Growth and reproduction of dusky dolphins (*Lagenorhynchus obscurus*) in Aotearoa New Zealand

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Abstract

Dusky dolphins (*Lagenorhynchus obscurus*) are a semi-pelagic species widely distributed in the southern hemisphere. Our understanding of dusky dolphin life history in New Zealand waters has been limited by the small sample sizes and limited geographic coverage of previous studies. Here, I assess age, growth, allometry and reproductive biology from 138 individuals (51 females, 73 males and 14 unsexed individuals). Data originated from stranding and bycatch events around the Aotearoa New Zealand coast from 1960 to 2023. The total body length of females and males varied between 83 to 195cm (mean = 158.1; SD = 27.6; *n* = 51), and 87 to 192cm (mean =160.1; SD = 25.8; *n* = 73), respectively. Morphological measurements of males (*n* = 55) and females (*n* = 39) were analysed across 25 external measurements, exhibiting negative, positive, and isometric allometry. No growth differences between sexes were observed. Size and shape dimorphism was analysed across 29 external morphological measurements of physically mature individuals. No sexual size or shape dimorphism was observed in the appendage, girth, or blubber measurements. Significant dimorphism between sexes was observed in the snout to genital slit length. Age was estimated from decalcified thin sections of teeth; maximum ages recorded in males and females were 22 and 14 years, respectively. Physical maturity was estimated from asymptotic length obtained using Gompertz growth models. Males and females were estimated to obtain physical maturity at 171.5 and 170cm, respectively. Reproductive parameters were assessed (*n* = 39) through gross and histological examination of gonads across in males (*n* = 22) and females (*n* = 17). The average length at attainment at sexual maturity for males was 170.4cm. For females, the average length at attainment of sexual maturity was 167.5cm, though a lack of age overlap prevented age at sexual maturity being assessed for either sex. Five foetuses ranged in total body length from 25.5 to 81cm, with the smallest born males and females measuring 91.5 and 102cm, respectively. Length at birth could not be determined due to a lack of overlap between measurements of unborn foetuses and newborn neonates.

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Chapter 1 Introduction

Photo Credit: Rob Pine

1.1 Age & Growth

Life history studies play a crucial role in understanding the reproductive and survival characteristics of various species (Bennett, 2023). Such studies include investigating the lifespan, age of sexual maturity, breeding frequency, duration of lactation, foraging habits, and dietary preferences of a species (Bennett, 2023; González-Suárez & Revilla, 2013). By examining these traits, we can evaluate the susceptibility of species to extinction in response to changing environments (González-Suárez & Revilla, 2013; Hernández-Yáñez et al., 2022; Jackson et al., 2022). Additionally, life history studies contribute to our understanding of the diversity of mammal species in various habitats and evolutionary backgrounds (Jones & Safi, 2011). Consequently, life history studies provide valuable insight into the ecological and evolutionary dynamics of mammalian biodiversity.

For example, we can use our understanding of the age structure of cetacean populations, to assess population health and adaptability. Such knowledge further informs conservation strategies, allowing sustainable bycatch limits and the discovery of critical habitats for the various life stages (Hammond et al., 2023). By analysing age data, an understanding of how each species allocates resources throughout different life stages (including growth, reproduction, and survival) can be garnered. Furthermore, insights into their reproductive cycles, longevity and overall fitness can be ascertained (Chivers, 2018).

Various methods are used to study the age and growth of cetaceans, including the analysis of ear plugs and examination of teeth for growth layers, for age estimation in baleen and toothed whales, respectively (Murphy, et al., 2018a; Perrott, et al., 2018; Trumble et al., 2013). Length-age curves, developed from measurements of known-age individuals, are also used to estimate the age of cetaceans across different species (Perrin et al., 1980). Other non-invasive methods, photographic identification, can also be used to monitor individual cetaceans over time, providing valuable information on growth rates and longevity (Elliser et al., 2022).

Variations in the age and growth rates of delphinids occur due to a multitude of factors, including genetic predispositions, environmental conditions including food abundance and habitat quality, and the intricacies of social structure within their pods (Connor et al., 2000; Coscarella et al., 2011; Wells et al., 2003). This diversity in body size among delphinids may be attributed to various influences such as the effects of aquatic weightlessness, migratory patterns, and selective pressures shaped by thermoregulation and feeding behaviours in aquatic environments (Montgomery et al., 2013; Sun et al., 2019).

The largest delphinid species, the killer whale (*Orcinus orca*), can attain maximum body lengths of 9 and 7.7 meters in males and females, respectively (Ford, 2009; Macgregor, 2021), reaching maximum ages of 50 to 60 and 80 to 90 years, respectively (Ford, 2009; Macgregor, 2021). Bottlenose dolphins (*Tursiops truncatus*) typically live over 40 years, with adult body lengths up to 3.8 meters reported (Leatherwood & Reeves, 2012; Wells & Scott, 2018; Wells & Scott, 2009). On opposite end of the size spectrum, Hector’s dolphins (*Cephalorhynchus hectori*) typically attain a maximum body length of ~1.5 meters, while some females grow up to 1.6 meters (Rayment et al., 2009; Slooten et al., 2006). Dusky dolphins (*Lagenorhynchus obscurus*) are intermediate within the Delphinidae family, typically reaching lengths of 170 to 200cm (Best & Meÿer, 2010; Cipriano, 1992; Manzanilla-Naim, 2011; Van Waerebeek & Würsig, 2009). Globally, age and growth of dusky dolphins has been studied in the South African, Peruvian and New Zealand populations. Across each population, body length varies, with most variation observed in the Peruvian population, where maximum lengths of 205 and 211cm have been reported for males and female, respectively (Manzanilla-Naim, 1989; Van Waerebeek & Würsig, 2009). Meanwhile, maximum lengths in South African and New Zealand populations have been reported at ~ 190cm for both sexes and between 170 to 180cm for both sexes, respectively (Best & Meÿer, 2010; Cipriano, 1992; Würsig, 2007).

Longevity within the South African population is poorly described, with only three captive South African dusky dolphins having been aged (8, 18 and ca. 21 years old), with no sex provided on any of those three individuals (Best 1976). Manzanilla (1989) reported on the reproductive status and age (based on dentine layers) of 41 dusky dolphins (27 females, 14 males), from Peru in the eighties, with the males ranging between 15 to 22 years old, the oldest female estimated to be 11.5 years old. In New Zealand, Cipriano's (1992) study included 11 individuals ranging from 1973 to 1988. The two oldest specimens analysed were males, estimated to be between 35 to 36 years and 26 to 30 years old (Webber, 1987). The oldest female specimen was estimated to be 22 to 24 years old. The two oldest specimens analysed were males ranging between 35 to 36 years and 26 to 30 years old. The oldest female specimen was assigned an age range of 22 to 24 years old.

1.2 Morphology

Morphology focuses on the examination of the size, shape, and structure of living organisms (Caffrey, 2023). Additionally, it delves into the exploration of the interconnections and associations between the various components that constitute these organisms (Caffrey, 2023). Morphometric studies enable researchers to investigate numerous characteristics of an organism's body form and size, a practice known as allometry (Dujardin, 2017; Murphy & Rogan, 2006). This encompasses not just morphological variation between sexes of a species, such as sexual changes in growth rates and patterns, but also regional variation in morphology within a species (Murphy & Rogan, 2006).

Qualitative and quantitative morphology are two different ways of describing the shape and size of an organism. Qualitative morphology is the study of the form and structure of an organism based on its physical appearance. It involves the observation of external features such as size, shape, colour, and texture. Quantitative morphology is the study of the form and structure of an organism based on numerical measurements (Hirtle et al., 2022). Cetaceans have a diverse variety of morphological adaptations that allow them to thrive in their marine environment. Many of these adaptations differ between species because the degree of resource partitioning within a population is influenced by the local environment (Kernaléguen et al., 2015). The division of scarce resources among species aids in the prevention of rivalry in an ecological niche (Nduna, 2019). As a result, the local environment, availability of prey, and sex all play important roles in the morphology, physiology, and life history of cetaceans (Kernaléguen et al., 2015).

The external morphology of delphinids exhibits considerable variation across different species, reflecting the adaptations to a diverse array of marine environments. Despite the diversity, they share common odontocete characteristics such as a fusiform body shape, a single external blowhole, and distinctive cranial structures that support their echolocation abilities (Cozzi et al., 2016; Huggenberger & Cozzi, 2018). The variations in body size, shape, colour patterns, beak shape and length, dorsal fin, fluke, and melon are particularly notable and serve as adaptations to specific ecological niches (Au & Lammers, 2007; Cozzi et al., 2016; Huggenberger & Cozzi, 2018). While these morphological traits are shared across the delphinid family, specific adaptations within individual species illustrate the diversity in their ecological roles and habitats.

Killer whale, for instance, are distinguished by their large size and stark black-and-white colouration, (Ford & Raverty, 2014; Weber et al., 2014; Wright et al., 2023). In contrast, the common dolphin (*Delphinus delphis*) features a sleek and aerodynamic body shape, complemented by an intricate pattern of coloration. This includes a dark grey or black cape that gradually lightens towards the sides, culminating in a creamy-white ventrum (Caro et al., 2011; Cozzi et al., 2016; Murphy & Rogan, 2006). Similarly, the bottlenose dolphin is recognised for its versatility and adaptability, featuring a robust body and prominent dorsal fin that allow it to thrive in both coastal and open sea habitats (Cozzi et al., 2016; Félix et al., 2018; Huggenberger & Cozzi, 2018). Furthermore, variations in beak length among species highlight the evolutionary adaptations for feeding, with some species having evolved long, slender beaks suited for snatching prey from tight spaces (Galatius et al., 2020; Huggenberger & Cozzi, 2018). Other species have adapted to having shorter beaks for capturing certain prey types located closer to the surface or in the mid-water column, the shorter beak aids in precision and timing in catching fast-moving and agile prey (Galatius et al., 2020; Huggenberger & Cozzi, 2018).

The dusky dolphin showcases distinct morphological features characterized by a streamlined, fusiform body shape that facilitates efficient swimming and manoeuvrability (Figure 1.1). Moreover, the dusky dolphin exhibits a small head with a steep forehead, a feature common among many dolphin species that aids in echolocation (Cipriano & Webber, 2010; Coombs et al., 2022). Their flippers are long, thin, and pointed, contributing to their agility in the water. They have well-developed, conical teeth suited for grasping slippery prey, consistent with the homodont dentition typical of dolphins, which allows for a diet comprising mainly of fish and squid (Van Waerebeek & Würsig, 2009). Their beak is short and dark, and they possess a large dorsal fin that is sharply hooked, aiding in stabilization during swimming. Adaptations such as a powerful tail stock and flukes enable this species to generate significant thrust and perform complex aerial behaviours, which are thought to play roles in social signalling, feeding, and predator avoidance (Würsig & Würsig, 2009). Overall, the morphology of the dusky dolphin reflects a blend of adaptations for social interaction, high-speed swimming, and ecological versatility within its marine habitat.

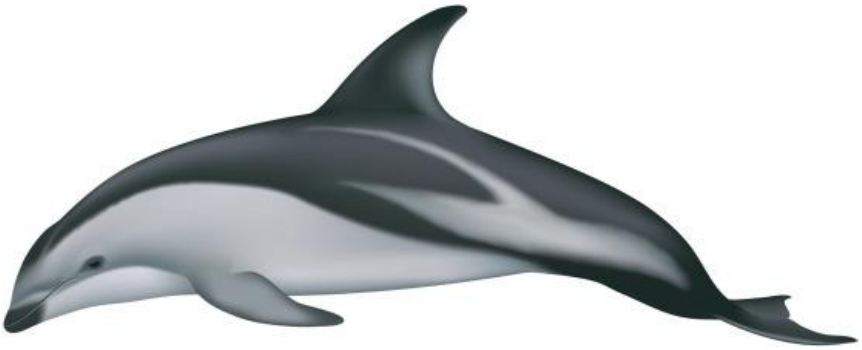


Figure 1.1 Morphology of dusky dolphin showing distinct features, including a short rostrum, robust body, intricate colour patterns, and a falcate dorsal fin. © Uko Gorter

1.3 Allometry

Allometry refers to the disproportionate variations in shape, size, or function that occur when comparing distinct isolated characteristics of body size in animals (Betty et al., 2022; Lindstedt & Schaeffer, 2002). Most body-size relationships are expressed as a straightforward power function of the form $y = ax^b$, where x is the organisms total body length, y denotes a biological characteristic, and a and b denote the scaling exponent and experimentally determined constant, respectively (Arhonditsis et al., 2019; Murphy & Rogan, 2006).

