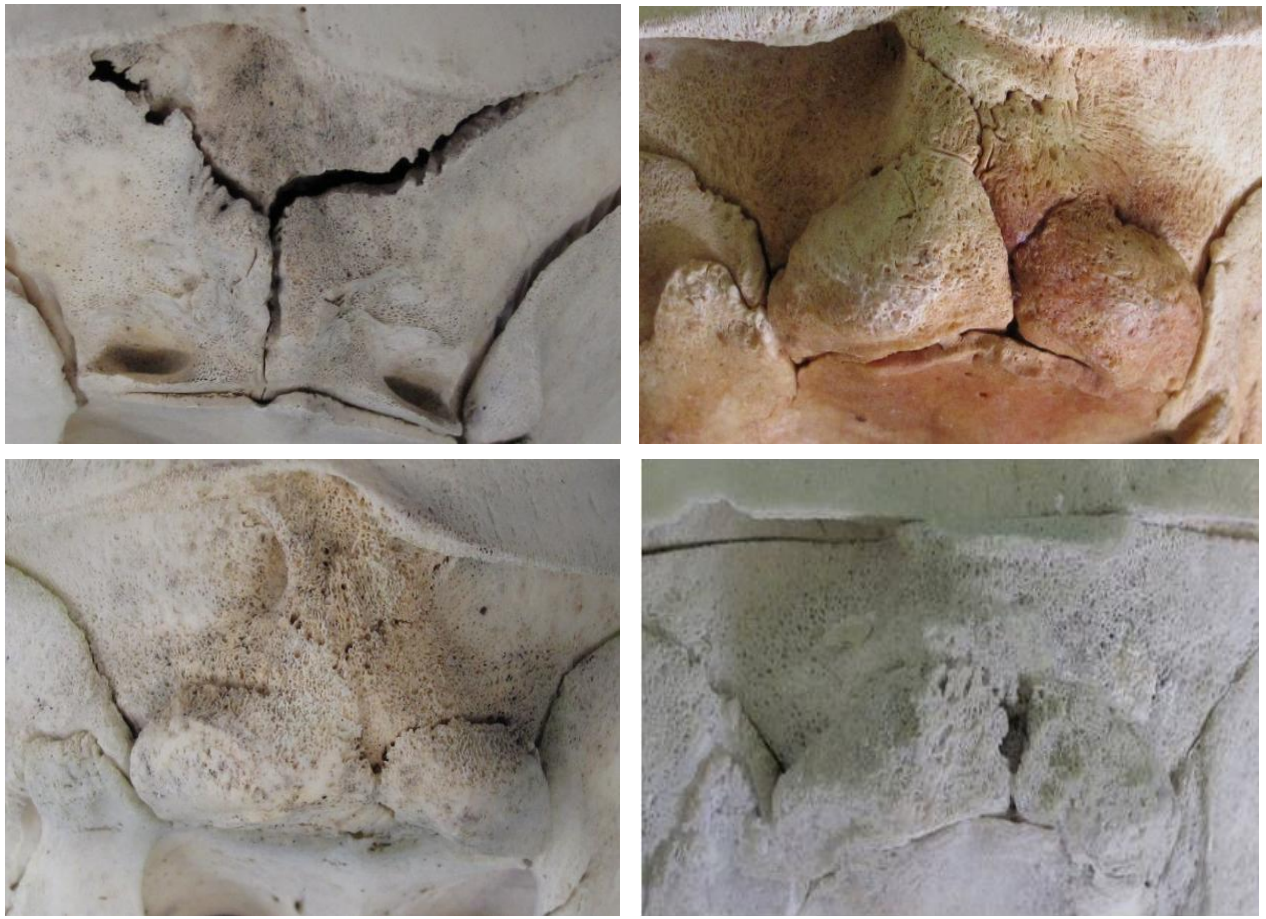
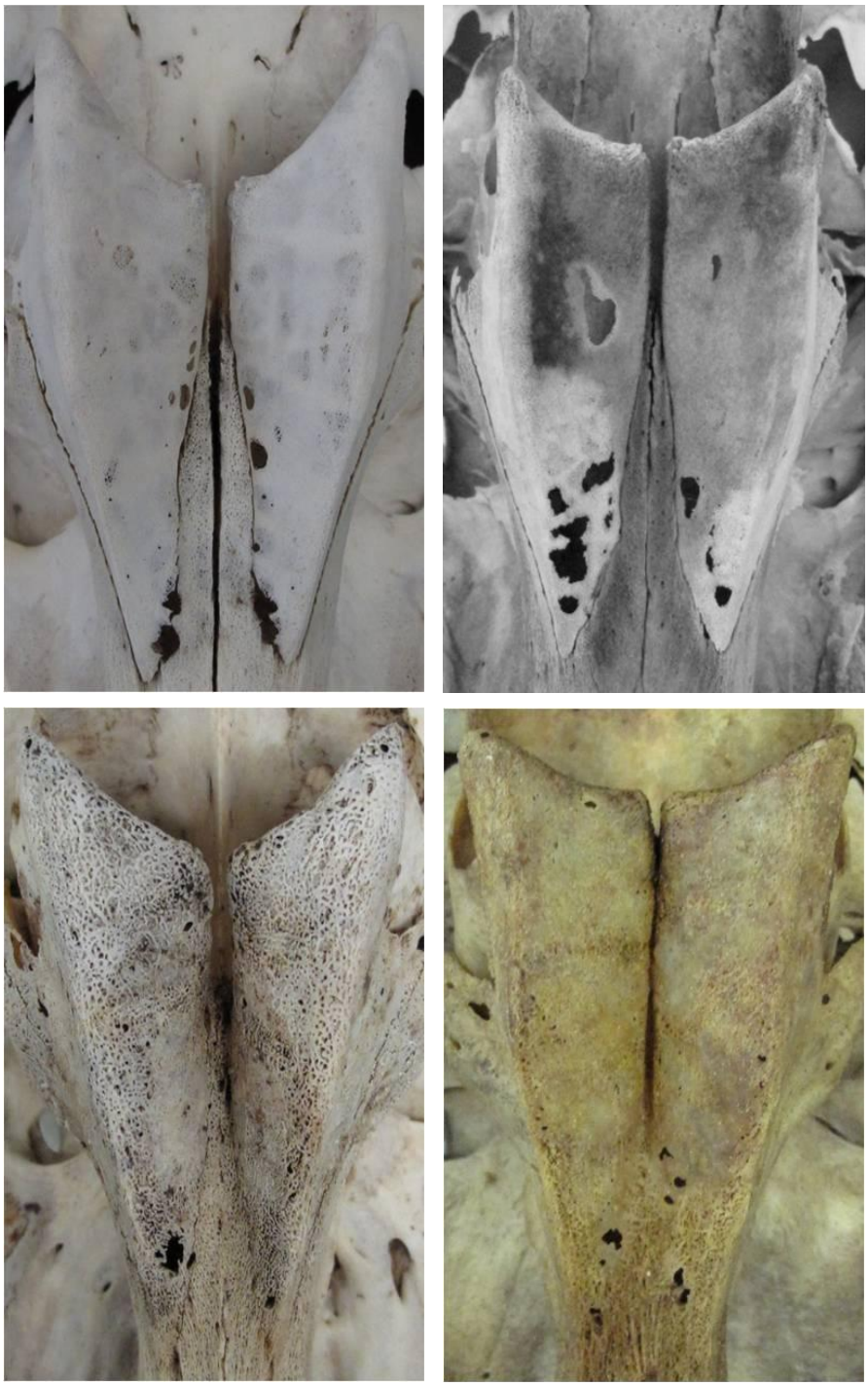
Appendices



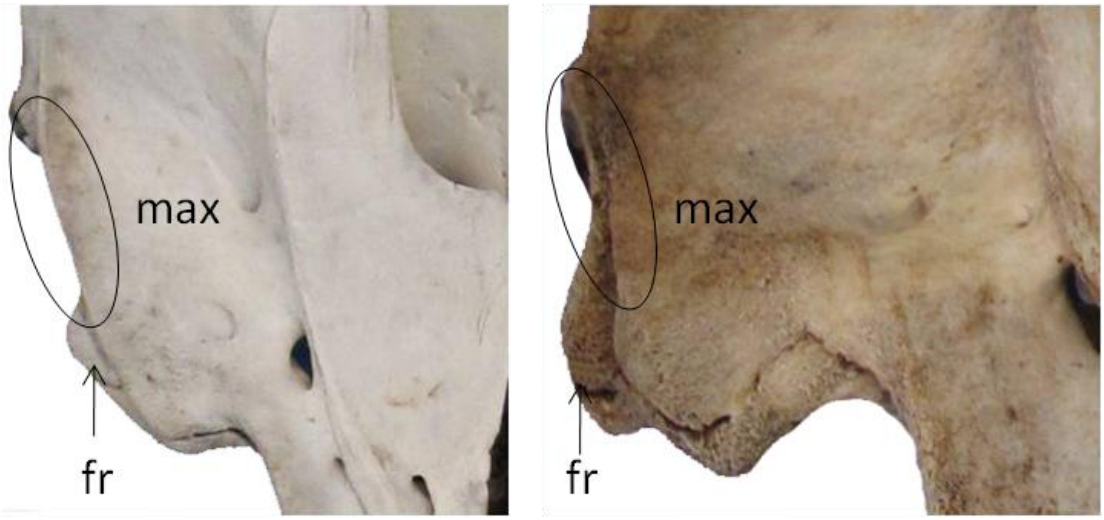
Appendix 1. NZCDP dentition data sheet for recording tooth counts and tooth condition of *Delphinus* sp. skull specimens from New Zealand waters according to seven predefined tooth wear categories. Note: L.R. = lower right jaw; L.L. = lower left jaw; U.R. = upper right jaw; U.L. = upper left jaw.



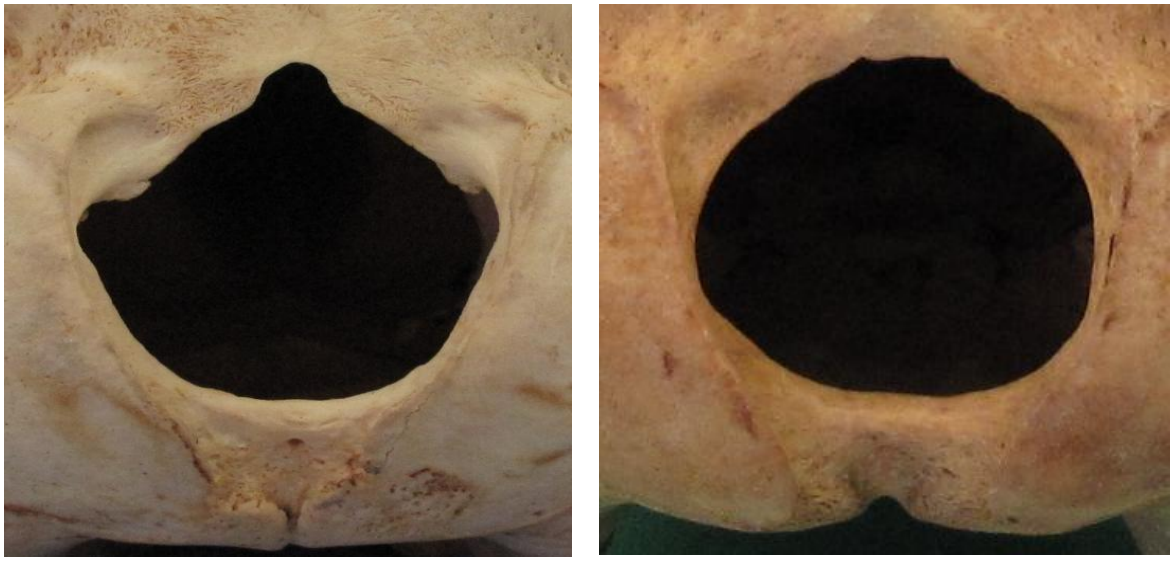
Appendix 2. Examples of the different degrees of suture fusion (0 to 3) of the frontal-frontal and frontal-interparietal sutures of *Delphinus* sp. from New Zealand waters. Note: Top left = stage 0; top right = stage 1; bottom left = stage 2; bottom right = stage 3. Top and bottom right photographs taken with the courtesy of the Museum of New Zealand Te Papa Tongarewa.