Allometry is considered as: positive, negative, or isometric. When $b \neq 1$, the characteristic being analysed grows disproportionately to overall size and will either be positive or negative (Voje, 2017). Positive allometry, $b > 1$, suggests the characteristic grows at a greater rate than the total body length or in comparison to other characteristics (Voje, 2017). Negative allometry, $b < 1$, suggests the characteristic grows at a slower rate in comparison to the total body length or other characteristics (Voje, 2017). When $b = 1$, characteristics grow proportionately to the total body length or in comparison to other characteristics, this is referred to isometric allometry (Voje, 2017).

Biological variation in a wide variety of physiological, morphological, ecological, and life-history characteristics has a strong correlation with variation in organism size, and the principle of allometry provides key hypotheses for explaining this trait variation (Voje, 2017). Understanding differences in growth rates can provide information about the evolutionary or plastic response to resource partitioning, providing additional insight into the ecology of the population or species.

1.3.1 Cetacean Allometry

Studying marine mammals in their natural habitat can be a challenging task (Ballance, 2018). Accordingly, morphological and allometric research is usually conducted on marine mammals post-mortem.

Murphy & Rogan (2006) examined the growth, allometric relationships and sexual dimorphism of 105 males, 149 females and 38 unsexed specimens of short-beaked common dolphins, stranded and bycaught in Ireland between 1990 to 2003. A total of 24 standard external morphometric measurements for each individual specimen were measured (Figure 1.2). Results of this study indicated male and female short-beaked common dolphins demonstrate similar growth patterns in several characteristics (Murphy & Rogan, 2006), demonstrating negative allometry in both sexes.

Betty et al., (2022) assessed age, growth, allometry, and sexual dimorphism of southern hemisphere long-finned pilot whales (*Globicephela melas edwardii*) that stranded in New Zealand between 1978 and 2017. The data comprised of 1520 individuals across 776 females, 515 males, and 229 individuals of unknown sex. Thirteen standard external morphometric measurements (Figure 1.2), from which significant allometry was identified for ten morphological characteristics in females and eleven in males. Except for genital slit length, which showed isometric development in females, nearly all linear body measures were negatively allometric in both male and female long-finned pilot whales.

Such exemplars highlight that while morphology and allometry may vary between species and sexes, different species may also share similar allometric relationships as shown across short-beaked common dolphin and the southern hemisphere long-finned pilot by Murphy & Rogan (2006) and Betty et al., (2022), respectively. These studies demonstrate how morphometric research provides valuable insights into growth, sexual dimorphism, and allometric relationships that are often challenging to investigate in populations in their natural habitat. By comparing findings across species, researchers can identify common developmental trends and ecological adaptations, creating a framework for understanding the morphological and life history traits of other cetaceans, including dusky dolphins.

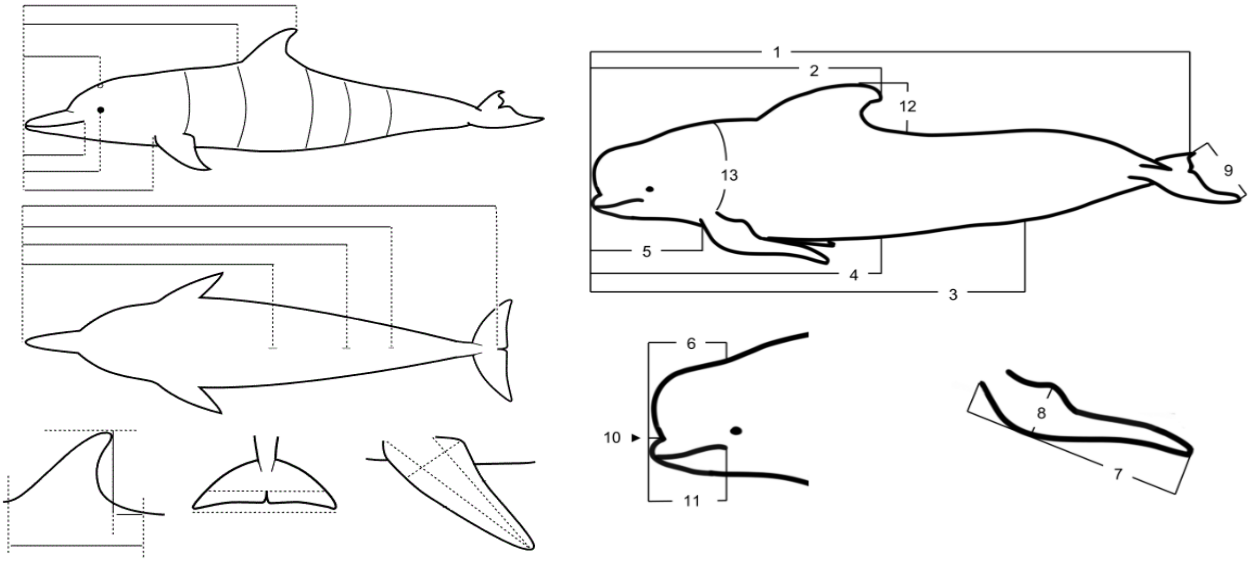


Figure 1.2 External morphometric measurements from common dolphins (*Delphinus delphis*) (left) adapted from Murphy & Rogan (2006) and southern hemisphere long-finned pilot whale (*Globicephela melas edwardii*) (right), adapted from Betty et al., (2022).

1.4 Life History Strategies

Life history strategies across the animal kingdom can be broadly categorized along a continuum between R-selected and K-selected extremes, reflecting how species balance reproduction and survival in response to environmental pressures (Bakewell et al., 2020; Figueredo et al., 2005). ‘R-selected’ species are adapted for environments with abundant resources and high mortality rates (Singh, 2019). They reproduce quickly and prolifically, with minimal investment in offspring. Examples include many fish, amphibians, and insects, which produce large numbers of offspring but experience low survival rates (Allen et al., 2017; Singh, 2019). Conversely, K-selected species thrive in stable environments with intense competition for limited resources. These species invest heavily in fewer offspring, ensuring higher survival rates through extended parental care, slower development, and greater longevity (Bakewell et al., 2020; Braendle et al., 2011; Figueredo et al., 2005; Healy et al., 2019). Examples of terrestrial K-selected species include elephants, primates, large carnivores, and marine mammals, all of which exhibit low reproductive rates and significant parental investment (Figueredo et al., 2005; Shilovsky et al., 2022).

Among marine mammals, K-selection is most pronounced in cetaceans, which exhibit some of the slowest life history traits seen in any mammalian group. Like other K-selected species, cetaceans invest heavily in each offspring, reflected in their long gestation periods, extended lactation, and delayed sexual maturity (Huang et al., 2011). The higher level of parental investment ensures that offspring have a better chance of survival in the challenging marine environment, where energy expenditure is high, and food sources may be unpredictable (Adamczak et al., 2023; Singh, 2019). These life history traits enable cetaceans to effectively navigate their environment, ensuring the survival of each offspring and promoting long-term stability of their populations (Adamczak et al., 2023). By studying cetacean life histories within a broader comparative framework, scientists gain a deeper understanding of how evolutionary forces shape reproductive strategies in cetaceans.

1.5 Cetacean Ontogeny

The process of individual development from a single cell, an egg cell or a zygote to an adult organism is known as ontogeny. The ontogeny of cetaceans includes two key life stages: immature and mature; the life stage of immature can be further segregated into neonate, assuming the individual exhibits key characteristics including neonatal skin folds, rostral hairs, and absence of teeth. Throughout these key stages, dusky dolphins go through morphological changes as they grow to sexually mature adults. While there is significant research body on the ontogeny and morphology of many marine mammals (Adamczak et al., 2023; Agbayani et al., 2020; Barroso et al., 2012; Betty et al., 2022; Cooper et al., 2009; Cozzi et al., 2016; Ford & Raverty, 2014; Huggenberger & Cozzi, 2018; Lanzetti et al., 2022; Marchesi et al., 2020; Pavlov et al., 2021; Stolen et al., 2002; Sun et al., 2019; Yousuf et al., 2010), limited research on dusky dolphins currently exists.

Growth rates play a significant role in life history by facilitating a variety of ecological trade-offs between rapid and gradual growth (Arendt, 1997; Jennings et al., 2016). Faster-growing individuals outcompete siblings for food and are more resistant to predators (Jennings et al., 2016; Ricklefs, 1984). Faster growth also aids in weaning or reaching maturity earlier, which can boost survivability by accelerating the development of adult foraging skills or by increasing the amount of time spent foraging (Jennings et al., 2016). Differences in growth rate or mean body size during ontogeny can provide information about evolutionary or plastic responses to resources partitioning, resources availability and predation risk (Dmitriew, 2011).

Growth rates in cetaceans are highly influenced by the fat and protein content of the mother's milk (Sommers, 1998). The lipid-rich hypodermis of cetaceans, known as blubber, aids in movement, thermoregulation, buoyancy control, and streamlining (Struntz et al., 2004). At births, neonates demonstrate low blubber mass, depth, and lipid content. For the first few months of life, a neonate requires a large portion of its sustenance from the fatty-rich milk of its mother, as it is yet to be able to independently hunt (Sommers, 1998; Struntz et al., 2004).

1.6 Length at Birth

The body length of cetaceans at birth varies significantly across different species, showcasing the remarkable diversity of marine mammals. For example, blue whales (*Balaenoptera musculus*), have newborn calves that measure approximately 7 meters (23 feet) in length (Perrin et al., 2009). This significant birth size is noteworthy and highlights the immense size of these animals. In comparison to their body size, small odontocetes give birth to the largest cetacean neonates (Caspar & Begall, 2022). An example of this is the harbour porpoises (*Phocoena phocoena*), which give birth to calves approximately 70 to 80cm (Börjesson & Read, 2003; Hooker, 2018; Learmonth et al., 2014; Lockyer, 1984; Norman et al., 2018). The initial size of these newborns is crucial for their early survival, as it impacts their vulnerability to predators and ability to regulate body temperature (Börjesson & Read, 2003; Chivers, 2018; Fortune et al., 2012; Norman et al., 2018). The size of cetacean calves at birth provides insights into the mother's investment in pregnancy, with larger species typically having longer gestation periods and giving birth to proportionally larger offspring (Christiansen et al., 2022; Clapham et al., 1999). Understanding the length at birth provides guidance for conservation efforts, as it can guide strategies aimed at protecting these marine mammals at different stages of their lives.

Peruvian dusky dolphins are born at an average length of 91cm (*n* = 183) (Van Waerebeek & Read, 1994). These dolphins exhibit a growth rate of 0.261cm per day (Van Waerebeek & Read, 1994). Comparatively, the New Zealand population has previous reported length at births ranging from 97 to 120cm (*n* = 5), with individuals demonstrating milk in their stomachs (Würsig, 2007). Conversely, within the South African population, dusky dolphins are estimated to be born at lengths of 86 to 87 cm, based on measurements of 13 live or freshly dead neonates, which ranged from 81.5 to 91 cm (average 86.6 cm), and 16 dead and decomposing neonates, which ranged from 72 to 88 cm (average 81.8 cm). However, the total sample size of 29 individuals, and the inclusion of decomposing neonates with poor body condition may influence the reliability of these estimates (Best & Meÿer, 2010). Among these populations, the Peruvian dolphins appear to have intermediate birth sizes, with the New Zealand population showing the largest reported lengths at birth and the South African population the smallest.

1.7 Sexual Maturity and Physical Maturity

Mammals reach sexual maturity when they can produce viable offspring, which is determined by various factors including age, body size, and hormonal fluctuations (Chen et al., 2022; McKenzie et al., 2007). Male cetaceans attain sexual maturity through spermiogenesis, which leads to the development of mature male gametes (Betty et al., 2019; Plön & Bernard, 2007). Females reach sexual maturity after their initial ovulation by the presence of *corpora* on the ovaries (Anabella et al., 2017; DeMaster, 1984; Plön et al., 2012). The age at which sexual maturity is attained varies greatly among species and ranges from ca three years in harbour porpoise to 16 years in killer whales (Robeck & O'Brien, 2018; Webber et al., 2023; Wright et al., 2023). The age of sexual maturation typically varies between males and females, with females tending to reach sexual maturity earlier (LeDuc, 2009; Robeck & O'Brien, 2018). Estimates regarding the age and size at which dolphins reach sexual maturation hold significant value in facilitating comparative biological investigations and offering insights for the effective management of populations vulnerable to human-induced mortality (Bronikowski et al., 2022; Heydenrych et al., 2024; Kebke et al., 2022).

In contrast, physical maturity in cetaceans is the stage at which an individual reaches its maximum physical size and development, marked by the completion of skeletal growth (fusion of growth plates), maximum body length, and muscle mass (Aguilar & García-Vernet, 2018; Bishop, 2014). It is noteworthy that physical maturity generally occurs after sexual maturity, implying that numerous cetaceans are capable of reproducing prior to reaching their full growth potential (McPherson & Chenoweth, 2012; Wells & Scott, 2018). The time interval between sexual and physical maturity can vary significantly across species. Generally, larger whale species necessitate more time to attain both sexual and physical maturity in comparison to smaller species. For instance, certain large whale species may not achieve full physical maturity until they are more than 20 to 30 years old (Perrin et al., 1980). A comprehensive understanding of the differentiation between sexual and physical maturity is crucial for conservation and management endeavours. While the number of sexually mature individuals capable of reproduction may indicate population recovery, the overall health and resilience of the population also depend on the presence of physically mature individuals. These individuals are vital not only for contributing to genetic diversity but also for ensuring the population's ability to withstand environmental challenges. Individuals that reach physical maturity are generally better equipped to handle environmental stressors, such as food shortages or habitat degradation, and are more likely to have longer lifespans and increased reproductive success (Clutton-Brock & Sheldon, 2010; Hecht, 2021). The absence of physically mature individuals could suggest unfavourable environmental conditions, such as insufficient resources or other ecological pressures, which prevent individuals from reaching their full growth potential (Hecht, 2021). Thus, physical maturity is integral to the population's long-term survival and resilience, emphasizing the importance of considering both sexual and physical maturity in conservation strategies (Clapham et al., 1999; Reeves et al., 2003).

Growth curve analysis plays a crucial role in studying the development patterns, age-specific growth rates, and physical maturity (measured as asymptotic length) attainment in cetaceans. This analysis is essential for understanding their life history strategies and making informed decisions regarding conservation and management. Researchers utilize various models to analyse cetacean growth curves, with the von Bertalanffy growth function (Bertalanffy, 1938) being one of the most employed due to its ability to describe the sigmoidal growth pattern observed in many cetacean species. This model provides insights into the relationship between growth and time, offering estimates of maximum body size and the rate at which it is achieved (Bertalanffy, 1938). For example, studies on humpback whales (*Megaptera novaeangliae*) have utilized this model to demonstrate their rapid growth during early years, followed by a gradual plateau as they approach physical maturity (Lockyer et al., 1981). Such analyses are not only crucial for understanding the biological and ecological aspects of cetacean life but also for evaluating the impacts of human activities such as whaling and habitat changes on cetacean populations (Perrin et al., 2009). For instance, growth pattern studies have revealed how energy allocation during development reflects individual and population health, providing critical indicators for conservation efforts (Adamczak et al., 2023). Similarly, habitat modelling techniques based on growth and distribution data have informed effective management plans to mitigate anthropogenic threats, such as bycatch and habitat degradation (Redfern et al., 2006). Such insights enable conservationists to develop targeted management strategies, such as setting sustainable bycatch limits, protecting critical habitats, and monitoring population recovery trends.

By conducting growth curve analysis, researchers can infer important factors such as the age of sexual maturity, reproductive output, and even longevity, which in turn enables targeted conservation efforts to be established throughout their lifespan. By conducting growth curve analysis, researchers can deduce important factors including the age at which sexual maturity is reached, reproductive output, and even longevity. The age and size at which sexual and physical maturity is attained can vary among different populations. In the case of Peruvian dusky dolphins, they reach sexual maturity at a relatively young age and larger size compared to the New Zealand and South African populations. Female Peruvian dusky dolphins reach sexual maturity between 4.3 to 5 years, while males reach sexual maturity between 3.8 to 4.7 years (Van Waerebeek & Würsig, 2018). Both sexes reportedly reach a length of 175cm at sexual maturity (Van Waerebeek & Würsig, 2009). Additionally, both male and female Peruvian dusky dolphins reach a physically mature length at 185cm (Van Waerebeek & Würsig, 2009).

Manzilla (1989) reported on the reproductive status of 41 dusky dolphins (27 females, 14 males), from in Peru between 1985 and 1986, reporting that immature females ranged in total body length from 127 to 179.5cm (*n* = 8). In that study, the three largest immature females (174, 177, and 179.5cm) had developed ovarian follicles, while mature females (*n* = 18) reached total body lengths of 173 to 193cm. Of the 14 males in Manzanilla (1989), twelve were deemed mature with the presence of seminal fluid in the epididymis, ranged in TBL from 176 to 206cm. The remaining two immature males demonstrated total body lengths of 141 and 172cm. This research highlights how the length at sexual maturity varies within both the species and across populations.

Conversely, male South African dusky dolphins become sexually mature at a length of approximately 160cm, while females attain sexually mature at 170 to 175cm, at an average age of 6.3 years (Best & Meÿer, 2010; Van Waerebeek & Würsig, 2018). Both sexes are estimated to reach physical maturity at 179.9cm (Best & Ross, 1984; Van Waerebeek, 1993). For the New Zealand population of dusky dolphins, sexual maturity is estimated to be reached between 160 and 165cm, at an age of between 7 and 8 years for both sexes (Cipriano, 1992; Cipriano & Webber, 2010; Würsig, 2007). Physical maturity is estimated to occur at a length of 179.1cm (Van Waerebeek, 1993).

1.8 Sexual Dimorphism

Dimorphism, derived from the Greek words “di” meaning two and “morph” meaning form, refers to the existence of two distinct forms within a species. Specifically, “sexual dimorphism” described the phenomenon where the external appearances of males and females of a species differ. Alternatively, when male and female individuals have identical external appearances, they are referred to as “monomorphic” (Mesnick & Ralls, 2018; Würsig et al., 2023). Sexual dimorphism is widely observed across numerous species and animal groups and is prominent among odontocete species, with variations manifesting across body size, shape and size of the dorsal fin, tail fluke size, presence of postnatal humps, beak length, and colour pigmentation patterns. Mesnick & Ralls (2018), Murphy & Rogan (2006), and Ralls & Mesnick (2009) all provided independent exemplars of such differences, emphasizing the significant influence of sexual dimorphism in some odontocetes. To analyse these differences, the study of geometric morphometrics proves valuable as it focuses on quantifying shape and its variations. Klingenberg (2016) explains that shape, in this context, pertains to the arrangement of external features of an organism that can be measured, including lengths and proportions. Studying sexual dimorphism through morphological analysis provides a means to investigate heterogeneity, contributing to insights into health and population stability among marine mammals (Agbayani et al., 2020).

Sexual dimorphism can represent the social structure and behaviour of a species and is present in odontocetes (toothed whales), mysticetes (baleen whales) and pinnipeds (Betty et al., 2022; Ralls & Mesnick, 2009). The proportional size of the different sexes varies greatly among the more than 75 odontocetes species (Mesnick & Ralls, 2018; Ralls & Mesnick, 2009). Males are bigger than females in several species, with sperm whales (*Physeter macrocephalus*), killer whales, bottlenose whales (*Hyperoodon ampullatus*), narwhals (*Monodon monoceros*), belugas (*Delphinapterus leucas*), and pilot whales (*Globicephala* spp.) having the most significant dimorphism (Ralls & Mesnick, 2009; Würsig et al., 2023). Conversely, in other species such as Arnoux’s beaked whales (*Berardius arnuxii*), vaquita (*Phocoena sinus*), harbour porpoise, Hector’s dolphins, and Commerson’s dolphins (*Cephalorhynchus commersonii*), females are typically larger than males (Caspar & Begall, 2022; Ralls & Mesnick, 2018). Caspar and Begall’s (2022) indicated that small-bodied species predominantly exhibit female-biased sexual dimorphism and monomorphism, while species exceeding 2.5 meters in body length typically display varying degrees of male-biased sexual dimorphism.

Research on sexual dimorphism in dolphins has provided valuable insights into evolution and social dynamics. Perrin (1975) discovered that male spotted dolphins are notably larger with more prominent dorsal fins than females, indicating potential influences on mating competition and social hierarchy. Connor et al., (2000) states that the larger size of male bottlenose dolphins is crucial for mate competition and dominance establishment. Mann et al., (2000) also revealed that size differences between male and female bottlenose dolphins impact their foraging behaviour, affecting their ecological roles. These studies collectively emphasize the significance of sexual dimorphism in dolphins, not only in physical attributes but also in social interactions and ecological functions.

The origins of sexual dimorphism in odontocetes, like other animals, are believed to stem from evolutionary pressures that affect males and females differently. These selective forces are often tied to the distinct reproductive and ecological roles of each sex. Blanckenhorn (2005), Jennings et al., (2016), and Teder (2014) discuss how these roles shape physical development and behaviour, suggesting that sexual dimorphism is an outcome of adaptive strategies. For example, cetaceans exhibit a notable pattern where males undergo extended periods of development. This prolonged growth is thought to be associated with male-specific reproductive strategies. Conversely, females invest their energy and resources into reproduction, reaching physical maturity at an earlier age than males.

Ralls (1977) observed that most mammals are "not extremely dimorphic," noting the abundance of species with little to no sexual dimorphism (SD) across various mammalian orders, including those with larger females. Ralls' research demonstrated a trend towards female-biased dimorphism, though this could be influenced by the presence of pregnant females. Additionally, the study found that sexual size monomorphism was almost as common as the occurrence of larger males (Tombak et al., 2024). These findings challenge the traditional perspective in sexual selection research, which often assumes that males are larger due to their involvement in competition for mates and the advantages of greater size in intrasexual rivalry. This perspective, based on Darwinian sexual selection theory, has historically emphasised traits such as increased body size, specialised physical adaptations, or other attributes that enhance male reproductive success in species where males compete directly for access to females (Janicke et al., 2016; Padilla-Morales et al., 2024). However, observations of female-biased sexual dimorphism, sexual size monomorphism, and the presence of larger females in various species challenges the general validity of the assumption that males are typically larger, highlighting the need for a more comprehensive understanding of sexual selection dynamics. These observations emphasize the importance of adopting a broader perspective on sexual selection, one that considers the variety of reproductive strategies, ecological pressures, and the role of female size in enhancing reproductive success through factors such as gestation, lactation, and other life-history traits (Mollet et al., 2023; Tombak et al., 2024). This expanded perspective underscores that sexual selection operates in a complex and context-specific way.

Despite the extensive research conducted on sexual dimorphism in various cetacean species, there is a noticeable gap in the scientific literature regarding dusky dolphins. While studies have delved into aspects of their social behaviour, ecology, and general morphology (Markowitz, 2004; Würsig & Würsig, 1977), the specific area of sexual dimorphism within this species has not received adequate attention.

The Peruvian population of dusky dolphins has had more extensive research conducted with clear dimorphism in total body length (Van Waerebeek 1993). However, highly significant differences in two linear and three appendages body measurements were reported in this population; snout to blowhole and snout to anus, and maximum flipper width, base length of dorsal fin, depth of flukes and one girth measurement; girth at anus.

The degree of sexual dimorphism in the New Zealand population of dusky dolphins is not yet understood. Van Waerebeek (1993) analysed the mean and maximum lengths of South-West Africa and New Zealand populations of dusky dolphins and concluded that both populations are 8 to 10cm shorter than the Peruvian population (Table 1.1). More recent research conducted by Van Waerebeek and Würsig (2009) showed the dorsal fins of male dusky dolphins tend to be thicker, broader at the base and more rounded in comparison to female counterparts. The maximum length at maturity for New Zealand dusky dolphins further varied by less than 5% between males and females (Markowitz et al., 2023). Research on the sources of variation in the morphology of dusky dolphins can reveal information about the dolphin's life since the presence or absence of sexual dimorphism can represent the species' social structure and behaviour within pods.

Table 1.1 Total body length and age data available for dusky dolphins (*Lagenorhynchus obscurus*) from New Zealand, South Africa, and Peru.