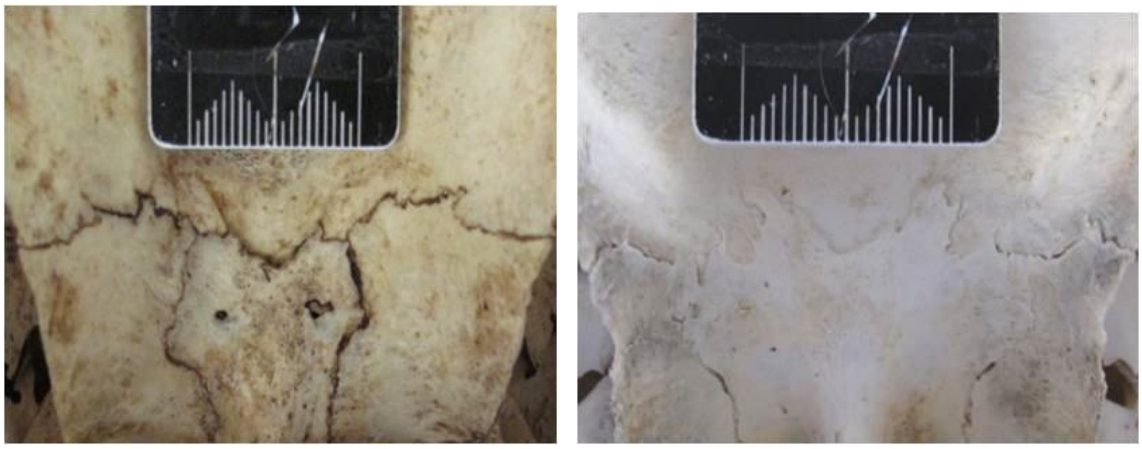
Appendix 3. Examples of the different degrees of suture fusion (0 to 3) of the pterygoid-palatine and palatine-palatine sutures of *Delphinus* sp. from New Zealand waters. Note: Top left = stage 0; top right = stage 1; bottom left = stage 2; bottom right = stage 3.



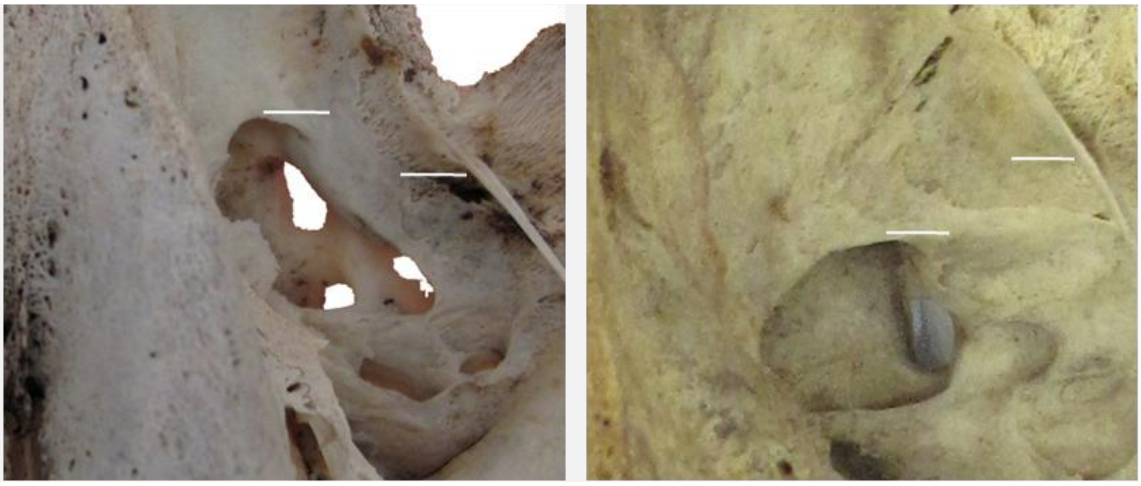
Appendix 4. Examples of the ontogenetic stages 1 (left) and 2 (right) of the non-metric character Nr. 7 (refer to Table 2.7 for definition) recorded on *Delphinus* sp. from New Zealand waters. Note: max = maxilla; fr = frontal. Area of interest indicated by oval.



Appendix 5. Examples of trait expression 1 (left) and 2 (right) of non-metric characters Nr. 11 (shape foramen magnum), 12 (dorsal notch), 14 (width of groove), and 16 (small foramen) (refer to Table 2.7 for definitions) recorded in *Delphinus* sp. skulls from New Zealand waters.

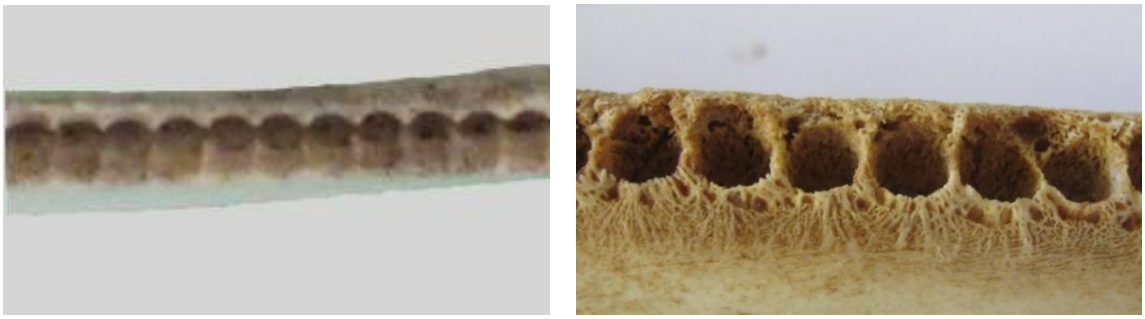


Appendix 6. Examples of trait expression 1 (left) and 2 (right) of non-metric characters Nr.19 (shape of vomer) and 20 (lateral fenestrations in vomer) (refer to Table 2.7 for definitions) recorded on *Delphinus* sp. skulls from New Zealand waters.



Appendix 7. Example of trait expression 1 (left) and 2 (right) of the non-metric character Nr.23 (large ventral foramen) (refer to Table 2.7 for definition) recorded on *Delphinus* sp. skulls from New Zealand waters.

Appendix 8. Example of trait expression 1 (left) and 2 (right) of the non-metric character Nr.24 (orbital fissure / anterior lacerate foramen) (refer to Table 2.7 for definition) recorded on *Delphinus* sp. skulls from New Zealand waters.



Appendix 9. Examples of the developmental stages 1 (left) and 2 (right) of the non-metric character Nr. 25 (interalveolar septa) (refer to Table 2.6 for definition) recorded on *Delphinus* sp. from New Zealand waters.

Appendix 10. Additional information for *Delphinus* sp. skulls from New Zealand waters available for the present study. Note: MU = Massey University, TM = Te Papa (Tongarewa) Museum; Lat. = latitude; Long. = longitude; HG = Hauraki Gulf; non = outside the HG but from within New Zealand waters; TBL = total body length in cm; Sex. mat. = sexually mature; Preg. = pregnant; Y = yes; N = no; Lac. = lactating. Specimens listed alphabetically.

Specimen Code	Stored at	Date	Carcass Location	Lat. (South)	Long. (East)	Region	Sex	TBL	Age	Sex. mat.
KS05-40Dd	MU	31.07.2005	Tawharanui Beach, Warkworth	-36.3667	174.8175	HG	F	184.0	-	-
KS06-04Dd	MU	10.09.2006	Matakatia Bay, Whangaparaoa	-36.6171	174.7671	HG	F	205.5	11	Y
KS07-09Dd	MU	17.08.2007	West Harbour Marina, Hobsonville	-36.8005	174.6343	HG	F	208.0	18	-
KS07-10Dd	MU	21.09.2007	Tryphena, Gt Barrier Island	-36.3003	175.4667	HG	M	167.0	3	-
KS07-12Dd	MU	16.12.2007	Red Beach, Whangaparaoa	-36.6002	174.7005	HG	F	207.0	>12	Y
KS08-03Dd	MU	27.02.2008	Mahia Beach, Wairoa, Hawkes Bay	-39.0833	177.8670	non	F	200.0	>14	Y
KS08-04Dd	MU	15.04.2008	Whangarei Harbour, Whangarei	-35.8172	174.5172	non	F	198.0	>20	-
KS08-06Dd	MU	30.07.2008	Omaha Beach, Whangaparaoa	-36.3335	174.7675	HG	F	-	1.5	-
KS08-09Dd	MU	24.08.2008	Riverhead River, Auckland	-36.7507	174.5843	HG	F	206.0	12	Y
KS08-10Dd	MU	10.09.2008	Pakiri Beach, Warkworth	-36.2504	174.7341	HG	M	212.0	13	Y
KS08-14Dd	MU	16.11.2008	Milford Beach, Auckland	-36.7668	174.7669	HG	F	>200	>20	Y
KS09-09Dd	MU	23.06.2009	Tiritiri Island, Whangaparaoa	-36.6001	174.8835	HG	F	>156.0	2	N
KS09-10Dd	MU	09.07.2009	Motutapu Island, Auckland	-36.7667	174.9174	HG	M	-	8.75	-
KS09-11Dd	MU	14.07.2009	Shakespeare Bay, Whangaparaoa	-36.6004	174.8007	HG	F	169.5	2.75	N
KS09-13Dd	MU	18.07.2009	Algies Bay, Whangaparaoa	-36.4177	174.7340	HG	M	214.0	8	Y
KS09-14Dd	MU	21.07.2009	Kawakawa Bay, Auckland	-36.9342	175.1668	HG	F	212.0	>10	Y
KS09-18Dd	MU	30.07.2009	Sandspit Harbour, Warkworth	-36.3838	174.7173	HG	F	197.0	>10	Y
KS09-19Dd	MU	05.08.2009	Circular Bay, Waiheke Island	-36.7667	175.1176	HG	F	186.0	7	N
KS09-24Dd	MU	14.09.2009	Riverhead River, Auckland	-36.7502	174.5841	HG	M	207.0	12	Y
KS10-01Dd	MU	18.01.2010	Glinks Gully, Dargaville	-36.0675	173.8504	non	F	162.0	-	N
KS10-05Dd	MU	07.03.2010	Northcote Point, Auckland	-36.8010	174.7338	HG	F	194.5	-	Y

Appendix 10 continued.