	New Zealand		**South Africa**		**Peru**	
	Female	**Males**	**Females**	**Males**	**Females**	**Males**
Year of key studies	1992[6], 2007[7], 2010[9]		1993[3], 2010[8]		1982-1983[4],1985-1990 [1], 1993[11], 2009[2]	
Research methods	Growth curves and growth layer groups (GLGs) used to assess length and age to determine maximum age and length as well as maturity classes based on age and length.[6]		Length–weight regressions to estimate growth and age/maturity. Visual comparison between the weights of non-juvenile individuals in different seasons. Compared length/weight regressions to observe health among population.[8]		GLGs to assess if one year of age acquainted to 1 growth layer in dentine during El Nino[4]	
Average length at birth	97-120cm (*n* = 5) all had only milk in their stomachs[6,7]		86-87cm (*n* = 29)[8] mean overlap. Weight at birth 8354g (*n* = 10)[8]		Growth rate of 0.261cm/day; born at mean length of 91cm and 9.6kg [1]. Neonates (*n* = 87) and near-term foetuses (*n* = 96) [1].	
Length at sexual maturity	160-165cm (*n* = 21)[6,7,9] sexes pooled		170-175cm [8] (*n* = 16)	166-176cm [8] (*n* = 37)	175cm (*n* = 394)[13] sexes pooled	
Average age of sexual maturity (yrs.)	7-8 [6,7,9]	7-8 [6,7,9]	Currently Unknown	Currently Unknown	4.3-5 [11]	3.8-4.7[11]

Average length at physical maturity	170-180cm ($n = 12$)[6] Sexes pooled		Currently Unknown	Currently Unknown	Currently Unknown	Currently Unknown
Average age at physical maturity length (yrs.)	Currently Unknown	Currently Unknown	Currently Unknown	Currently Unknown	Currently Unknown	Currently Unknown
Maximum length (cm)	170-180[6,7] ($n = 8$) New Zealand individuals ca. 8–10 cm shorter than Peruvian specimens of both sexes[2]	170-180[6,7] ($n = 12$)	190-191cm ($n = 53$)[8] Southwestern Africa individuals ca. 8–10 cm shorter than Peruvian specimens of both sexes[2]	190-191cm ($n = 51$)[8]	205cm [2,4]	211cm [2,4]
Maximum age (years)	22-24[6] ($n = 1$)	35-36[6] ($n = 1$) 26-30[6] ($n = 1$)	21[15] ($n = 1$) Three captive individuals that died were aged, oldest was around 21 years old.		11.5 ($n = 27$)[9, 14]	15-22[14] ($n = 14$)
Sexual dimorphism	Males have slightly larger dorsal fins, with a broader base and greater surface area than females. No sexual dimorphism in colour pattern was noted. [3,6,9]		No difference in size between sexes[8]. Males have larger flipper and fluke indices[8]. Male flippers range from 40-47.49cm ($n = 10$), female flippers range from 39.5-45cm ($n = 14$)[8]. Male flukes range from 54-63.99cm ($n = 7$), female flukes range from 51-58cm ($n = 15$)[8].		Small but highly significant differences in six body measurements; girth at anus, maximum flipper width, base length of dorsal fin, depth of flukes, snout to vent and snout to anus.[3]	

1.Van Waerebeek & Read (1994), 2. Van Waerebeek & Würsig (2009), 3. Van Waerebeek, (1993a), 4. Manzanilla-Naim (2011), 5. Best & Ross (1984), 6. Cipriano (1992), 7. Würsig (2007), 8. Best & Meÿer (2010), 9. Cipriano & Webber (2010), 10. Leatherwood et al., (1983), 11. Van Waerebeek & Würsig (2018), 12. Jefferson et al., (2008), 13. Van Waerebeek (1993), 14. Manzanilla-Naim (2011), 15. Best (1976).

1.9 Reproduction

Mating systems can be broadly classified into two main types: monogamy and polygamy, each exhibiting distinct sexual dimorphism characteristics. Mating systems, however, are shaped not only by competition and choice but also by the temporal and physical availability of mates, as well as phylogenetic effects and resource distribution. In monogamous systems, individuals have exclusive mates for at least one oestrous cycle, associated with physical monomorphism between females and males due to the limited sexual selection pressures (Würsig et al., 2023). In contrast, polygamous systems, where individuals mate with multiple partners, exhibit high levels of sexual dimorphism due to male competition for female attention or female mate choice. Polygamy can be further subdivided into polygyny, polyandry, and polygynandry. Polygyny is characterized by males competing with other males and mating with multiple females, with minimal involvement in offspring care, leading to pronounced sexual dimorphism (Würsig et al., 2023). In polyandrous systems, multiple males mate with a single female, and males often assume the responsibility for offspring care; here, females exhibit dimorphism through external markings, and males typically possess large testes relative to their body size due to sperm competition (Würsig et al., 2023). Polygynandry, which incorporates elements of both polyandry and polygyny, involves both sexes mating with multiple partners during one reproductive period. This system tends to result in monomorphic coloration and size, often making it difficult to distinguish from monogamy based on physical traits alone (Würsig et al., 2023).

The reproductive strategies among cetaceans also vary, from the highly social and polygynous systems observed in some delphinid species to the more solitary systems of many large whales, influencing both mating behaviour and parental investment (Clapham, 2000; Connor et al., 2001; Markowitz et al., 2010). These variations reflect a complex interplay between ecological conditions, social structures, and evolutionary pressures, underscoring the adaptability and diversity of cetaceans within their habitats.

Cetaceans exhibit a wide array of reproductive characteristics across different species, populations, and sexes. These characteristics encompass both the anatomical features of reproductive organs, and the behaviours associated with reproduction. Male cetaceans are known for their relatively large testes that can vary significantly in size, even within populations, potentially as a response to different mating systems (Robeck, 2005). Indicators such as sexual dimorphism, testes size, and sociality serve as crucial social and biological markers for determining mating systems among cetaceans (Ralls and Mesnick, 2019). Female cetaceans have evolved various adaptations for gestation and birth within marine environments, alongside extensive postnatal care and intricate reproductive cycles (Chivers, 2018; Oftedal, 1997).

1.9.1 Male Reproduction

The reproductive development of young cetaceans has not been extensively studied. This is in part due to the challenges associated with acquiring comprehensive samples that accurately represent the different stages of growth and development prior to reaching sexual maturity (Atkinson, 2009; Plön & Bernard, 2007). Different factors can be used to assess the sexual development of cetaceans, including the average size of seminiferous tubules, the relative presence of Sertoli cells, interstitial tissue, germinal cells (such as spermatogonia, spermatocytes, spermatids, and spermatozoa), the activity in the epididymis, and the presence and proportion of spermatozoa in the epididymis (Atkinson, 2009; Palmer et al., 2023; Plön & Bernard, 2007).

Notable variation in the reproductive characteristics exist among populations and ecotypes of the same species (Chen et al., 2011; de Bruyn et al., 2013). For instance, Murphy et al., (2020) reported that male harbour porpoises in the North Atlantic attain sexual maturity at a significantly greater body length than those in the North Sea. Moreover, individuals in this region also intermingled with the larger, recently proposed sub-species of Iberian harbour porpoises, which further contributes to the increased body length required for sexual maturity in males, as highlighted by Murphy et al., (2020) and Palmer et al., (2023).

In a review of available data on combined testis sizes in relation to proposed mating systems for cetaceans, Plön and Bernard (2007) determined that a monogamous or extreme polygynous mating system can be inferred from relatively small testes in relation to body weight. Conversely, relatively large testes are indicative of frequent copulations and sperm competition (Plön et al., 2012; Plön & Bernard, 2007). The investigation of male seasonality in cetaceans poses challenges due to the necessity of collecting samples consistently throughout the year (Miller, 2016). However, the reliance on opportunistic sampling from stranded or bycaught animals often hinders the attainment of a representative sample (Miller, 2016).

A recent study by Palmer et al., (2023) showed that a combined testicular weight for New Zealand common dolphins ranged from 2 to 57.8g for immature individuals (*n* = 35), 135 to 283g for pubescent individuals (*n* = 2), and 492 to 5796.5g for mature individuals (*n* = 24), while testicular length ranged from 27 to 274mm for immature individuals, 318 to 429mm for pubescent individuals, and 275 to 965mm for mature individuals. Palmer et al., (2023) reported evidence of reproductive seasonality which is has also been observed in the eastern North Atlantic common dolphin population. Reproductive seasonality has also been observed in belugas, with a minimum testicular volume of 816.37cm^3 in August and a maximum testicular volume of 1742.87cm^3 in December, with an average increase in volume by a factor of 1.57 (Richard et al., 2017).

Dusky dolphins demonstrate a polygynandrous mating system, which relies upon sperm competition (Pearson, 2019), as evidenced by large testes, which can account for up to 5.4% of total body weight (Table 1.2) during mating season (Cipriano, 1992; Deutsch, 2008; Markowitz et al., 2010; Van Waerebeek & Read, 1994). A subadult from the South African population with a total body length of 173cm had a combined testis weight of only 134g (Best, 1976). This compares to adult males from the same population whose combined testes weighs up to 1.6kg (Best, 1976).

Cipriano (1992) analysed the testes of nine adult male dusky dolphins in New Zealand. Of the nine individuals examined, five had enlarged testes (995 to 2143g each, including epididymis) with semen present in the epididymis. The remaining four males ranged measuring 165 to 175cm, were aged between 12 to 26 years, with inactive testes ranging between 252 to 479g. Van Waerebeek and Read (1994) analysed the testis weight (including epididymis) of 125 dusky dolphins of all ages from Peru. Testicular weights ranged from 53 to 5120g and 53 to 4930g for the left and right testis, respectively, with a maximum combined testes weight of 9730g reported (Van Waerebeek & Read, 1994).

Table 1.2 Male reproductive data available for dusky dolphins (*Lagenorhynchus obscurus*) from New Zealand, South Africa, and Peru

	New Zealand		**South Africa**		**Peru**	
	Left	**Right**	**Left**	**Right**	**Left**	**Right**
Mature testis mass	277.4-2143g[2] (*n* = 9)	252.5-2085g[2] (*n* = 9)			53-5,120g ($\bar{X}$ = 1,464g; *n* = 125)[1]	53-4,930g ($\bar{X}$ = 1,486g; *n* = 125)[1]
Mature testis mass (without epididymides)			>1.76m in length, large testes 500 g or more combined (*n* = 8)[3]			
Mature testis length					12.3-58.5cm (*n* = 132)[1]	13.5-58.0cm (*n* = 133)[1]
Mature testis length (without epididymides)			24cm[3] (*n* = 10)	24cm[3] (*n* = 10)		
Months when testis are largest	Spring-summer[2] (September to February)		Late summer[3] (February to March)		Increased in August, maximum in September and October, and then decreased again in November.[1]	
Immature testis mass	12-637g (*n* = 3 juveniles, *n* = 1 subadult)[2]	12.9-663g (*n* = 3 juveniles, *n* = 1 subadult)[2]			Heaviest 300g (*n* = 38)[1]	Heaviest 310g (*n* = 38)[1]
Immature testis mass (without epididymides)			Up to 165cm had testes weighing >80g combined (*n* = 18)[3]			
Immature testis length					23cm (*n* = 38)[1]	24cm (*n* = 38)[1]
Immature testis length (without epididymides)						

1.Van Waerebeek & Read (1994), 2. Cipriano (1992), 3. Best & Meÿer (2010)

1.9.2 Female Reproduction

Sexual maturity in cetaceans (see section 1.6) plays a significant role in determining the timing and success of breeding. The breeding cycle of female cetacean species comprises three distinct phases, namely gestation, lactation and resting periods (also known as anoestrous) (Chivers, 2018). For the majority of these species, this cycle spans a duration of two years or longer (Mikhalev, 2019). However, it is worth noting that annual breeding is an exceptional occurrence, which has only been documented in minke whales (*Balaenoptera acutorostrata*) and harbour porpoises (Chivers, 2018). In odontocetes, gestation ranges from 9 to 17 months depending on the species (Huggenberger & Cozzi, 2018; Reidenberg & Laitman, 2009). The gestation period in dusky dolphins varies across different populations (Table 3.1), with the New Zealand population reporting a gestation period of 11.4 months (Cipriano, 1992). In contrast, the South African population reports a slightly shorter gestation period of ten to eleven months, while the Peruvian population exhibits the longest gestation period at 12.9 months (Best & Meÿer, 2010; Van Waerebeek & Read, 1994). In comparison to other marine mammal groups, cetaceans exhibit prolonged gestation periods due to the full development of offspring in the womb, which enable newborns to possess immediate sensory and motor capabilities such as sight, hearing, swimming, and vocalization upon birth (Huggenberger & Cozzi, 2018; Palmer et al., 2022). Accordingly, newborns can be one-fifth of the length of the mother at birth (Huggenberger & Cozzi, 2018).

The lactation period in baleen whales lasts for approximately 6 months, during which the young experience rapid growth (Chivers, 2018). In contrast, odontocetes have a lactation period that extends beyond a year, resulting in a slower growth rate for their calves (Chivers, 2018; Mikhalev, 2019). In New Zealand dusky dolphins, the lactation period is 18 months (Leatherwood et al., 1983), compared to 12 months for the Peruvian population (Leatherwood et al., 1983; Van Waerebeek & Read, 1994). Currently, no information is available on the lactation period for the South African population. The extended period of lactation in odontocetes is attributed to the complex social structure of odontocetes, requiring more time for calves to learn the essential social behaviours for survival (Chivers, 2018). During this period, the calf learns important skills such as communication, hunting, and navigation from the mother and other members of the pod (Chivers, 2018). These skills are essential for the calf to survive and thrive in its environment. Calving intervals range from one year in smaller dolphin species to around eight years in larger dolphin species (Huggenberger & Cozzi, 2018).

The anoestrous period, a phase of the inactivity and recovery for the female, typically allows the female to rebuild energy reserves for the next reproductive cycle (Chivers, 2018). This period can last for several months or even years, depending on the species and environmental conditions (Chivers, 2018). There is currently no information available on the resting period for the New Zealand population of dusky dolphins. In contrast, the South African population has a resting period of approximately 2 to 3 years (Best & Meÿer, 2010). For the Peruvian population, the resting period is shorter, around 3.7 months, though data suggest this period may be biased due to the inclusion of females experiencing preimplantation pregnancy, a stage in which fertilised eggs do not immediately implant in the uterus (McKenzie et al., 2007; Van Waerebeek & Read, 1994; Van Waerebeek & Würsig, 2009). During preimplantation pregnancy, fertilized eggs may undergo early embryonic development but remain in a suspended state before implantation occurs (McKenzie et al., 2007). This delay in implantation can lead to variations in the timing of the reproductive cycle, potentially skewing estimates of the resting period and affecting the interpretation of reproductive data for this population. The anoestrous period is subsequently followed by the the oestrus cycle, i.e., follicles rupture and release matured ova, which then transform into the *corpus luteum* (CL) (Inbaraj et al., 2021). The CL's primary function is to secrete progesterone and support pregnancy, if it occurs (Inbaraj et al., 2021). If pregnancy does not occur, the CL will still form but will regress more quickly (Inbaraj et al., 2021).

After pregnancy or ovulation, the CL regresses and becomes the *corpus albicans* (CA), which is made up of fibrous scar tissue. The CA remains on the ovary for a significant period before disappearing, but in cetaceans, it remains visible on the ovary's surface throughout their lifespan (Inbaraj et al., 2021). Each CA indicates a previous ovulation, allowing for the analysis of an individual’s reproductive history (Berta et al., 2015; Inbaraj et al., 2021). The timing of the oestrus cycle is closely aligned with seasonal environmental conditions, ensuring that mating and subsequent conception occur during periods when resources are abundant. This reproductive seasonality is crucial for the survival of the calf, as it ensures that the birth coincides with favourable conditions for the neonates development (Norman et al., 2018; Robeck & O’Brien, 2018).

The inter calving interval, which is the time between births, vary widely among species and populations (Atkinson, 2024; Mikhalev, 2019). For instance, killer whales can have inter calving intervals up to five years, while bottlenose dolphins in some regions have been observed to give birth every two to three years (Matkin et al., 2014; Olesiuk et al., 2005; Robinson et al., 2017; Wright et al., 2023). Harbour porpoises typically have a much shorter interval, around ten to eleven months (Keener et al., 2018; Read & Hohn, 1995). In New Zealand and South Africa, dusky dolphins exhibit an inter calving interval of two to three years (Best & Meÿer, 2010; Markowitz, 2004). However, detailed information on the inter calving interval for the Peruvian population is currently lacking. This period is influenced by several factors, including duration of gestation, lactation, and the resting period (Atkinson, 2024; Chivers, 2018). Environmental factors, such as food availability, significantly impact the inter calving interval in delphinids (Davidson et al., 2017).

In regions where nutrients are abundant, delphinids often experience shorter inter calving intervals due to enhanced maternal health and more favourable conditions for gestation and calf rearing (Bezamat et al., 2019; Rechsteiner et al., 2013; Sim et al., 2015). In contrast, populations in areas with limited resources may face longer calving intervals, as reduced nutritional intake can negatively affect maternal health and reproductive success. Social factors also influence the length of the inter calving intervals in delphinids (Davidson et al., 2017). The presence of predators can lead to increased stress and a greater need for maternal vigilance, which can result in the prolonging of calving intervals (Fearnbach et al., 2011; Mann, 2019). Additionally, competition within a population for limited resources can further influence reproductive timing (Möller & Harcourt, 2008). High competition may strain individuals, impacting their overall health and reproductive cycles (Möller & Harcourt, 2008).

Table 1.3 Female reproductive data available for dusky dolphins (*Lagenorhynchus obscurus*) in New Zealand, South Africa, and Peru.

	New Zealand		**South Africa**		**Peru**	
Gestation period	11.4 months[1]		10-11 months[4]		12.9 months[3]	
Lactation period	18 months[2]				12 months[3] ($n = 87$, $n = 15$ pregnant and lactating)	
Resting period			2-3 years ($n = 15$)[4]		3.7 months[3,5] (Most likely biased as females experiencing preimplantation pregnancy were grouped in this category) (total $n = 144$ sexually mature, $n = 22$ resting)	
Birth season	November to January[1]		January to March[4]		August to October[1]	
Annual pregnancy rate					0.555 ($n = 165$ sexually mature females)[3]	
	Left	**Right**	**Left**	**Right**	**Left**	**Right**
Ovary length						
Ovary weights	14.8g ($n = 1$, adult)[1]	1.6g ($n = 1$, adult)[1]				

1. Cipriano (1992), 2. Leatherwood et al., (1983), 3. Van Waerebeek & Read (1994), 4. Best & Meÿer (2010), 5. Van Waerebeek & Würsig (2009)

1.10 Study Species – Dusky Dolphin (*Lagenorhynchus obscurus*)

The *Lagenorhynchus* genus consists of five delphinid species, Pacific white-sided dolphin (*L. obliquidens*), white-beaked dolphin (*L. albirostris*), Atlantic white-sided dolphin (*L. acutus*), dusky dolphin (*L. obscurus*) and Peale's dolphin (*L. australis*) (Cipriano & Webber, 2010; Harlin-Cognato, 2010). While the hourglass dolphin (*Lagenorhynchus cruciger*) is still classified within the *Lagenorhynchus* genus, Vollmer et al. (2019) recently proposed reassigning the species to the genus *Sagmatias*. This recommendation stems from phylogenetic, morphological, and acoustic analyses that revealed significant genetic and phenotypic differences, suggesting that *L. cruciger* is more closely aligned with species in the genus *Sagmatias*. Irrespective of taxonomic debate, all current members of the *Lagenorhynchus* genus have a relatively short rostrum, a pronounced falcate dorsal fin, a robust body form, and a complex pattern of body colour characterised by bands, stripes, and flares of numerous hues (Harlin-Cognato, 2010).

Dusky dolphins are classified as a semi-pelagic since they can be found in both coastal and continental shelf waters (Würsig & Pearson, 2014). The range of dusky dolphins includes South America, from northern Peru, south to Cape Horn and from southern Patagonia north to the Falkland Islands (Malvinas); off southwestern Africa, from False Bay in South Africa to Lobito Bay in Angola; and off South Island New Zealand (Figure 1.3). Additional poorly described populations further occupy the seas surrounding the mid-Atlantic oceanic islands of the Tristan da Cunha Archipelago, the Prince Edward Islands, and Crozet and Amsterdam Island in the southern Indian Ocean (Cipriano & Webber, 2010; Harlin-Cognato, 2010; van Waerebeek et al., 1995; Van Waerebeek & Würsig, 2009). To date, the majority of the research conducted on *dusky dolphins* has been conducted off Peru. However, molecular phylogeography suggests regional dusky dolphin populations are genetically isolated from one another and should be treated as separate stocks, if not subspecies (Harlin-Cognato, 2010).

Dusky dolphins were first documented in New Zealand waters over a hundred and fifty years ago and originally identified as *Clymenia obscura* (Cipriano & Webber, 2010; Hector, 1872, 1878; Würsig & Würsig, 2009). In present-day New Zealand, dusky dolphins are most observed in two specific areas: between the Kaikoura Peninsula and the Haumuri Bluffs, and in Admiralty Bay, Marlborough Sounds (Cipriano & Webber, 2010; Gaskin, 1972; Würsig, 2007; Würsig & Würsig, 2009). These areas, however, reflect regions of concentrated research rather than the species' full distribution across New Zealand waters. While much of the research on dusky dolphins has focused on the South Island, these locations do not represent the primary centres of their distribution within New Zealand. Population estimates for the species in New Zealand are limited but thought to be around 12,000 animals (Markowitz, 2004; Orbach et al., 2018).

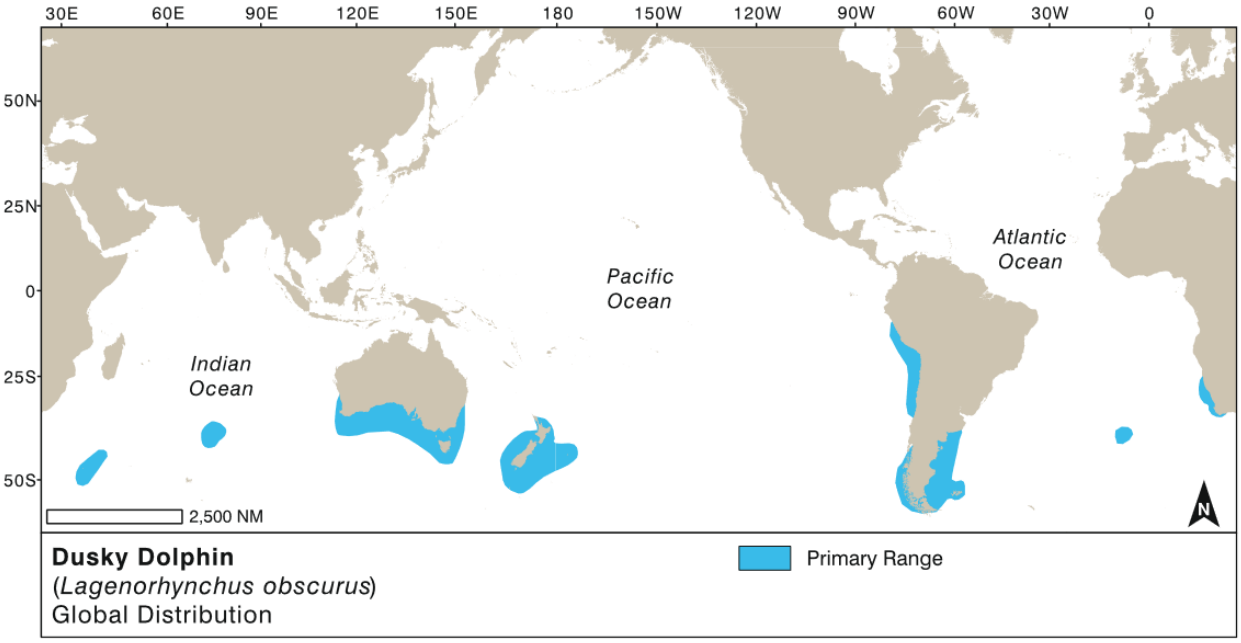


Figure 1.3 Dusky dolphin distribution from Jefferson, T. A., Webber, M. A., & Pitman, R. L. (2008). Cetaceans. In T. A. Jefferson, M. A. Webber, & R. L. Pitman (Eds.), Marine Mammals of the World (pp. 22–305). Academic Press. https://doi.org/10.1016/B978-0123

Despite their southern hemisphere range (Figure 1.3), there remains significant knowledge gaps concerning key biological aspects of the New Zealand population. This includes a lack of insight to age structure, growth rates, allometry, and sexual dimorphism of the New Zealand population, which hinders current understand of the population dynamics. Accordingly, the overarching aim of my thesis is to address some of these critical knowledge gaps by examining the age, growth and reproductive characteristics of this population. My specific study objectives were to;

Study Objectives

1: Assess age structure, growth rates, allometry and sexual dimorphism of dusky dolphins in Aotearoa New Zealand waters;

and

2: Estimate the reproductive parameters in male and female dusky dolphins in Aotearoa New Zealand waters.