Specimen	Stored at	Date	Carcass Location	Lat. (South)	Long. (East)	Region	Sex	TBL	Age	Sex. mat.
KS10-06Dd	MU	12.03.2010	Parapara Beach, Golden Bay	-40.717	172.6839	non	F	187.0	-	Y
KS10-07Dd	MU	12.03.2010	Tukurua Pt, Golden Bay	-40.7335	172.7002	non	F	190.0	-	Y
KS10-09Dd	MU	23.03.2010	Bethells Beach, West Coast	-36.884	174.4340	non	F	180.0	-	N
KS10-16Dd	MU	13.05.2010	Ruakaka, Whangarei	-35.9005	174.4507	non	M	230.0	-	Y
KS10-18Dd	MU	01.06.2010	Mahia Beach, Wairoa, Hawkes Bay	-39.0674	177.8674	non	F	182.0	-	-
KS10-26Dd	MU	11.08.2010	At Sea, East of Tiritiri Island	-36.6002	174.9009	HG	M	217.0	-	-
KS10-27Dd	MU	03.09.2010	Aranga, Mauganui Bluff	-35.767	173.5672	non	M	169.5	-	N
KS10-78Dd	MU	11.10.2010	Goldsworth Bay, Warkworth	-36.4336	174.7506	HG	M	201.0	-	-
KS11-08Dd	MU	13.02.2011	Toroa Point, Torbay, Auckland	-36.6841	174.7506	HG	M	176.0	-	-
KS11-10Dd	MU	23.04.2011	Motuihe Island, Auckland	-36.8004	174.9341	HG	M	190.0	-	-
KS11-12Dd	MU	02.05.2011	Te Puru Beach, Coromandel	-37.0342	175.5168	HG	M	171.0	-	N
KS11-14Dd	MU	12.05.2011	Mairangi Beach, Auckland	-36.7336	174.7504	HG	F	195.0	-	Y
KS11-27Dd	MU	16.06.2011	Kariotahi Beach, West Coast, Auckland	-37.2834	174.6503	non	M	133.0	-	N
MM000547	TM	18.06.1932	Chatham Island	-43.9849	176.6354	non	-	-	-	-
MM000981	TM	-	Marsen Point, Northland	-35.8333	174.5000	non	-	-	-	-
MM001092	TM	25.06.1956	Wellington	-41.2899	174.8951	non	M	-	-	-
MM001688	TM	1975	Tauranga	-37.6605	176.2186	non	-	-	-	-
MM001822	TM	10.02.1979	Wellington	-41.1706	174.7442	non	M	-	-	-
MM001850	TM	14.02.1981	Western Cook Strait	-41.3067	174.3352	non	-	-	-	-
MM002220	TM	-	-	-	-	-	-	-	-	-
MM002221	TM	-	-	-	-	-	-	-	-	-
MM002246	TM	-	At Sea, off Napier	-39.5337	177.4896	non	-	-	-	-
MM002436	TM	-	~48-50miles SE of Portland Isl., Hawkes Bay	-39.7325	178.4564	non	-	-	-	-
W08-06Dd	MU	30.06.2008	Wairoa, Hawkes Bay	-39.0176	177.4169	non	F	180.0	-	Y
W08-11Dd	MU	18.08.2008	Paekakariki, Wellington	-40.9836	174.9343	non	F	159.0	1.75	N

Appendix 10 continued.

Specimen Code	Stored at	Date	Carcass Location	Lat. (South)	Long. (East)	Region	Sex	TBL	Age	Sex. mat.
W08-17Dd	MU	30.09.2008	Taranaki, New Plymouth	-39.0500	174.0836	non	F	208.0	29	Y
WB05-26Dd	MU	27.07.2005	Red Beach, Whangaparaoa	-36.6001	174.7005	HG	M	160.0	2	N
WC06-10Dd	MU	07.04.2006	At Sea, off Napier	-39.4837	176.967	non	F	206.0	>31	Y
WC08-16Dd	MU	11.09.2008	At Sea, off Napier	-39.4837	176.9339	non	F	204.5	>33	Y
WC98-30Dd	TM	13.09.1998	At Sea, off Napier	-39.4668	176.9667	non	F	190.0	>11	-
WS00-34Dd	TM	10.10.2000	Kawau Bay, Warkworth	-36.3834	174.7170	HG	F	198.0	11	-
WS04-19Dd	MU	23.08.2004	Opahi Bay, Warkworth	-36.4842	174.7009	HG	M	174.0	6	Y
WS04-28Dd	TM	16.12.2004	Lucas Creek, Auckland	-36.7338	174.6675	HG	F	195.0	-	Y
WS04-29Dd	TM	16.12.2004	Lucas Creek, Auckland	-36.7339	174.6675	HG	F	195.0	-	Y
WS04-34Dd	TM	20.12.2004	Arkles Bay, Whangaparaoa	-36.6338	174.7342	HG	F	189.0	10	-
WS05-06Dd	TM	--.01.2005	Warkworth River, Warkworth	-36.3842	174.6510	HG	M	220.0	10	-
WS05-18Dd	MU	21.12.2004	Coromandel Beach, Coromandel	-36.7502	175.4676	HG	M	213.0	>11	-
WS05-24Dd	MU	08.05.2005	Waitemata Harbour, Auckland	-36.8171	174.7005	HG	F	189.0	8	-
WS05-28Dd	MU	29.03.2005	Himatangi Beach,Palmerston North	-40.3669	175.2173	non	M	>129.0	1	-
WS06-06Dd	MU	14.02.2006	Cape Jackson, Marlborough	-41.0342	174.2671	non	M	182.0	2	N
WS06-09Dd	MU	07.04.2006	Port Taranaki, New Plymouth	-39.0503	174.0671	non	F	212.0	14	Y
WS06-15Dd	MU	01.09.2006	Mahurangi River, Warkworth	-36.4001	174.6671	HG	M	153.0	3	N
WS07-01Dd	MU	30.12.2006	Motuana Bay, Ponui Isl, Auckland	-36.8841	175.1676	HG	F	189.5	9	Y
WS07-02Dd	MU	20.12.2006	Clarks Beach,Manukau Harbour	-37.1334	174.6843	non	M	241.0	>15	Y
WS07-09Dd	MU	12.04.2006	Awatuna, West Coast, South Island	-42.6001	171.0841	non	M	177.0	3.5	N
WS97-17Dd	TM	14.04.1997	Wellington	-41.3008	174.8174	non	F	190.0	-	-

Appendix 11. Potential age range of *Delphinus* sp. skull specimens of unknown age from New Zealand waters based on the suture index. Note: Age classes were differentiated based on the range of the suture index obtained from individuals of known age (listed first); years = years; > = minimum age; parentheses indicate minimum suture index, due missing scores of: [1] = one, [2] = two, or [3] = three sutures as a result of bone damage or remaining flesh. Cranially mature specimens of known age with ≥ 3 missing sutures (n = 4) were not listed.

Specimens	Age class I (1 – 3 yrs)	Suture index 0.0 - 3.0
KS07-10Dd	1	1.0
KS08-06Dd	1.5	0.5
KS09-09Dd	1.75	1.5
KS09-11Dd	2	1.0
W08-11Dd	2	2.0
WB05-26Dd	2	0.5
WS05-28Dd	2.75	0.0
WS06-06Dd	3	1.5
WS06-15Dd	3	3.0
WS07-09Dd	3.5	2.5
KS10-09Dd	-	2.0
KS10-27Dd	-	1.0
KS11-27Dd	-	(0.5)[1]

Specimens	Age class II (6 – 10 yrs)	Suture index 4.0 - 7.5
KS09-13Dd	8	6.5
KS09-19Dd	7	(4.0)[1]
WS04-19Dd	6	5.5
WS04-34Dd	10	7.0
WS05-06Dd	10	4.0
WS05-24Dd	8	5.0
WS07-01Dd	9	(5.5)[2]
KS05-40Dd	-	4.5
KS10-18Dd	-	5.5
KS10-78Dd	-	(4.5)[3]
KS11-08Dd	-	5.5
KS11-12Dd	-	7.5
MM000547	-	7.5
MM001822	-	5.5
W08-06Dd	-	6.0

Appendix 11 continued.

Specimens	Age class III (≥ 11 yrs)	Suture index ≥ 8.0
KS06-04Dd	11	8.5
KS07-09Dd	18	9.0
KS08-04Dd	>20	8.0
KS08-09Dd	12	8.0
KS08-10Dd	13	(8.5)[1]
KS09-14Dd	>10	10
KS09-18Dd	>10	(8.0)[2]
KS09-24Dd	12	8.5
W08-17Dd	29	8.0
WC06-10Dd	>31	9.5
WC08-16Dd	>33	10
WC98-30Dd	>11	9.0
WS00-34Dd	11	9.0
WS05-18Dd	>11	8.5
WS07-02Dd	>15	10
KS10-16Dd	-	8.5
KS10-05Dd	-	9.5
KS10-06Dd	-	8.5
KS10-07Dd	-	8.5
KS10-26Dd	-	(8.5)[1]
KS11-10Dd	-	9.5
KS11-14Dd	-	10
MM000981	-	10
MM001688	-	9.5
MM001850	-	(8.0)[2]
MM001092	-	9.5
MM002220	-	8.5
MM002221	-	8.5
MM002246	-	(8.0)[2]
WS04-28Dd	-	8.5
WS04-29Dd	-	8.0
WS97-17Dd	-	(9.0)[1]

Appendix 12. Cranial maturity status for *Delphinus* sp. skull specimens from New Zealand waters based on the suture index. Sex, age, and preliminary cranial maturity status (Pril.cranial mat.status) are also given. Note: M = male; F = female; Im = cranially immature; Mat = cranially mature; yrs = years; rostral fusion < = fusion < 50% of the length of the rostrum; =: fusion extended to 50% of the length of the rostrum; > = fusion > 50% of the length of the rostrum; N = no; Y = yes; missing sutures = number of sutures that could not be scored due to bone damage / remaining flesh. Parentheses indicate predicted cranial maturity status of individuals for which 1 to 3 sutures could not be scored due to bone damage /remaining flesh. The cranially mature female specimen KS08-14Dd = > 20 years, was excluded from suture score calculations, because 6 sutures could not be scored due to bone damage.

Code	Sex	Pril.cranial mat.status	Age (yrs)	Rostral fusion	Missing sutures	Suture index	Cranially mature
KS05-40Dd	F	Im	-	=	0	**4.5**	N
KS06-04Dd	F	Mat	11	>	0	**8.5**	Y
KS07-09Dd	F	Mat	18	=	0	**9.0**	Y
KS07-10Dd	M	Im	3	<	0	**1.0**	N
KS07-12Dd	F	Mat	>12	>	3	**7.5**	(Y)
KS08-03Dd	F	Mat	>14	>	3	**5.5**	(Y)
KS08-04Dd	F	Mat	>20	>	0	**8.0**	Y
KS08-06Dd	F	Im	1.5	<	0	**0.5**	N
KS08-09Dd	F	Mat	12	=	0	**8.0**	Y
KS08-10Dd	M	Mat	13	>	1	**8.5**	Y
KS09-09Dd	F	Im	2	<	0	**1.5**	N
KS09-10Dd	M	-	8.75	>	1	**7.0**	N
KS09-11Dd	F	Im	2.75	<	0	**1.0**	N
KS09-13Dd	M	-	8	=	0	**6.5**	N
KS09-14Dd	F	Mat	>10	>	0	**10**	Y
KS09-18Dd	F	Mat	>10	>	2	**8.0**	Y
KS09-19Dd	F	Im	7	=	1	**4.0**	N
KS09-24Dd	M	Mat	12	>	0	**8.5**	Y
KS10-01Dd	F	Im	-	<	0	**3.5**	N
KS10-05Dd	F	Mat	-	>	0	**9.5**	Y
KS10-06Dd	F	Mat	-	>	0	**8.5**	Y
KS10-07Dd	F	Mat	-	>	0	**8.0**	Y
KS10-09Dd	F	Im	-	=	0	**2.0**	N
KS10-16Dd	M	Mat	-	>	0	**8.5**	Y
KS10-18Dd	F	-	-	>	0	**5.5**	N
KS10-26Dd	M	Mat	-	=	1	**8.5**	Y
KS10-27Dd	M	Im	-	<	0	**1.0**	N
KS10-78Dd	M	Mat	-	>	3	**4.5**	(N)

Appendix 12 continued.