Chapter 2 Methods

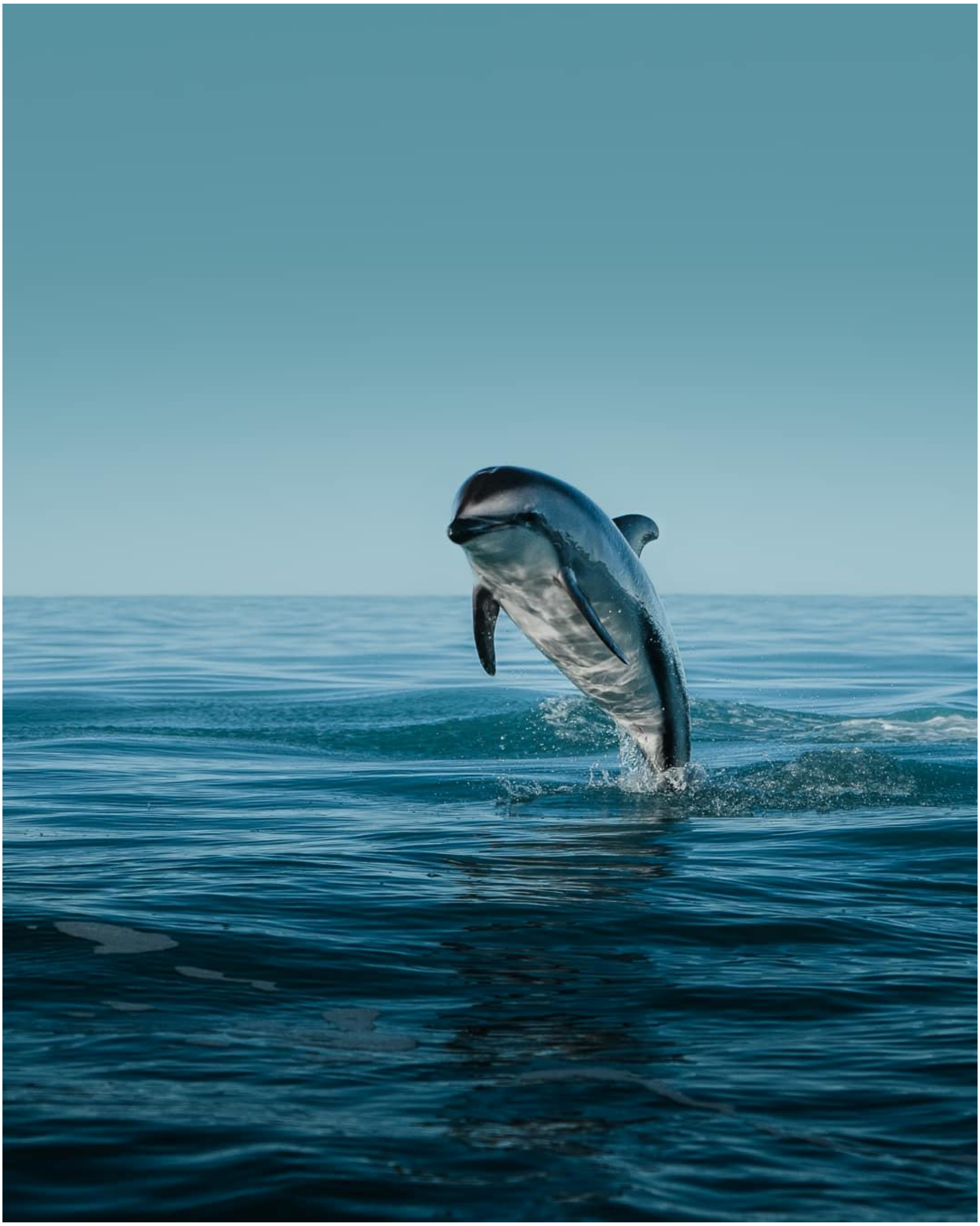


Photo credit: Jared Kreiss

2.1 Data Collection

Between 1872 and 2023, a total of 216 stranding and bycatch incidents involving dusky dolphins (*Lagenorhynchus obscurus*) were included in the New Zealand Whale Stranding Database (NZWSDB), administered by the New Zealand Department of Conservation Te Papa Atawhai (DOC). While the NZWSDB contains data dating to 1872, the documentation of events became more consistent after 1978, when DOC took over the administration of database. Indeed, prior to 1980, only 44 incidents were captured within the NZWSDB. Of those 44 cases, only 16 animals had morphometrics reported. Of those, six individuals (one female and five males) were previously reported on by Cipriano (1992).

The data analysed in this study consisted of a subset of 143 individuals, which were a subset of the NZWSDB dataset. Species confirmation was via either confirmed via DNA, photographs and/or diagnostic morphometry in the context of incident location (e.g. absence of pronounced rostrum, TBL and coastline to exclude misidentified *Cephalorhynchus*). All 143 individuals (51 females, 73 males, 14 individuals of unknown sex, and five foetuses) included in this study had available morphometric measurements, which were collected by the Department of Conservation (1960 to 2023; n = 93) and Massey University Te Kunenga ki Pūrehuroa (1997 to 2023; n = 50).

External measurements were recorded from individuals following Murphy and Rogan (2006) and Betty et al., (2022), with a total of 26 measurements assessed (Figure 2.1, Table 2.1). Due to the opportunistic nature of sampling during stranding events, not all individuals had all measurements recorded, resulting in varying sample sizes across different measurements, calculations, figures, and tables. Regression analysis was conducted to ensure measurement accuracy, account for inter-observer error, and identify outliers, which is crucial for maintaining the integrity of the data and ensuring that any variation in the measurements is due to biological differences rather than methodological inconsistencies. Each measurement was plotted independently against total body length for males and females to assess relationships and identify any potential measurement errors or outliers that could skew the results (Murphy & Rogan, 2006).

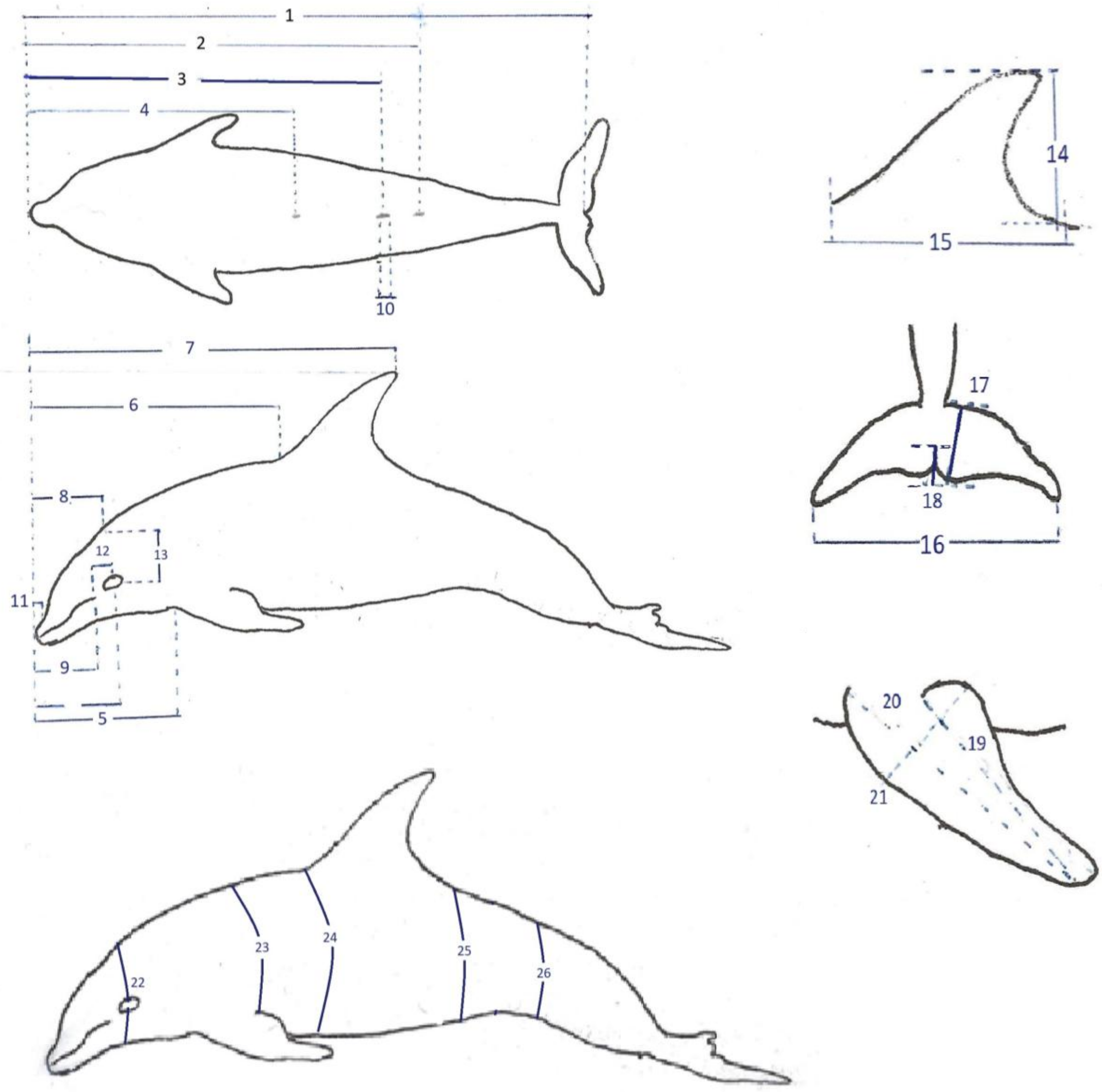


Figure 2.1 Body morphometric measurements taken of dusky dolphins in New Zealand.

Table 2.1 Measurements taken with abbreviations

	External Characteristics Measured	Abbreviation
1	Body length, Tip of rostrum to tail notch	TBL
2	Snout to anus	Snout-anus
3	Snout to genital slit	Snout-genital
4	Snout to navel	Snout-navel
5	Snout to origin flipper	Snout-flipper
6	Snout to origin dorsal fin	Snout-dorsal
7	Snout to tip dorsal fin	Snout-tip dorsal
8	Snout to blowhole	Snout-blowhole
9	Snout to corner of mouth	Snout-cnr mouth
10	Genital slit length	Genital slit
11	Rostrum length	Rostrum length
12	Corner of mouth to eye	Cnr mouth-eye
13	Eye to blowhole	Eye-blowhole
14	Dorsal fin height	Dorsal height
15	Dorsal fin lat base	Dorsal base
16	Width of fluke	Fluke width
17	Length of fluke	Fluke length
18	Fluke notch	Fluke notch
19	Length of flipper – Internal	Flipper-int
20	Length of flipper – Exterior	Flipper-ext
21	Flipper width	Flipper width
22	Girth at eye	Girth-eye
23	Girth at flippers	Girth-flippers
24	Axillary girth	Axill-girth
25	Girth at navel	Girth-navel
26	Girth at anus	Girth-anus

2.2 Sex Determination

Sex was determined anatomically, via the genital region located on the ventrum (Ijsseldijk et al., 2020; Figure 2.2). Females exhibit distinctive anatomical features such as the presence of mammary slits, which are situated on either side of the genital slit. Additionally, females possess a continuous external genital slit that functions as a passage for both the vagina and anus. In contrast, males have distinct genital and anal slits, where the anal opening is several centimetres caudal to the genital slit (Markowitz et al., 2010; MMAPL, 2023b; Schroeder, 1990).

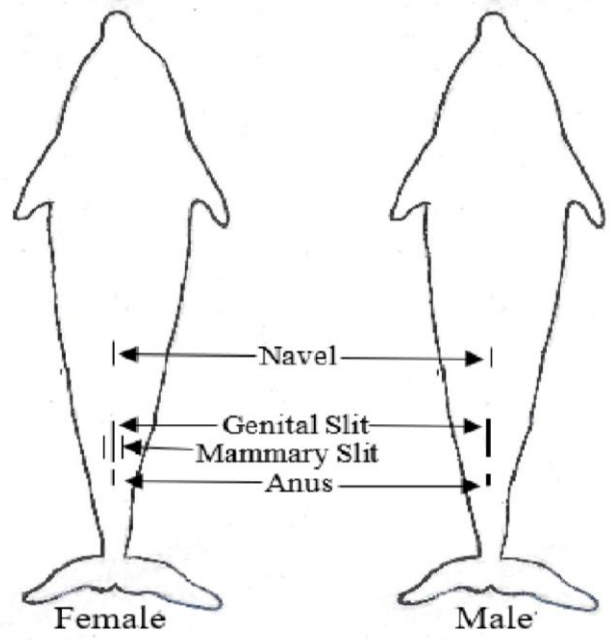


Figure 2.2 Anatomical differences between sexes

2.3 Age Estimation

Age estimation in odontocetes is predominately predicted through identifying and counting Growth Layer Groups (GLGs), where each layer represents one year of life, in the dentine of thin, decalcified, and stained sections of teeth (Evans & Hindell, 2004; Murphy et al., 2018b; Palmer et al., 2022). During necropsy, three to six teeth were extracted from the centre of the upper and lower jaw of individuals, which were then preserved in either 70% ethanol, frozen, or dried for analysis (Betty et al., 2019; Palmer et al., 2022). Analysis involved the sectioning and staining of the teeth to reveal the GLGs (Hamilton & Evans, 2018). The GLGs were then counted by multiple readers to ensure accuracy.

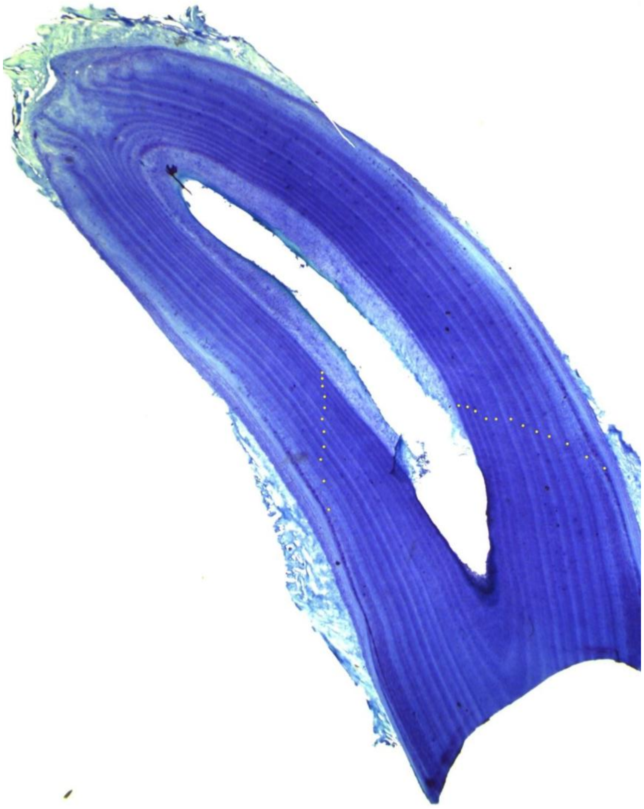


Figure 2.3 Section of stained tooth showing growth layer groups (GLGs) in the dentine of dusky dolphins (*Lagenorhynchus obscurus*; KS11-51Lo) stranded on New Zealand Aotearoa coast in 2011 and aged 11 years. Image CERG Pathology Unit, Massey University. Note: dots represent each GLG.

Teeth for aging were available from 23 cadavers (10 females, 12 males, and 1 individual of unknown sex) assessed postmortem between 2010 and 2023 at Massey University. Teeth sections were carefully examined using a binocular microscope, with magnifications ranging from 10x to 40x. All readings and age estimates were conducted blindly, without any prior knowledge of any biological information. Each section was thoroughly examined twice by a single experienced reader during three independent reads (Palmer et al., 2022, 2023). The best age estimates or age ranges obtained from these readings were then compared. In cases where a discrepancy greater than one GLG occurred, a second experienced reader re-examined the section with knowledge of the initial estimate. If a consensus could not be reached, an alternate section was chosen and reviewed by both readers until a final estimate was determined, following Betty et al., (2022). Individuals that could not be accurately aged due to tooth wear or damage were excluded from further analysis. To identify neonates, the presence or formation of the neonatal line in the dentine of the tooth was carefully observed.

2.4 Age Class

Foetuses were defined as any individual in utero or beachcast exhibiting characteristics diagnostic of a foetus (Reidenberg & Laitman, 2009; Stěrba et al., 2000) including closed eyes indicating incomplete development of visual capability, and highly malleable fins and flukes, facilitating adaptation to the intrauterine environment and easier passage through the birth canal (Barbara & Smuts, 1999; Cipriano, 1992; Cockcroft & Ross, 1990; Stěrba et al., 2000; Weir et al., 2010).

Neonates were defined as young calves that exhibit diagnostic characteristics of newborns (Stockin et al., 2008). The main characteristics used to distinguish between neonates from foetuses were the presence of teeth (Thewissen, 2018; Werth & Crompton, 2023), and secondly a detached, healed umbilicus and open eyes as a to transition from the prenatal to postnatal stage of development. Foetal folds (Barbara & Smuts, 1999; Cockcroft & Ross, 1990; Tezanos-Pinto, 2009) and marginal papillae were also used as notable characteristics in both foetuses and neonates.

Any individual which lacked features indicative of a foetus or neonate but sexually immature (see section 3.6) I considered immature. Mature individuals were defined by developed gonads (refer to sexual maturity section 3.6).

2.5 Growth Curve

Gompertz growth models are most suitable for describing the growth of most small cetaceans (Grandi et al., 2022; Stolen et al., 2002). Therefore, Gompertz growth curves were utilized to assess the growth patterns and the length at physical maturity (asymptotic length) of dusky dolphins. This was achieved by employing the following equation to model their growth:

$$L_{(t)} = A^{[-b^{-kt}]}$$

In this model, $L_{(t)}$ represents the total body length (TBL) at age t, A is the asymptotic value (the maximum length achievable as age approaches infinity), b is the constant of integration, and k is the growth rate constant.

2.6 Allometry

Allometric measures were taken to the nearest 0.5cm and analysed using methods modified from Betty et al., (2022) and Murphy and Rogan (2006). Regression plot analysis was conducted to lower inter-observer error, transcription error, and outliers. Every measurement (morphological data) underwent a logarithmic transformation [Log10(x)] to normalise the data, as this transformation helps linearise relationships between body size and other measurements, allowing for more accurate comparisons of proportionality and scaling. For both males and females separately, each measurement was plotted against the TBL. Data that deviated from the fitted line by more than three standard deviations was excluded from the dataset.

To analyse the growth patterns and make comparisons between sexes, allometric growth equations were utilized for the 26 body measurements. These equations took the form of:

$$y = axb$$

where y represents the character being measured (dependent variable), x represents the total body length (independent variable), b represents the growth coefficient, and a represents the intercept (Schmidt-Nielsen, 1984). Following Read and Tolley (1997), negative allometry was indicated when the growth coefficient was significantly smaller than 1 ($b < 1$), positive allometry was indicated when the growth coefficient was significantly greater than 1 ($b > 1$), and isometric allometry was indicated when the coefficient was not significantly different from 1.

To test the null hypothesis $H0$: $b = 1$, the test statistic (ts) was calculated as:

$$ts = (b - 1)/\mathrm{SE}b$$

where b represents the slope, SEb represents the standard error of the slope, df represents the degrees of freedom ($n - 2$), and α represents the significance level of 0.05. Student's t-test tables were used for this calculation and were analysed using R (R Core Team, 2023). To conduct a comparative analysis of growth coefficient values between males and females, a slope analysis was performed utilizing Student's t-test tables with a degree of freedom (df) of $n - 2$ and a significance level (α) of 0.05.

2.6.1 Average Age and Body Length at Attainment of Sexual Maturity

Average age and body length at attainment of sexual maturity was evaluated and adapted from Palmer et al., (2023). The SOFI method was applied to estimate the average age at which sexual maturity was attained (ASM) in the following manner:

$$ASM = j + \sum_{i=j}^{k} p_i x_i$$

$$Variance\ (S^2) = \sum \frac{(p_i q_i) x_i}{N_i - 1}$$

Here, j denotes the first indeterminate age class, and k is the last indeterminate age class. The Variable p_i and q_i represent the proportion of immature and mature individuals in the age class i respectively, such that $p_i + q_i = 1$. The term x_i is the number of age classes amalgamated to achieve a sample size of greater than two in age class i, I_i is the count of immature individuals, M_i is the count of mature individuals, and N_i is the total number of individuals in the age class i, where $N_i = I_i + M_i$. Proportions p_i and q_i are calculated as follows: if $I_i \neq N_i$, then $p_i = \frac{I_i}{N_i}$ and $q_i = \frac{M_i}{N_i}$; if $I_i = N_i$, then $p_i = \frac{I_i - 0.5}{N_i}$ and $q_i = \frac{I_i + 0.5}{N_i}$; and if $M_i = N_i$, then $p_i = \frac{I_i + 0.5}{N_i}$ and $q_i = \frac{I_i - 0.5}{N_i}$.

The average length at attainment of sexual maturity (LSM) was estimated by adapting the SOFI method for use with constant length intervals (5cm), instead of age:

$$LSM = j + \sum_{i=imin}^{imax} p_i x_i$$

$$Variance\ (S^2) = \sum_{i=imin}^{imax} \frac{p_i (1 - p_i) x_i}{n_i - 1}$$

Where j is the lower limit of the length class containing the smallest mature individual, $imin$ is the length class with the shortest mature individual, $imax$ is the length class with the longest mature individual, p_i is the proportion of immature individuals in the length class i, x_i is the proportion of length classes combined within length class i, and n_i is the total number of individuals in the i-th length class.

2.7 Sexual Dimorphism

The evaluation of sexual dimorphism was restricted to physically mature individuals, defined as those with a total body length (TBL) greater than or equal to the asymptotic length. Two methods were employed to assess dimorphism, following Betty et al., (2022), Murphy & Rogan,

(2006) and Palmer et al., (2023): analysis of sexual size dimorphism without adjusting for body size, which considers both size and shape, and analysis of sexual shape dimorphism, which accounts for variations in body length. Prior to analysis, all physically mature morphometric data were subjected to tests for homogeneity of variance (Levene's test) and normality (Shapiro-Wilk test). R Studio was employed to analyse all data pertaining to sexual dimorphism (R Development Core Team 2021). Spearman's rank correlation coefficients were utilized to examine the relationships between sex and morphometric measurements.

ANOVA was used to investigate the variation in size and/or shape between males and females, while ANCOVA was used to examine sexual variation in body shape only, by eliminating the effect of dolphin size on individual measurement types, using TBL as the covariate (Betty et al., 2022). As the data exhibited a deviation from normality, all morphological data was transformed on a logarithmic scale [Log10(x)] prior to ANCOVA analysis. Each measurement was analysed independently for males and females using both Welch's univariate analysis of variance (ANOVA) and univariate analysis of covariance (ANCOVA) (Betty et al., 2022).

Seventeen measurements with insufficient sample size ($n < 20$) were excluded from the linear discriminant function analysis. The remaining twelve measurements, which had sufficient sample sizes ($n \geq 20$), included eight linear and four appendage measurements. Missing values in these measurements were calculated using multiple imputation with the linear regression method. The linear discriminant function analysis was performed on these twelve measurements using R to assess the differences between the sexes.

Sexual dimorphism was further assessed and evaluated using the size dimorphism index (SDI), a method employed Janicke & Fromonteil (2021) and Lindenfors et al., (2007). The SDI equation calculates the relative size difference in size between sexes, providing a measure of the magnitude of dimorphism. To calculate the SDI between sexes, the mean measurements of physically mature males and females were utilised for each external measurement. SDI values > 0 suggest male-biased dimorphism, indicating that males are, on average, larger than females, while values < 0 suggest female-biased dimorphism, indicating that females tend to be larger. The results of these calculations are provided in Appendix Table 1. The calculation for size dimorphism index is as follows:

$$SDI = \frac{males\ mean}{females\ mean} - 1$$

2.8 Reproduction

2.8.1 Females

Determining female reproductive status involved the examination of the ovaries, uteri, and mammary glands following Murphy et al., (2020) on 17 females examined at postmortem at Massey University between 1997 and 2023. To be classified as sexually mature, females required at least one ovarian *corpus albican* (CA) or *corpus luteum* (CL) or be pregnant and/or lactating. If none of these criteria were met, females were categorized as sexually immature. The reproductive status of mature females was categorized as follows: (1) pregnant, indicating the presence of a foetus in the uterus and a *corpus luteum* (CL) on one ovary, (2) pregnant and lactating, characterized by the presence of a foetus, a CL on one ovary, and the production of milk detected in the mammary glands, (3) lactating, denoting the production of milk, and (4) resting mature, referring to a sexually mature female that is not pregnant or lactating, following Perrin and Donovan (1984).

To obtain accurate measurements, vernier callipers were utilised to determine the maximum length, width, and depth of each individual ovary, recorded to the nearest 0.1mm. Additionally, the weight of each ovary was recorded with a precision of 0.1g. A combined ovarian weight was calculated for females where both ovaries (*n* = 13) were collected. Ovaries containing corpora were then manually sectioned into 2mm slices and examined under a 5x magnifying lamp. This examination aimed to determine the total number of corpora present and measure the diameters of any *corpus luteum* (CL) and *corpus albicans* (CA). Notably, during the sectioning process, the hilar region of the ovaries, which is the area where they attach to the broad ligament of the uterus, was left intact to maintain the cohesion of the sections (Cozzi et al., 2016; Saksouk & Johnson, 2004).