Code	Sex	Pril.cranial mat.status	Age (yrs)	Rostral fusion	Missing sutures	Suture index	Cranially mature
KS11-08Dd	M	Im	-	=	0	**5.5**	N
KS11-10Dd	M	Im	-	=	0	**9.5**	Y
KS11-12Dd	M	Im	-	<	0	**7.0**	N
KS11-14Dd	F	Mat	-	>	0	**10**	Y
KS11-27Dd	M	Im	-	<	1	**0.5**	N
MM000547	-	-	-	=	0	**7.5**	N
MM000981	-	-	-	>	0	**10**	Y
MM001092	M	Mat	-	>	0	**9.5**	Y
MM001688	-	-	-	>	0	**9.5**	Y
MM001822	M	-	-	<	0	**5.5**	N
MM001850	-	-	-	=	2	**8.0**	(Y)
MM002220	-	-	-	=	0	**8.5**	Y
MM002221	-	-	-	>	0	**8.5**	Y
MM002246	-	-	-	>	2	**8.0**	(Y)
MM002436	-	-	-	-	1	**6.0**	N
W08-06Dd	F	Im	-	=	0	**6.0**	N
W08-11Dd	F	Im	1.75	<	0	**2.0**	N
W08-17Dd	F	Mat	29	>	0	**8.0**	Y
WB05-26Dd	M	Im	2	<	0	**0.5**	N
WC06-10Dd	F	Mat	>31	>	0	**9.5**	Y
WC08-16Dd	F	Mat	>33	>	0	**10**	Y
WC98-30Dd	F	Mat	>11	>	0	**9.0**	Y
WS00-34Dd	F	Mat	11	=	0	**9.0**	Y
WS04-19Dd	M	Im	6	<	0	**5.5**	N
WS04-28Dd	F	Mat	-	=	0	**8.5**	Y
WS04-29Dd	F	Mat	-	>	0	**8.0**	Y
WS04-34Dd	F	Mat	10	>	0	**7.0**	N
WS05-06Dd	M	-	10	=	0	**4.0**	N
WS05-18Dd	M	Mat	>11	>	0	**8.0**	Y
WS05-24Dd	F	Im	8	=	0	**5.0**	N
WS05-28Dd	M	Im	1	<	0	**0.0**	N
WS06-06Dd	M	Im	2	<	0	**1.5**	N
WS06-09Dd	F	Mat	14	>	3	**6.5**	(Y)
WS06-15Dd	M	Im	3	<	0	**3.0**	N
WS07-01Dd	F	Mat	9	>	2	**5.5**	N
WS07-02Dd	M	Mat	>15	>	0	**10**	Y
WS07-09Dd	M	Im	3.5	<	0	**2.5**	N
WS97-17Dd	F	Im	-	=	1	**9.0**	Y

Appendix 13. Mean ± SD, range and sample size of condylobasal length (CBL) and rostrum length (RL) for *Delphinus* sp. skull specimens from New Zealand waters by sex and maturity status separately for each rostrum rating category. Note: Im = cranially immature; Mat = cranially mature; n = sample size; n/a = not applicable. For description of rating categories refer to section 2.2.4.

CBL	Rating category 1			Rating category 2			Rating category 3			Rating category 1 and 2		
Sex	**Mean ± SD**	**Range**	**n**	**Mean ± SD**	**Range**	**n**	**Mean ± SD**	**Range**	**n**	**Mean ± SD**	**Range**	**n**
Males (Im)	430.5 ± 43.5	345.7 - 461.2	7	n/a	301.1 - 445.4	2	418.6 ± 22.6	399.4 - 454.2	5	417.4 ± 57.9	301.1 - 461.2	9
Females (Im)	445.3 ± 9.4	437.7 - 455.7	3	n/a	424.4 - 430.1	2	394.3 ± 34.4	349.8 - 433.7	4	438.1 ± 12.1	424.4 - 455.7	5
Males (Mat)	469.2 ± 24.4	446.4 - 494.9	3	n/a	449.7 - 460.6	2	n/a	438.6	1	462.2 ± 17.6	446.4 - 494.9	5
Females (Mat)	444.5 ± 16.3	426.5 - 467.1	6	448.3 ± 19.4	422.7 - 468.5	6	432.6 ± 19.4	417.3 - 466.0	5	446.4 ± 17.2	422.7 - 468.5	12

RL	Rating category 1			Rating category 2			Rating category 3			Rating category 1 and 2		
Sex	**Mean ± SD**	**Range**	**n**	**Mean ± SD**	**Range**	**n**	**Mean ± SD**	**Range**	**n**	**Mean ± SD**	**Range**	**n**
Males (Im)	268.5 ± 32.6	203.7 - 292.6	7	n/a	165.5 - 284.5	2	255.4 ± 19.8	237.7 - 284.5	5	285.9 ± 45.3	165.5 - 292.6	9
Females (Im)	277.0 ± 5.9	271.2 - 283.0	3	n/a	265.8 - 267.5	2	240.5 ± 28.9	203.8 - 274.3	4	272.8 ± 7.1	265.8 - 283.0	5
Males (Mat)	296.7 ± 21.9	281.2 - 321.8	3	n/a	276.1 - 291.6	2	n/a	274.2	1	291.6 ± 17.9	276.1 - 321.8	5
Females (Mat)	277.5 ± 13.9	261.3 - 294.5	7	279.1 ± 14.7	265.4 - 298.1	6	269. ± 14.4	261.5 - 294.6	5	278.3 ± 13.8	261.3 - 298.1	13

Appendix 14. Congenital beak deformity documented in the cranially mature New Zealand female *Delphinus* sp. specimen KS09-18Dd, named Wrybill (K.A. Stockin, pers. comm.) in external view (top, photograph by K.A. Stockin) and skeletal (bottom) view.

Appendix 15. Median, interquartile range (I.Q.R), range and sample size (n) for condylobasal length (CBL) and rostrum length (RL) of *Delphinus* sp. skull specimens from New Zealand waters separately for maturity status (Im = cranially immature; Mat = cranially mature) and sex.

CBL	Median (I.Q.R)	Range	n
Males (Im)	445.4 (397.7 - 455.8)	301.1 - 461.2	9
Males (Mat)	460.6 (449.7 - 466.2)	446.4 - 494.9	5
Females (Im)	437.7 (430.1 - 442.5)	424.4 - 455.7	5
Females (Mat)	444.1 (432.3 - 463.1)	422.7 - 468.5	12

RL	Median (I.Q.R)	Range	n
Males (Im)	283.2 (245.5 - 285.8)	165.5 - 292.6	9
Males (Mat)	287.2 (281.2 - 291.6)	276.1 - 321.8	5
Females (Im)	271.2 (267.5 - 276.6)	265.8 - 283.0	5
Females (Mat)	280.8 (265.8 - 291.4)	261.3 - 298.1	13

Appendix 16. Sex, maturity status, total body length (TBL), age, skull weight, skull weight to skull length (SW/CBL^3) ratio and skull length to skull width (SW/ZW^3) ratio for each *Delphinus* sp. skull specimen from New Zealand waters included for skull weight analyses. Note: M = male; F = female; C = captive; Im = cranially immature; Mat = cranially mature; yrs = years; SW = skull weight; CBL = condylobasal length; ZW = zygomatic width. Specimens listed alphabetically.

Code	Sex	Status	TBL (cm)	Age (yrs)	Skull weight (g)	$SW/CBL^3 x10^{-6}$ ratio	$SW/ZW^3 x10^{-5}$ ratio
KS07-09Dd	F	Mat	208.0	18	505.0	6.26	8.17
KS07-12Dd	F	Mat	207.0	>12	626.0	6.92	9.26
KS08-09Dd	F	Mat	206.0	12	518.0	6.41	7.91
KS08-10Dd	M	Mat	212.0	13	669.0	7.52	10.70
KS08-14Dd	F	Mat	>200.0	>20	567.0	5.56	8.59
KS09-10Dd	M	Im	-	8.75	693.0	7.85	9.57
KS09-13Dd	M	Im	214.0	8	797.0	8.18	11.63
KS09-14Dd	F	Mat	212.0	>10	639.0	6.36	8.13
KS09-18Dd	F	Mat	197.0	>10	561.0	-	7.75
KS10-06Dd	F	Mat	187.0	-	495.0	6.56	7.92
KS10-16Dd	M	Mat	230.0	-	772.0	7.62	9.96
KS10-18Dd	F	Im	182.0	-	431.0	5.64	7.57
KS11-14Dd	F	Mat	195.0	-	508.0	6.55	8.40
MM001688	-	Mat	-	-	783.0	8.11	10.37
MM001850	-	Im	-	-	685.0	7.99	10.01
MM002221	-	Mat	-	-	851.0	-	9.69
W08-17Dd	F	Mat	208.0	29	586.0	5.70	8.44
WC06-10Dd	F(C)	Mat (C)	206.0	>31	423.0	4.99	7.47
WC08-16Dd	F(C)	Mat (C)	204.5	>33	426.0	4.42	5.32
WS00-34Dd	F	Mat	198.0	11	476.0	-	8.85
WS04-29Dd	F	Mat	195.0	-	460.0	-	8.16
WS05-24Dd	F	Im	189.0	8	495.0	5.23	8.00
WS07-02Dd	M	Mat	241.0	>15	911.0	7.52	10.29

Appendix 17. Mean ± SD, range and sample size for total body length (TBL), and for cranial characters recorded on cranially mature male and female *Delphinus* sp. skull specimens from New Zealand waters. Unpaired t-test and ANCOVA results (with condylobasal length (CBL) and length of right mandible (LRM) as covariates) from comparisons between males and females are also shown. Note: values in bold = < 0.05; **= < 0.01; na= not analyzed; df = degrees of freedom; p = p-value. Welch correction was applied to characters in italics. For character abbreviations refer to section 2.2.4.

	Male *Delphinus* sp.			Female *Delphinus* sp.			Unpaired t-test			ANCOVA	
Character	Mean ± SD (mm)	Range (mm)	n	Mean ± SD (mm)	Range (mm)	n	t	df	p	CBL p	LRM p
TBL(cm)	215.7 ± 16.3	190.0 - 241.0	7	199.9 ± 7.7	187.0 - 212.0	21	3.200	27	**	na	na
CBL	463.6 ± 19.3	446.4 - 494.9	5	446.4 ± 17.2	422.7 - 468.5	11	1.815	15	0.090	na	na
RL	291.6 ± 17.9	276.1 - 321.8	5	279.0 ± 13.3	261.3 - 298.1	14	1.660	17	0.115	0.621	0.997
ANOC(R)	176.5 ± 5.1	171.6 - 185.4	8	173.9 ± 5.0	163.0 - 185.5	20	1.257	26	0.220	0.880	0.427
ANOC(L)	178.8 ± 5.1	172.1 - 187.1	8	174.9 ± 5.3	162.7 - 186.0	19	1.747	25	0.093	0.522	0.228
REXN	344.8 ± 19.8	327.0 - 376.9	5	331.5 ± 16.0	309.2 - 351.3	13	1.487	16	0.156	0.292	0.520
ANFPR	33.6 ± 8.4	24.3 - 47.2	8	29.8 ± 6.7	18.7 - 52.9	22	1.287	28	0.209	0.371	0.557
LFPR	125.93 ± 7.2	117.5 - 139.6	7	115.3 ± 14.1	92.0 - 145.1	18	1.884	23	0.072	0.919	0.141
WRB	98.0 ± 6.5	91.7 - 109.6	8	92.0 ± 3.4	87.2 - 101.3	21	*1.940*	*8*	**0.016**	0.621	0.087
WPRB	51.7 ± 3.5	47.1 - 56.4	8	49.6 ± 2.3	45.2 - 54.8	20	1.853	26	0.075	0.766	0.307
WTB	23.9 ± 2.8	18.6 - 27.1	8	23.9 ± 3.9	14.0 - 29.0	19	0.001	25	0.999	0.179	0.217
WT30	11.0 ± 1.8	8.8 - 13.5	8	9.9 ± 2.1	7.1 - 14.6	21	1.356	27	0.186	0.694	0.802
WR60	64.8 ± 2.9	60.7 - 69.1	8	61.0 ± 3.5	55.4 - 69.0	23	2.655	28	**0.013**	0.239	0.253
WR1/2	53.8 ± 5.1	43.7 - 57.0	6	53.7 ± 4.1	46.8 - 60.7	17	1.057	21	0.303	0.565	0.501
WR3/4	45.0 ± 3.8	38.8 - 48.9	5	39.9 ± 3.3	35.2 - 46.7	14	2.874	17	**	0.135	0.078
LSOW	169.6 ± 8.4	158.8 - 180.4	8	161.7 ± 6.2	153.4 - 174.9	22	2.809	28	**	0.181	0.359
GWPR	72.1 ± 2.6	69.0 - 77.0	8	71.4 ± 3.0	66.3 - 77.8	21	0.555	27	0.584	0.679	0.824
GWRPR	34.6 ± 2.9	29.3 - 39.3	8	32.1 ± 5.0	20.7 - 39.8	22	1.337	28	0.192	0.194	0.368
GWLPR	25.7 ± 1.2	20.0 - 29.3	7	23.0 ± 4.0	17.3 - 31.4	21	1.590	26	0.124	0.914	0.683
GWM	183.9 ± 7.3	171.3 - 192.5	7	175.3 ± 6.7	165.5 - 192.5	21	2.878	26	**	0.066	0.285

Appendix 17 continued.

Character	Male common dolphins			Female common dolphins			Unpaired t-test			ANCOVA	
	Mean ± SD (mm)	Range (mm)	n	Mean ± SD (mm)	Range (mm)	n	t	df	p	CBL p	LRM p
GWRM	69.9 ± 5.0	65.0 - 78.5	7	65.6 ± 3.8	61.0 - 78.8	22	2.430	27	**0.022**	0.144	0.243
GWLM	77.8 ± 3.2	73.8 - 82.4	8	74.2 ± 4.3	67.8 - 87.6	21	2.184	27	**0.038**	0.106	0.805
GWEN	46.5 ± 2.2	42.8 - 49.9	8	45.8 ± 2.2	42.0 - 49.6	22	0.791	28	0.435	0.678	0.335
GLLPTF	70.9 ± 6.8	63.6 - 83.5	8	70.2 ± 3.3	63.0 - 77.7	20	*0.287*	*8*	*0.782*	na	na
GLRPTF	72.3 ± 6.2	62.8 - 81.1	8	70.8 ± 2.8	65.8 - 76.9	21	*0.663*	*8*	*0.526*	na	na
HLPTF	54.5 ± 4.1	48.8 - 60.1	8	52.6 ± 4.6	41.2 - 59.1	20	1.028	26	0.314	0.786	0.423
HRPTF	55.5 ± 3.2	51.1 - 60.0	8	53.8 ± 5.2	43.9 - 62.2	21	0.872	27	0.391	0.526	0.569
WLPTF	59.9 ± 4.7	52.0 - 66.3	8	58.2 ± 4.9	43.3 - 63.8	21	0.835	27	0.411	0.971	0.403
WRPTF	63.7 ± 5.0	54.0 - 70.3	8	60.8 ± 5.1	42.4 - 66.3	21	1.363	27	0.184	0.459	0.225
LOL	51.6 ± 2.2	48.6 - 54.5	7	51.4 ± 2.1	47.1 - 56.6	20	0.229	25	0.776	0.925	0.477
ROL	52.3 ± 2.9	47.8 - 55.9	8	51.2 ± 2.0	48.9 - 56.3	17	1.183	23	0.249	0.880	0.692
MaxDLTF	41.3 ± 1.6	39.9 - 44.6	8	39.2 ± 2.6	34.7 - 44.0	21	2.520	27	**0.047**	0.157	0.379
MaxDRTF	41.5 ± 1.3	39.9 - 43.5	8	39.2 ± 2.4	34.6 - 44.8	21	2.087	27	**0.018**	0.112	0.242
LLUTR	246.4 ± 14.5	233.0 - 270.3	5	238.6 ± 10.3	225.7 - 256.1	13	1.291	16	0.125	0.128	0.277
LRUTR	246.6 ± 13.4	236.3 - 269.5	5	239.3 ± 10.9	255.8 - 257.1	13	1.207	16	0.245	0.098	0.300
TRIN	338.1 ± 18.7	322.3 - 369.7	5	324.7 ± 14.9	304.3 - 347.0	13	1.600	16	0.129	0.125	0.193
GLLPT	77.3 ± 3.7	72.0 - 81.2	6	75.9 ± 5.1	67.4 - 83.2	19	0.605	23	0.551	0.465	0.115
GLRPT	77.0 ± 4.1	72.2 - 83.3	6	75.7 ± 4.6	66.8 - 83.3	19	0.656	23	0.519	0.528	0.099
WPT	48.4 ± 4.0	43.0 - 55.9	7	47.5 ± 2.6	42.8 - 52.9	21	0.733	26	0.467	0.497	0.809
GWIN	54.5 ± 1.8	52.3 - 56.5	8	51.5 ± 2.6	46.2 - 55.5	22	1.854	28	0.074	0.460	0.052
PROW	173.4 ± 7.3	162.8 - 183.1	8	165.3 ± 5.7	157.4 - 177.5	20	3.186	26	**	0.422	0.216
POOW	194.7 ± 7.9	184.3 - 206.6	8	187.0 ± 6.7	177.8 - 201.8	20	2.415	26	**0.023**	0.664	0.366
ZW	192.2 ± 9.5	181.0 - 206.9	7	185.3 ± 7.5	175.2 - 200.1	21	1.973	26	0.059	0.601	0.478

Appendix 17 continued.

Character	Male *Delphinus* sp. Mean ± SD (mm)	Range (mm)	n	Female *Delphinus* sp. Mean ± SD (mm)	Range (mm)	n	Unpaired t-test t	df	p	ANCOVA CBL p	LRM p
WBOC	90.9 ± 7.1	81.4 - 102.9	8	89.5 ± 4.3	80.4 - 99.1	21	0.645	27	0.523	0.141	0.687
WBOCS	54.9 ± 3.8	49.6 - 60.9	8	51.7 ± 3.5	44.8 - 57.5	20	2.109	26	**0.045**	0.649	0.186
LLSQ	52.6 ± 2.0	49.6 - 55.3	8	50.1 ± 3.1	46.3 - 58.6	21	2.228	27	**0.034**	0.980	0.936
LRSQ	52.4 ± 2.6	49.8 - 56.3	7	50.1 ± 3.0	46.2 - 58.3	19	1.742	24	0.094	0.549	0.839
LLLAC	45.6 ± 3.1	41.9 - 50.4	6	43.6 ± 3.0	35.8 - 48.2	19	1.247	23	0.167	0.484	0.633
LRLAC	42.5 ± 4.2	35.2 - 48.6	8	41.2 ± 2.9	33.1 - 45.4	21	1.014	27	0.320	0.813	0.711
WPA	160.8 ± 3.5	156.8 - 167.7	8	156.1 ± 7.5	144.8 - 173.6	19	1.685	25	0.105	0.161	0.855
GWPA	153.1 ± 5.9	147.6 - 164.4	8	147.8 ± 4.6	140.4 - 156.6	20	2.572	26	**0.016**	0.161	0.071
LWPA	145.9 ± 5.0	137.4 - 150.7	7	140.0 ± 7.0	128.6 - 152.6	19	2.171	24	0.053	0.078	0.223
GWEX	165.5 ± 10.2	152.9 - 181.4	8	156.7 ± 6.2	141.0 - 169.4	21	1.972	27	0.059	0.502	0.545
WEXR	58.9 ± 1.5	54.0 - 68.2	8	58.2 ± 4.4	51.4 - 68.0	20	0.370	26	0.714	0.422	0.218
WEXL	59.4 ± 3.0	53.3 - 63.8	8	57.0 ± 4.1	48.4 - 64.0	21	1.243	26	0.225	0.496	0.792
HBC	130.2 ± 4.5	124.4 - 136.3	8	128.1 ± 3.4	119.5 - 135.0	19	1.344	25	0.191	0.647	0.980
HFCFM	90.6 ± 3.1	85.9 - 95.2	8	91.9 ± 5.1	84.1 - 100.4	19	0.743	26	0.464	0.104	0.098
WFM	36.4 ± 1.8	32.8 - 38.5	8	35.9 ± 2.2	32.9 - 41.4	19	0.517	25	0.610	0.422	0.119
HFM	34.9 ± 3.6	27.4 - 38.9	8	33.3 ± 3.5	28.3 - 39.7	19	1.124	25	0.272	0.171	0.096
LLM	397.8 ± 22.3	375.5 - 431.5	5	381.3 ± 16.4	361.6 - 412.1	17	1.821	20	0.084	0.898	0.979
HLM	67.8 ± 3.8	63.5 - 74.6	7	65.1 ± 2.4	61.3 - 69.9	21	2.2278	26	**0.031**	0.900	0.979
LMF	112.3 ± 4.4	107.7 - 120.3	8	108.7 ± 6.8	99.7 - 122.0	21	1.357	27	0.186	0.490	0.784
LLLTR	239.0 ± 9.8	228.9 - 256.7	6	231.4 ± 13.3	213.5 - 260.3	18	1.092	21	0.287	0.092	0.093
LRM	397.9 ± 22.3	375.3 - 432.5	5	380.6 ± 16.4	358.6 - 412.4	18	1.939	21	0.066	0.816	na
HRM	68.3 ± 4.4	64.2 - 75.9	7	65.8 ± 2.3	62.0 - 70.1	20	*1.473*	*7*	*0.184*	na	na
RMF	112.5 ± 4.6	106.5 - 120.0	8	108.8 ± 7.0	98.8 - 123.6	21	1.355	27	0.187	0.428	0.523
LLRTR	238.1 ± 10.3	227.1 - 257.0	7	232.6 ± 12.6	214.0 - 258.6	19	0.881	22	0.388	0.063	0.065

Appendix 18. Trait expression frequency of non-metric cranial characters in male and female *Delphinus* sp. from New Zealand waters for characters independent of maturity status (cranially immature and mature specimens pooled). Note: (L) and (R) = left and right side of the skull, respectively; ant = anterior; post = posterior; blw = below; abv = above; pres = present; abs = absent; piri = piriform; umb = umbrella shaped; squ = square shaped; nar = narrow; n = sample size; numbers separated by semicolon = first number = number of individuals with first trait expression and second number = number of individuals with alternative trait expression. χ^2 = Chi-Square statistic; df = degrees of freedom; FE = Fisher's Exact test, which was used when sample size in any cell was < 5; p = p-value; * = < 0.001. For character abbreviations refer to section 2.2.6.**

Non-metric character	Trait expression	Total n	n per trait expression		Chi-Square χ^2 (d f= 1)	p
			Male	Female		
PMIOF	ant; post	52	17; 5	21; 9	0.072	0.789
PLIOF	ant; post	52	1; 20	1; 30	FE	1
DPM	blw; abv	53	15; 3	29; 6	FE	1
CPPT	pre; abs	57	0; 23	1; 33	FE	1
HV	blw; abv	54	4; 19	8; 23	FE	0.525
CPN (L)	pre; abs	58	1; 23	1; 33	FE	1
CPN (R)	pre; abs	53	10; 11	21; 11	1.033	0.310
EAPLPR	ant; post	45	16; 2	21; 6	FE	0.445
SFM	piri; oval	55	20; 4	28; 3	FE	0.686
O	pre; abs	54	10; 14	10; 20	0.120	0.729
NFOCEX (L)	abs; ≥ 1	57	19; 5	32; 1	FE	0.073
SB	umb; squ	45	15; 2	28; 0	FE	0.137
PPEV	post; ant	55	15; 6	21; 13	0.194	0.660
VS	nar; wide	50	8; 14	17; 11	2.029	0.154
LFV (L)	pre; abs	56	30; 3	25; 8	FE	0.185
PIOSF	post; ant	54	18; 4	25; 7	FE	1
PAELVF (L)	ant; post	50	1; 19	3; 27	FE	0.641
MNC (R)	ant; at/post	56	19; 4	6; 27	FE	***

Appendix 19. List of *Delphinus* sp. skull specimens from New Zealand waters, for which rostrum length to zygomatic width (RL/ZW) ratios in the range of the long-beaked common dolphin have been obtained. Note: M = male; F = female; Im = cranially immature; Mat = cranially mature; HG = Hauraki Gulf; non = non-HG regions; yrs = years; TBL = total body length; suture index ≥ 8 = cranial maturity; * = specimen with rostrum category 3 (refer to section 2.2.4). Only suture indices with no missing values for individual sutures are listed. Specimens listed alphabetically.

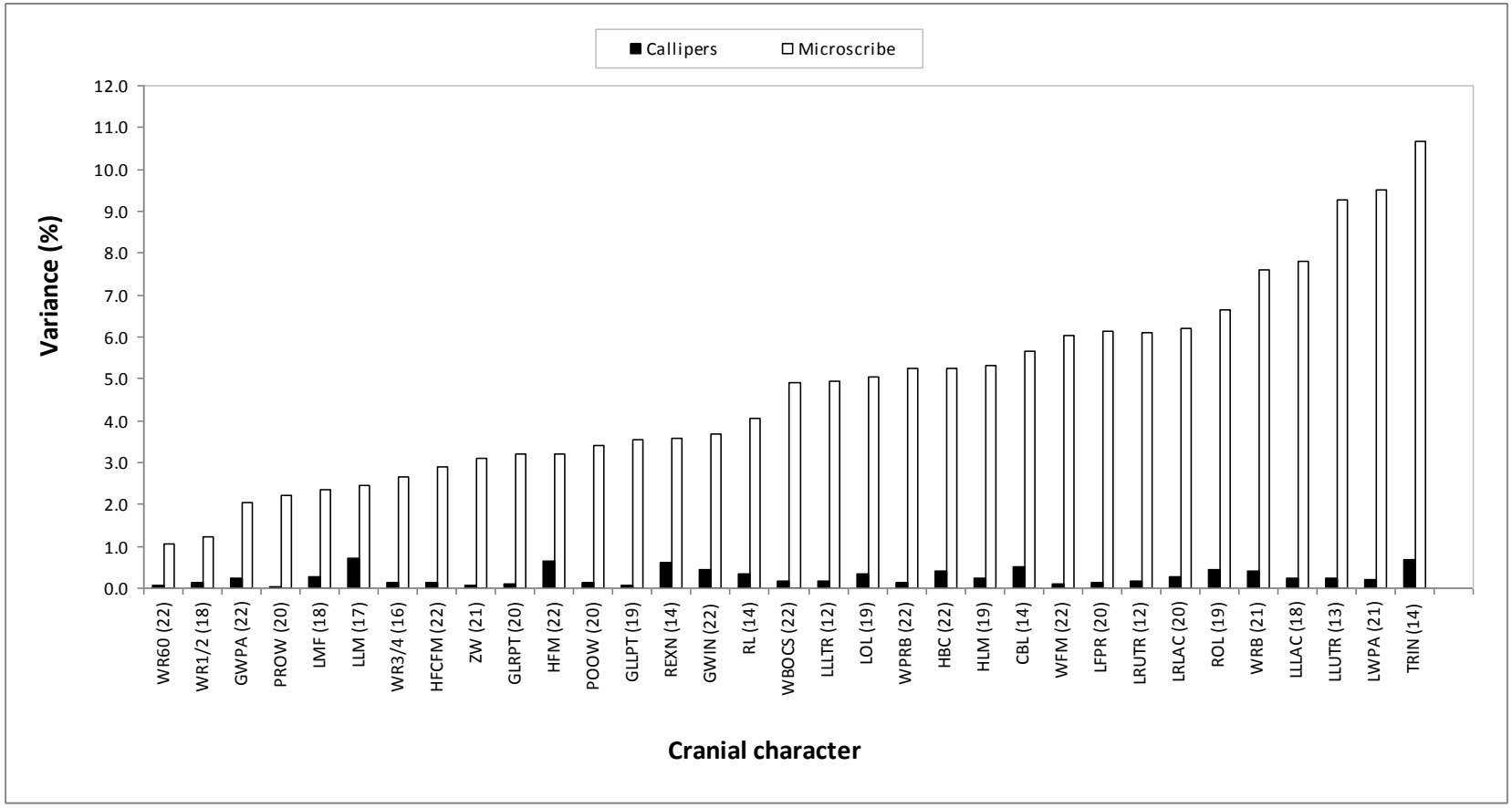
Code	Sex	Status	Region	Age (yrs)	TBL (cm)	Suture Index	RL (mm)	ZW (mm)	RL/ZW
KS08-14Dd	F	Mat	non	>20	>200	-	294.5	187.6	1.57
KS09-13Dd	M	Im	HG	8	214.0	6.5	290.0	189.9	1.53
KS09-24Dd	M	Mat	HG	12	207.0	8.5	291.6	184.0	1.59
KS10-78Dd	M	Im	HG	-	201.0	-	283.2	186.7	1.52
KS11-08Dd	M	Im	HG	-	176.0	5.5	292.6	184.6	1.59
KS11-12Dd	M	Im	HG	-	171.0	7.0	278.9	178.1	1.57
MM001822	M	Im	non	-	-	5.5	285.8	178.3	1.60
W08-06Dd	F	Im	non	-	180.0	6.0	276.6	176.7	1.57
WS05-06Dd*	M	Im	HG	10	220.0	4.0	284.5	184.5	1.54
WS06-09Dd	F	Mat	HG	14	212.0	-	298.1	185.7	1.61
WS07-02Dd	M	Mat	non	>15	241.0	10	321.8	206.9	1.56

Appendix 20. Trait expression frequency of non-metric cranial characters in *Delphinus* sp. from New Zealand waters according to region (Hauraki Gulf (HG) and non-Hauraki Gulf waters (non-HG)), pooled (all) and separately for both sexes. Note: Only characters independent of sex were considered when sexes were pooled, (L) and (R) = left and right side of the skull respectively; n = sample size; ant = anterior; post = posterior; blw = below; abv = above; pres = present; abs = absent; piri = piriform; umb = umbrella shaped; squ = square shaped; nar = narrow; n = sample size; numbers separated by semicolon = first number = number of individuals with first trait expression and second number = number of individuals with alternative trait expression. χ^2 = Chi-Square statistic; df = degrees of freedom; FE = Fisher's Exact test, which was used when sample size in any cell was < 5; p = p-value; numbers in bold = < 0.05. For character abbreviations refer to section 2.2.6.

Non-metric character	Trait expression	Sexes pooled					Males				Females				
		Total n	n per trait expression		Chi-Square χ^2		Total n	n per trait expression		Fisher's Exact	Total n	n per trait expression		Chi-Square χ^2	
			HG	non-HG	(df=1)	p		HG	non-HG	p		HG	non-HG	(df=1)	p
PMIOF	ant; post	55	22;8	17;8	0.018	0.892	27	9;5	10;3	0.678	28	13;3	7;5	FE	0.231
PLIOF	ant; post	56	1;27	2;26	FE	1	25	0;12	2;11	0.480	29	1;15	0;13	FE	1
DPM	blw; abv	54	23;6	21;4	FE	0.736	21	9;1	8;3	0.587	33	14;5	13;1	FE	0.209
CPPT	pre;abs	62	0;34	1;27	FE	0.451	29	0;15	0;14	-	33	0;19	1;13	FE	1
HV	blw; abv	59	7;27	5;20	0.003	0.956	29	2;13	3;11	0.651	30	5;14	2;19	FE	0.226
CPN (L)	pre; abs	62	1;33	1;27	FE	1	30	0;15	1;14	1	32	1;18	0;13	FE	1
CPN (R)	pre; abs	59	18;16	18;7	1.172	0.225	25	4;9	9;3	**0.047**	30	12;7	7;4	FE	1
EAPLPR	ant; post	50	22;7	19;2	FE	0.271	24	11;1	10;2	1	26	11;6	9;0	FE	0.063
SFM	piri; oval	59	28;4	22;5	FE	0.721	30	13;2	11;4	0.651	29	15;1	11;1	FE	1
O	pre; abs	58	13;18	8;19	FE	0.719	29	8;7	3;11	0.128	29	5;11	5;8	FE	0.714
SB	umb; squ	49	23;2	23;1	FE	1	22	8;2	12;1	0.571	26	15;0	11;0	-	-
PPEV	post; ant	59	23;9	13;14	2.540	0.111	27	9;4	8;6	0.695	32	14;5	5;8	2.644	0.104
VS	nar; wide	55	15;15	14;11	0.030	0.863	28	4;10	8;6	0.252	27	11;5	6;5	0.119	0.730
LFV (L)	pre; abs	60	28;5	23;4	FE	1	29	13;2	13;1	1	31	15;3	10;3	FE	0.676
PIOSF	post; ant	56	27;4	17;8	FE	0.108	26	12;1	9;4	0.322	30	15;3	8;4	FE	0.392
PAELVF (L)	ant; post	54	4;25	0;25	FE	0.115	26	1;10	0;15	0.423	28	3;15	0;10	FE	0.533

Appendix 21. Non-metric cranial characters employed for the mean measure of divergence (MMD) computation between New Zealand *Delphinus* sp. skull specimens from Hauraki Gulf (HG) and non-Hauraki Gulf (non-HG) waters pooled and separately for both sexes. Note: ant = anterior; blw = below; pres = present; post = posterior; nar = narrow; x = number of observations displaying the given trait; n = total sample size; M = male, F = female. For character abbreviations refer to section 2.2.6.

		Sexes pooled				Male				Female			
Non-metric	Trait	HG		non-HG		HG		non-HG		HG		non-HG	
character	expression	x	n	x	n	x	n	x	n	x	n	x	n
PMIOF	ant	22	30	17	25	9	14	10	13	13	16	7	12
DPM	blw	23	29	21	25	9	10	8	11	14	19	13	14
HV	blw	7	34	5	25	2	15	3	14	5	19	2	21
O	pres	13	31	8	27	8	15	3	14	5	16	5	13
PPEV	post	25	34	15	29	9	13	8	14	14	19	5	13
VS	nar	15	30	14	25	4	14	8	14	11	16	6	11
PIOSF	post	27	31	17	25	12	13	9	13	15	18	8	12
PAELVF (L)	ant	4	29	0	25	1	11	0	15	3	18	0	10



Appendix 22. Percentage variance for repeated measures (n = 3) of cranial characters recorded on cranially mature *Delphinus* sp. skulls from New Zealand waters by two different data acquisition methods (callipers: filled bars; microscribe: open bars). Note: Numbers in parentheses represent sample size. Characters arranged from lowest to highest percentage variance obtained for the microscribe data set. For character abbreviations refer to section 2.2.4.

Appendix 23. Mean ± SD and range for cranial measurements (mm) obtained with vernier callipers and a microscribe from cranially mature *Delphinus* sp. skull specimens from New Zealand waters. Mean absolute difference (MAD) with associated SD and 95% Confidence Interval (95% CI) in mm between mean calliper and microscribe measurements is also given. Relative error magnitude (REM) in relation to character size, given as a percentage, is also listed. Note: n = sample size. Values in bold indicate significance. Specimens of known and unknown sex were included. For character abbreviations refer to section 2.2.4.

		Callipers		Microscribe				
Character	n	Mean ± SD	Range	Mean ± SD	Range	MAD ± SD	95% CI	REM (%)
CBL	14	453.6 ± 17.7	432.1 - 494.9	454.8 ± 17.7	433.3 - 495.6	**1.2 ± 0.7**	**0.9 - 1.6**	0.3
GLLPT	19	77.0 ± 5.4	68.3 - 86.9	76.7 ± 5.7	66.1 - 86.6	0.5 ± 0.5	0.3 - 0.8	0.7
GLRPT	20	77.2 ± 5.2	67.0 - 85.9	76.7 ± 5.0	67.0 - 85.9	0.5 ± 0.4	0.3 - 0.7	0.6
GWIN	22	53.4 ± 2.2	49.4 - 57.2	53.5 ± 2.5	48.7 - 58.3	0.5 ± 0.4	0.4 - 0.7	1.0
GWPA	22	149.8 ± 5.7	140.4 - 164.4	149.0 ± 5.6	139.4 - 163.8	0.8 ± 0.5	0.6 - 1.0	0.6
HBC	22	130.1 ± 3.2	124.4 - 136.3	130.0 ± 3.3	124.1 - 135.9	0.3 ± 0.4	0.2 - 0.5	0.3
HFCFM	22	91.8 ± 4.9	83.9 - 100.4	91.8 ± 4.8	84.0 - 100.1	0.3 ± 0.3	0.2 - 0.4	0.3
HFM	22	34.0 ± 3.7	28.3 - 39.7	36.8 ± 2.4	33.0 - 41.7	**3.3 ± 2.1**	**2.5 - 4.2**	**9.4**
HLM	19	66.6 ± 3.2	61.3 - 74.6	66.4 ± 3.1	61.4 - 73.6	0.4 ± 0.2	0.3 - 0.5	0.6
LFPR	20	116.1 ± 14.2	92.0 - 139.6	116.0 ± 14.2	92.1 - 139.0	0.3 ± 0.2	0.2 - 0.3	0.2
LLLAC	18	44.3 ± 3.4	35.8 - 50.4	44.4 ± 3.7	35.8 - 51.5	0.4 ± 0.4	0.2 - 0.5	0.8
LLLTR	12	238.1 ± 10.2	223.0 - 256.7	238.3 ± 10.2	222.8 - 256.7	0.5 ± 0.5	0.2 - 0.8	0.2
LLM	17	387.1 ± 19.4	363.1 - 431.5	387.1 ± 19.3	362.5 - 430.4	0.8 ± 0.7	0.6 - 1.0	0.2
LLUTR	13	240.2 ± 12.9	225.7 - 270.3	240.2 ± 13.0	225.6 - 236.6	0.6 ± 0.6	0.3 - 0.9	0.2
LMF	18	110.5 ± 6.5	99.8 - 122.0	111.0 ± 6.7	100.2 - 122.2	0.6 ± 0.5	0.4 - 0.8	0.5
LOL	19	52.1 ± 2.0	48.8 - 56.6	53.3 ± 2.1	49.9 - 58.1	**1.1 ± 0.6**	**0.8 - 1.3**	2.1
LRLAC	20	41.6 ± 3.7	33.1 - 48.6	40.3 ± 3.6	32.2 - 47.7	**1.2 ± 0.5**	**1.0 - 1.4**	3.0

Appendix 23 continued.

		Callipers		Microscribe				
Character	**n**	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**	**MAD ± SD**	**95% CI**	**REM (%)**
LRUTR	12	242.5 ± 12.9	225.8 - 269.5	242.3 ± 13.0	225.2 - 268.6	0.8 ± 0.5	0.6 - 1.0	0.3
LWPA	21	141.5 ± 6.5	128.6 - 150.7	140.6 ± 6.6	127.4 - 149.7	**0.9 ± 0.5**	**0.7 - 1.1**	0.6
POOW	20	190.9 ± 8.3	177.8 - 206.6	190.5 ± 8.2	177.8 - 205.9	0.4 ± 0.3	0.3 - 0.6	0.2
PROW	20	168.9 ± 7.9	157.4 - 183.1	168.8 ± 8.0	157.0 - 182.9	0.2 ± 0.2	0.1 - 0.3	0.1
REXN	15	334.2 ± 17.4	311.6 - 376.9	333.5 ± 17.3	310.8 - 375.8	**1.0 ± 0.7**	**0.6 - 1.4**	0.3
RL	14	282.8 ± 15.6	261.5 - 321.8	281.7 ± 15.4	260.8 - 319.7	**1.1 ± 0.6**	**0.8 - 1.4**	0.4
ROL	19	52.2 ± 2.4	47.8 - 56.3	53.1 ± 2.1	49.8 - 56.8	**1.0 ± 0.6**	**0.7 - 1.3**	1.9
TRIN	14	329.9 ± 16.9	309.9 - 369.7	327.9 ± 16.4	307.2 - 365.2	**1.9 ± 1.0**	**1.3 - 2.4**	0.6
WBOCS	22	53.2 ± 4.4	44.8 - 63.4	52.8 ± 4.4	44.3 - 62.8	0.4 ± 0.3	0.3 - 0.5	0.7
WFM	22	36.4 ± 2.4	32.8 - 41.4	34.3 ± 3.9	28.3 - 41.7	**3.0 ± 1.9**	**2.2 - 3.8**	**8.4**
WPRB	22	50.8 ± 3.3	45.2 - 56.6	50.3 ± 2.6	46.4 - 55.3	0.8 ± 0.5	0.6 - 1.0	1.7
WR1/2	18	54.3 ± 3.2	46.8 - 58.7	54.0 ± 3.1	47.1 - 58.5	0.3 ± 0.2	0.2 - 0.4	0.6
WR3/4	17	41.6 ± 3.8	36.3 - 48.9	41.6 ± 3.6	35.9 - 48.1	0.5 ± 0.5	0.3 - 0.8	1.2
WR60	22	62.8 ± 4.0	55.4 - 70.3	62.5 ± 4.0	55.1 - 70.1	0.3 ± 0.2	0.3 - 0.4	0.6
WRB	21	94.5 ± 5.1	88.0 - 109.6	93.8 ± 4.9	87.8 - 109.8	0.8 ± 0.6	0.6 - 1.0	0.8
ZW	21	189.4 ± 8.9	175.2 - 206.9	188.7 ± 9.0	173.9 - 206.1	0.7 ± 0.5	0.5 - 0.9	0.4

Appendix 24. Rostrum length (mm), zygomatic width (mm) and rostrum length to zygomatic width (RL/ZW) ratio obtained for cranially mature *Delphinus* sp. skulls from New Zealand based on two different data acquisition methods (Cal = callipers and Mic = microscribe). Note: Diff = difference (mm) between measurements recorded by the two methods, where positive and negative values indicate larger measurements obtained with callipers and the microscribe, respectively. For rating categories refer to section 2.2.4.

Code	Rating	Rostrum length (mm)			Zygomatic width (mm)			RL/ZW ratio		
	category	Cal	Mic	diff	Cal	Mic	diff	Cal	Mic	diff
KS06-04Dd	3	294.6	293.8	0.8	198.9	199.3	-0.4	1.48	1.47	0.01
KS07-09Dd	2	265.4	264.5	0.9	183.6	183.2	0.4	1.45	1.44	0.01
KS07-12Dd	1	280.8	280.6	0.2	189.1	188.6	0.5	1.49	1.49	0.0
KS08-09Dd	1	261.5	260.8	0.8	187.1	186.2	0.9	1.40	1.40	0.0
KS08-10Dd	1	281.2	280.6	0.6	184.2	183.7	0.5	1.53	1.53	0.0
KS08-14Dd	1	294.5	293.7	0.8	187.6	186.9	0.7	1.57	1.57	0.0
KS09-14Dd	2	293.4	292.8	0.6	198.9	198.5	0.4	1.48	1.48	0.0
KS09-24Dd	2	291.6	290.5	1.1	184.0	183.5	0.5	1.59	1.58	0.01
KS10-05Dd	1	267.3	266.1	1.3	181.3	180.4	0.9	1.47	1.48	0.01
KS10-16Dd	1	287.2	286.5	0.7	197.9	197.0	0.9	1.45	1.45	0.0
KS10-26Dd	2	276.1	274.7	1.4	198.0	197.2	0.8	1.39	1.39	0.0
MM000981	1	273.0	272.4	0.6	184.4	184.3	0.1	1.48	1.48	0.0
MM002220	1	274.5	273.5	1.0	185.0	184.4	0.6	1.48	1.48	0.0
MM002221	3	286.0	286.1	-0.1	206.3	206.1	0.2	1.39	1.39	0.0
W08-17Dd	2	291.4	290.3	1.1	190.8	190.5	0.3	1.53	1.52	0.01
WS00-34Dd	3	262.5	261.6	0.9	175.2	174.3	0.9	1.50	1.50	0.0
WS04-28Dd	3	261.5	260.7	0.8	180.5	180.1	0.4	1.45	1.45	0.0
WS04-29Dd	3	263.9	263.1	0.8	178.0	177.2	0.8	1.48	1.49	0.0
WS05-18Dd	3	274.2	273.4	0.8	193.5	192.7	0.8	1.42	1.42	0.0
WS07-02Dd	1	321.8	320.7	1.1	206.9	206.1	0.8	1.56	1.56	0.0

Appendix 25. Mean ± SD and range (mm) for cranial measurements obtained with vernier callipers and a microscribe from cranially mature male and female *Delphinus* sp. skulls from New Zealand waters. Mean absolute difference (MAD) in mm between mean calliper and microscribe measurements for each sex per character are given. Unpaired t-test results for assessment of sexual dimorphism within a given data set (calliper and microscribe) are also shown. Note: M = male; F = female; n = sample size; p = p-value; values in bold = < 0.05; ** = < 0.01. For character abbreviations refer to section 2.2.4

			Callipers		Microscribe		Unpaired t-test				
			Mean ± SD		Mean ± SD		Callipers			Microscribe	
Character	Sex	n	(mm)	Range (mm)	(mm)	Range (mm)	t	p	df	t	p
CBL	M	5	463.6 ± 19.2	446.4 - 494.9	464.5 ± 19.2	447.4 - 495.6	0.231	1.277	10	0.215	1.324
	F	7	449.6 ± 17.1	432.1 - 468.5	451.0 ± 17.3	433.3 - 469.7					
GLLPT	M	5	76.5 ± 3.6	72.0 - 80.8	76.1 ± 3.7	71.0 - 80.3	0.711	0.379	14.0	0.7884	0.2736
	F	11	75.5 ± 5.5	68.3 - 83.2	75.3 ± 5.9	66.1 - 84.5					
GLRPT	M	6	77.0 ± 4.1	72.7 - 83.3	76.2 ± 3.7	71.9 - 81.2	0.627	0.5404	15.0	0.3696	0.7169
	F	11	75.5 ± 5.1	67.0 - 83.3	75.3 ± 5.0	67.0 - 83.3					
GWIN	M	7	54.5 ± 1.7	52.3 - 56.5	54.9 ± 1.8	52.8 - 57.3	2.38	**0.030**	17.0	2.588	**0.019**
	F	12	52.4 ± 1.9	49.4 - 55.5	52.4 ± 2.2	48.7 - 55.6					
GWPA	M	7	153.9 ± 5.9	148.4 - 164.4	153.2 ± 6.2	147.2 - 163.8	2.94	**	17.0	2.602	**0.015**
	F	12	147.3 ± 3.9	140.4 - 154.5	146.4 ± 4.2	139.4 - 154.0					
HBC	M	7	130.9 ± 4.3	124.4 - 136.3	130.7 ± 4.4	124.1 - 135.7	0.980	0.3409	17.0	0.8707	0.3961
	F	12	129.3 ± 2.7	126.5 - 135.0	129.3 ± 2.9	126.2 - 135.9					
HFCFM	M	7	89.9 ± 2.6	85.9 - 93.9	90.0 ± 4.0	87.1 - 93.9	1.415	0.1752	17.0	1.296	0.2123
	F	12	93.0 ± 5.3	84.1 - 100.4	92.8 ± 5.4	84.1 - 100.1					

Appendix 25 continued.

Character	Sex	n	Mean ± SD (mm) (Callipers)	Range (mm) (Callipers)	Mean ± SD (mm) (Microscribe)	Range (mm) (Microscribe)	Callipers t	Callipers p	Callipers df	Microscribe t	Microscribe p
HFM	M	7	36.0 ± 2.1	32.2 - 38.9	37.0 ± 1.9	33.0 - 38.8	1.787	0.092	17.0	0.107	0.916
	F	12	33.0 ± 4.1	28.3 - 39.7	36.9 ± 2.6	34.1 - 41.7					
HLM	M	7	68.1 ± 3.8	63.5 - 74.6	67.6 ± 3.5	63.1 - 73.6	1.752	0.100	15.0	1.537	0.145
	F	10	65.4 ± 2.6	61.3 - 69.3	65.3 ± 2.7	61.4 - 69.9					
LFPR	M	6	126.2 ± 7.8	117.5 - 139.6	126.1 ± 7.7	117.5 - 139.0	3.056	**	15.0	3.068	**
	F	11	108.4 ± 12.8	92.0 - 128.0	109.1 ± 12.4	92.1 - 127.5					
LLLAC	M	5	45.2 ± 3.3	41.9 - 50.4	45.3 ± 3.9	40.8 - 51.5	0.632	0.538	13.0	0.675	0.512
	F	10	44.0 ± 3.6	35.8 - 48.2	43.9 ± 3.7	35.8 - 48.4					
LLLTR	M	5	240.9 ± 10.9	231.9 - 256.7	240.7 ± 11.1	231.5 - 256.7	0.483	0.641	9.0	0.384	0.710
	F	7	237.7 ± 10.7	223.0 - 252.2	238.1 ± 10.7	222.8 - 252.5					
LLM	M	5	397.8 ± 22.3	375.5 - 431.5	397.2 ± 22.4	374.6 - 430.4	1.637	0.118	13.0	1.574	0.140
	F	10	380.5 ± 17.0	363.1 - 405.4	380.9 ± 17.1	362.5 - 405.1					
LLUTR	M	5	246.4 ± 14.5	233.0 - 270.3	246.5 ± 14.4	232.6 - 269.7	1.069	0.313	9.0	1.062	0.316
	F	6	237.8 ± 12.4	225.7 - 256.1	237.9 ± 12.5	232.6 - 269.7					
LMF	M	7	112.6 ± 4.6	107.7 - 120.3	113.3 ± 4.7	108.1 - 120.6	0.949	0.358	15.0	1.008	0.329
	F	10	109.6 ± 7.6	99.8 - 122.0	110.0 ± 7.7	100.2 - 122.2					
LOL	F	10	51.7 ± 2.1	49.2 - 56.6	52.7 ± 2.1	49.9 - 57.1	0.403	0.693	14.0	0.777	0.450
	M	6	52.1 ± 1.9	48.8 - 54.5	53.5 ± 2.0	51.0 - 57.0					

Appendix 25 continued.

Character	Sex	n	Mean ± SD (Callipers) (mm)	Range (mm)	Mean ± SD (Microscribe) (mm)	Range (mm)	Callipers t	Callipers p	df	Microscribe t	Microscribe p
LRLAC	M	7	41.9 ± 4.1	35.2 - 48.6	41.0 ± 4.0	35.0 - 47.7	0.313	0.758	15.0	0.644	0.523
	F	10	41.3 ± 3.7	33.1 - 45.4	40.3 ± 3.6	32.2 - 44.0					
LRUTR	M	5	246.6 ± 13.4	236.3 - 269.5	246.2 ± 14.0	232.5 - 268.6	0.933	0.373	10.0	0.852	0.414
	F	7	239.5 ± 12.6	225.8 - 257.1	239.6 ± 12.6	225.2 - 256.9					
LWPA	M	7	145.9 ± 5.0	137.4 - 150.7	145.2 ± 4.7	137.2 - 149.7	2.793	**	16.0	3.035	**
	F	11	138.0 ± 6.2	128.6 - 147.9	136.8 ± 6.3	127.4 - 147.0					
POOW	M	7	195.6 ± 7.4	186.1 - 206.6	195.0 ± 7.4	185.3 - 205.4	2.434	**0.028**	15.0	2.418	**0.029**
	F	10	187.1 ± 6.8	177.8 - 201.8	186.7 ± 6.6	177.8 - 200.8					
PROW	M	7	174.2 ± 7.5	162.8 - 183.1	174.2 ± 7.6	162.7 - 182.9	3.000	**	15.0	3.050	**
	F	10	164.8 ± 5.5	157.4 - 175.9	164.6 ± 5.3	157.0 - 175.2					
REXN	M	5	344.8 ± 19.8	327.0 - 376.9	343.4 ± 19.7	326.5 - 375.8	1.237	0.245	10.0	1.166	0.271
	F	7	331.8 ± 16.5	311.6 - 351.3	331.1 ± 16.9	310.8 - 350.7					
RL	M	5	291.6 ± 17.9	276.1 - 321.8	290.2 ± 17.5	274.7 - 319.7	1.334	0.212	10.0	1.283	0.228
	F	7	279.2 ± 14.3	261.5 - 294.6	278.4 ± 14.4	260.8 - 293.7					
ROL	M	7	52.9 ± 2.7	47.8 - 55.9	53.8 ± 2.3	50.2 - 56.4	0.923	0.372	14.0	5.260	0.313
	F	9	51.7 ± 22.4	48.9 - 56.3	52.6 ± 2.2	49.8 - 56.8					
TRIN	M	5	338.1 ± 18.7	322.3 - 369.7	335.8 ± 17.8	319.7 - 365.3	1.082	0.305	10.0	1.066	0.312
	F	7	327.1 ± 16.5	309.9 - 347.0	325.2 ± 16.8	307.2 - 344.8					

Appendix 25 continued.

Character	Sex	n	Mean ± SD (mm) (Callipers)	Range (mm) (Callipers)	Mean ± SD (mm) (Microscribe)	Range (mm) (Microscribe)	Callipers t	Callipers p	Callipers df	Microscribe t	Microscribe p
WBOCS	M	7	55.5 ± 3.6	49.6 - 60.9	55.2 ± 3.8	49.0 - 60.5	2.48	**0.024**	17.0	2.458	**0.025**
	F	12	51.4 ± 3.4	44.8 - 57.5	51.0 ± 3.5	44.3 - 57.4					
WFM	M	7	36.5 ± 1.8	32.8 - 38.5	36.3 ± 2.4	32.1 - 39.8	0.055	0.957	17.0	1.651	0.117
	F	12	36.5 ± 2.6	33.5 - 41.4	33.3 ± 4.4	28.3 - 41.7					
WPRB	M	7	52.3 ± 3.2	47.1 - 56.4	51.5 ± 3.1	46.4 - 56.3	1.846	0.082	17.0	1.498	0.152
	F	12	49.7 ± 2.8	45.2 - 54.8	49.7 ± 2.0	46.4 - 53.5					
WR05	M	5	55.8 ± 1.5	53.5 - 57.0	55.4 ± 1.6	52.9 - 56.8	1.526	0.151	13.0	1.415	0.181
	F	10	53.3 ± 3.6	46.8 - 58.7	53.1 ± 3.3	47.1 - 58.3					
WR34	M	5	45.0 ± 3.8	38.3 - 48.9	44.9 ± 3.7	38.9 - 48.1	3.301	**	12.0	3.212	**
	F	9	39.5 ± 2.5	36.4 - 43.8	40.1 ± 2.0	38.2 - 43.7					
WR60	M	7	65.1 ± 3.0	60.7 - 69.1	64.7 ± 3.0	60.1 - 68.4	2.280	**0.036**	17.0	2.290	**0.035**
	F	12	61.3 ± 3.7	55.4 - 68.4	61.0 ± 3.6	55.1 - 68.1					
WRB	M	7	98.0 ± 6.5	91.7 - 109.6	97.5 ± 6.7	91.2 - 109.8	2.992	**	16.0	3.179	**
	F	11	91.7 ± 2.2	88.0 - 95.1	90.8 ± 2.1	87.8 - 94.3					
ZW	M	6	194.1 ± 8.9	184.0 - 206.9	193.4 ± 8.6	183.5 - 206.1	1.950	0.069	16.0	1.916	0.073
	F	12	186.4 ± 7.4	175.2 - 198.9	185.7 ± 7.8	173.9 - 199.3					

Appendix 26. Cranial parameters for species identification of the common dolphin, *Delphinus* sp. Mean values and range (in parentheses) are given for geographic populations of the short-beaked (*D. delphis*) and long-beaked (*D. capensis*) form, and for populations with currently unknown species status (*Delphinus* sp.). Published values for *D.c. tropicalis* are also listed. Note: Cal = California; Engl / W = England / Wales; wNAtl = western North Atlantic; sAU = southern Australia; NZ = New Zealand; Ven = Venezuela; IndO = Indian Ocean; M = males; F = females; P = sexes pooled; RL/ZW (rostrum length to zygomatic width); TC = tooth count; TBL = total body length; CBL = condylobasal length; RL = rostrum length; na = not available; Ref. = reference; H & P = Heyning & Perrin, 1994; M = Murphy et al. 2006; W = Westgate, 2007; B = Bell, 2001 / et al., 2002; E & O = Esteves & Oviedo, 2007; J & VW = Jefferson & Van Waerebeek, 2002; DOS = De Oliveira Santos et al. (2002); T.S. = this study. Values are given separately for both sexes where available. Geographic populations listed according to species and RL/ZW ratios.

Species	Region	Sex	RL/ZW ratio	Upper left TC	Lower left TC	TBL (cm)	CBL (mm)	RL (mm)	ZW (mm)	Ref.
D. delphis	Cal	M	1.37 (1.21 - 1.46)	49 (42 - 54)	47 (41 - 53)	189.5 (172 - 201)	421.4 (392 - 442)	244.0 (218 - 264)	184.9 (173 - 195)	H & P
		F	1.36 (1.23 - 1.47)			180.1 (164 - 193)	406.3 (382 - 442)	244.0 (218 - 264)	179.6 (170 - 190)	H & P
	Engl / W	M	na (1.15 - 1.51)	na (41 - 53)	na (42 - 53)	213.4 (198 - 244)	450.2 (421 - 480)	278.2 (252 - 300)	193.5 (183 - 207)	M
		F	na (1.21 - 1.51)			203.6 (185 - 226)	432.7 (408 - 450)	266.9 (247 - 280)	185.9 (177 - 200)	M
	eNAtl	P	1.44 (1.31 - 1.57)	na (41 - 56)	na (42 - 53)	na (185 - 244)	na (396 - 487)	na (234 - 230)	na	M
	wNAtl	M	1.42 (1.31 - 1.54)	48 (43 - 52)	47 (42 - 52)	221.5 (na)	444.7 (412 - 481)	271.7 (248 - 298)	na	W
		F	1.44 (1.34 - 1.54)	48 (44 - 52)	47 (42 - 51)	202.2 (na)	434.9 (411 - 456)	265.8 (250 - 281)	na	W
	sAU	P	1.52 (1.36 - 1.73)	48 (43 - 54)	na	na	na	271.4 (225 - 311)	178.2 (152 - 202)	B
Delphinus sp.	**NZ**	**M**	**1.50 (1.39 - 1.59)**	**51 (45 - 55)**	**49 (45 - 53)**	**213.9 (190 - 241)**	**463.6 (446 - 495)**	**291.6 (276 - 322)**	**192.2 (181 - 207)**	**T.S.**
		F	**1.49 (1.40 - 1.61)**	**50 (47 - 55)**	**50 (43 - 55)**	**199.9 (187 - 212)**	**446.4 (423 - 469)**	**279.0 (261 - 298)**	**185.3 (175 - 200)**	**T.S.**
	Ven	P	1.60 (1.48 - 1.68)	51 (44 - 54)	48 (43 - 51)	na	na	267.6 (242 - 288)	168.5 (147 - 184)	E & O
D. capensis	Cal	M	1.60 (1.52 - 1.67)	53 (48 - 59)	51 (47 - 55)	219.1 (202 - 235)	473.6 (446 - 498)	302.0 (286 - 321)	189.1 (181 - 204)	H & P
		F	1.64 (1.55 - 1.77)			207.7 (193 - 224)	465.5 (445 - 486)	296.2 (281 - 314)	180.8 (173 - 191)	H & P
	Brazil	P	1.63 (1.51 - 1.77)	51 (49 - 56)	50 (47 - 52)	na	na	305.3 (284 - 342)	187.6 (171 - 198)	DOS
	IndO	P	1.64 (1.46 - 1.77)	54 (47 - 60)	52 (48 - 57)	na	486.0 (449 - 543)	312.4 (278 - 348)	191.1 (170 - 212)	J & VW
D.c. tropicalis	IndO	P	1.85 (1.60 - 2.06)	59 (54 - 67)	57 (52 - 64)	na	502.9 (456 - 575)	336.2 (298 - 398)	179.8 (160 - 206)	J & VW