2.8.2 Males

Testicular tissue was available for males (*n* = 20; Table 3.6) examined postmortem at Massey University between 1997 and 2020. Associated data, including age (years) TBL (cm), and testicular variables: testes length (mm), testes weight with epididymis (g), testes weight without epididymis (g), testes width (mm), testes depth (mm), index of testicular development (g/mm), and mean seminiferous tubule diameter (μm). The index of testicular development was determined by dividing the combined testes weight (excluding epididymis) by the combined testes length, as calculated by Hohn et al., (1985). The index variable was log-transformed, as it was discovered to be a more accurate predictor of sexual maturity compared to its original form. To analyse the relationships between these variables, charts and tables were utilized. To obtain accurate measurements, vernier callipers were utilised to determine the maximum length, width, and depth of each individual testis to the nearest 0.1mm. In instances where the testis exceeded the calliper's capacity, standard rulers were used, providing measurements to the nearest 1mm. Additionally, the weight of each testis was recorded with a precision of 0.1g.

Histological examination of testis was conducted to determine the stages of sexual maturity, following standard histological techniques (Cotter & Loda, 2017), which included dehydration, clearing, and embedding in paraffin wax. The tissue was then sectioned at a thickness of 5µm and stained with haematoxylin and eosin. The resulting histological slides were examined under a microscope at magnifications ranging from 100x to 400x. To determine the stage of sexual maturity, all seminiferous tubules in an ~1cm^2 section of the testicular tissue were assessed following Palmer et al., (2023).

The mean diameter of the seminiferous tubules was determined by measuring the basement membranes of 10 tubule cross-sections. These measurements were obtained from images captured using the Axiocam 105 camera, along with the associated Zeiss software (Carl Zeiss Microscopy GmbH, 2023). To ensure an accurate cross-section of the longitudinal axis, only clear circular tubules were measured, following the approach adopted in other studies on cetacean reproduction (Betty et al., 2019; Murphy et al., 2005; Palmer et al., 2023). In cases where the tissue exhibited moderate autolysis, measurements were not taken due to the inability to clearly distinguish the basement membrane.

The categorization of individuals into distinct stages of maturity was adapted from Murphy et al., (2005). Individuals in an immature stage were distinguished by the presence of only Sertoli cells and spermatogonia within the seminiferous tubules. Pubescent individuals were divided into two categories, early pubescence, and late pubescence (Murphy et al., 2005). Early pubescent individuals had both spermatogonia and spermatocytes present, with a reduction in Sertoli cells and interstitial tissue (Murphy et al., 2005). Late pubescent individuals on the verge of attaining sexual maturity, were characterised by the presence of some spermatids, though spermatozoa were not yet present. Mature individuals were identified by the presence of all stages of spermatogenesis within the tubules, including spermatids and spermatozoa (Murphy et al., 2005).

Chapter 3 Results

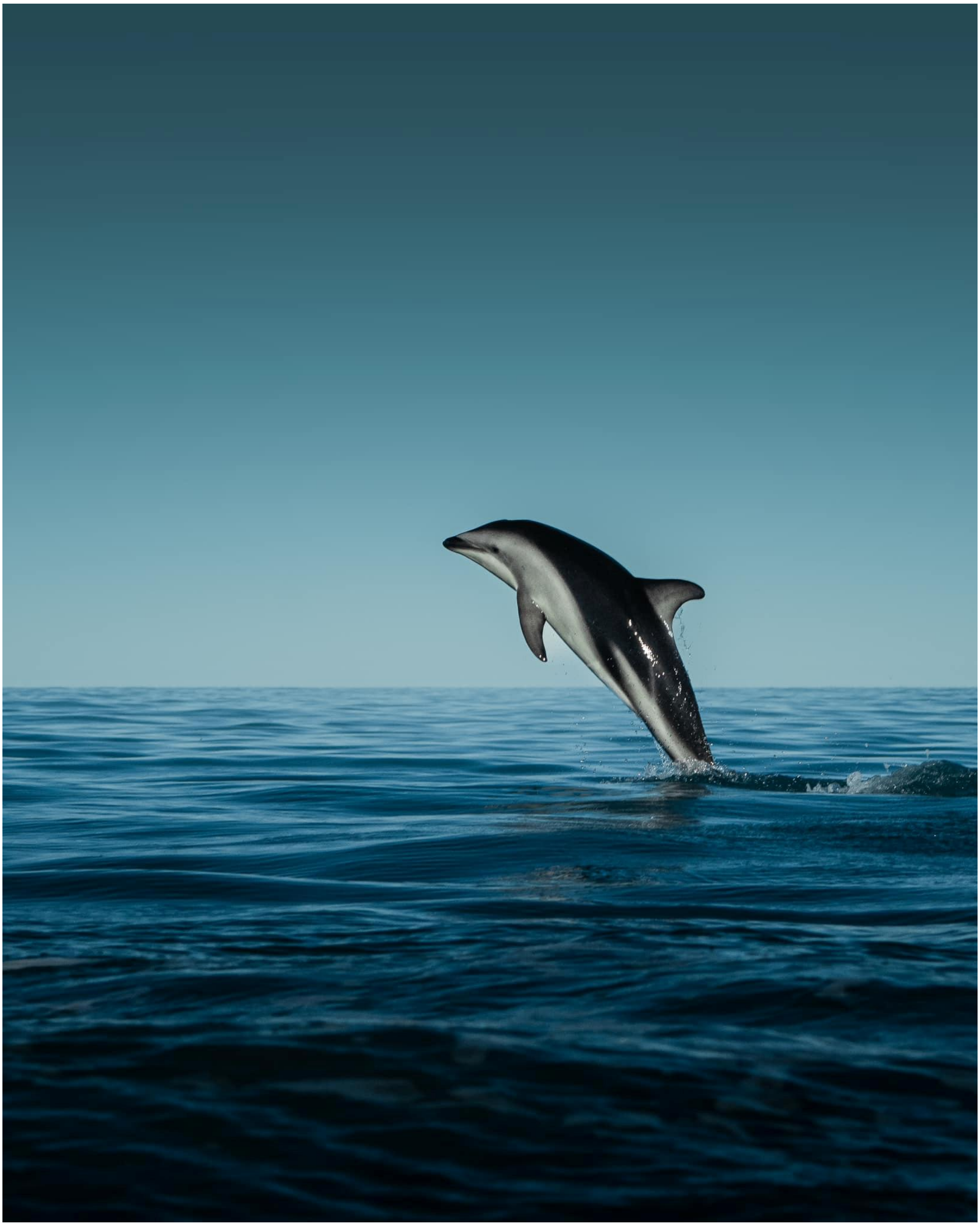


Photo credit: Jared Kreiss

3.1 Age & Growth

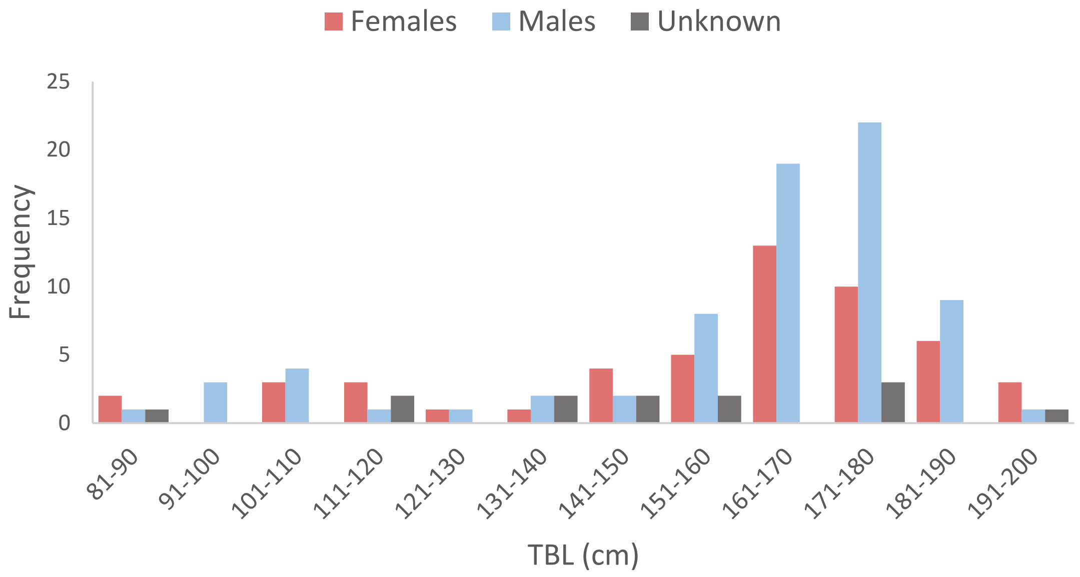
A total of 137 dusky dolphins (*n* = 73 males, *n* = 51 females, *n* = 13 unknown) from 1960 to 2023 were included for age and growth assessment (Table 3.1). Total body length (TBL) ranged from 83 to 200cm (*n* = 137), with a modal size class of 171 to 180cm (median ± SE, 166.5 ± 4.2cm, Figure 3.1a). Females ranged from 83 to 195cm (mean ± SE, 158.1 ± 3.9cm, *n* = 51), with a modal size class of 161 to 170cm. Males ranged from 87 to 192cm (mean ± SE, 160.1 ± 3.2cm, *n* = 73), with a modal size class of 171 to 180cm. Individuals of unknown sex ranged from 88 to 200cm (mean ± SE, 150.3 ± 7.9cm, *n* =13), with a modal size class of 171 to 180. Aged females (*n* = 10) and males (*n* = 12) from animals submitted to Massey University for postmortem assessment ranged from 0 to 14 years and 0.25 to 22 years, respectively (Figure 3.1b). An additional individual of unknown sex (KS22-78Lo) was aged at 0.25 years.

3.2 Length at Birth

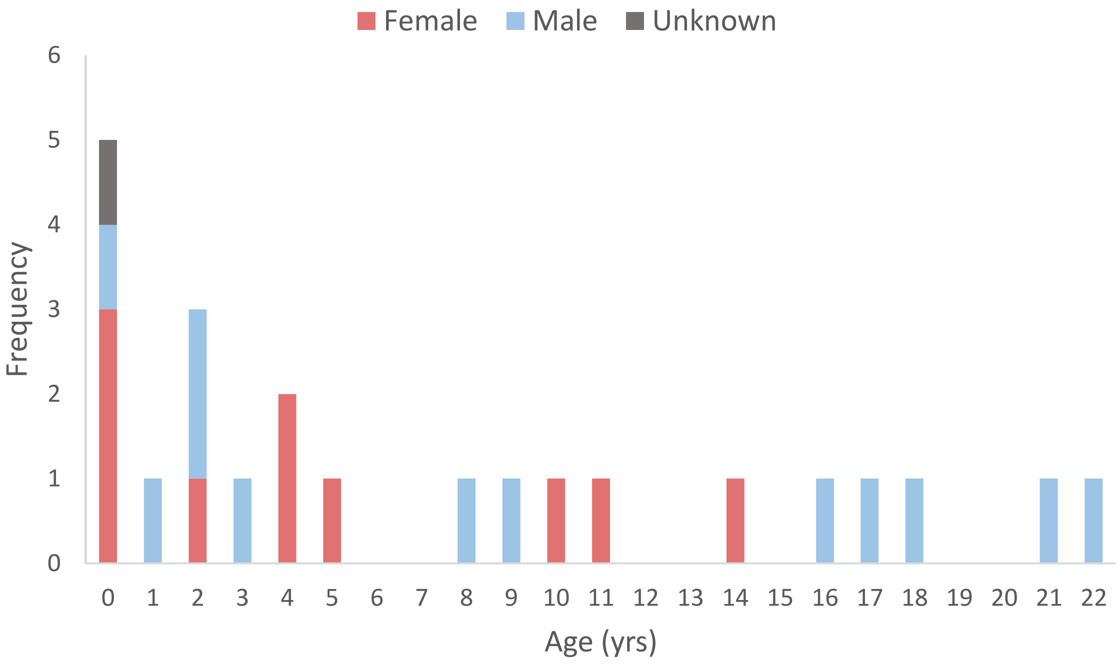
Foetuses (*n* = 5) ranging from 25.5 to 81cm TBL were recorded from cadavers assessed by Massey University. The smallest born male (KS14-48Lo) and female (WS04-06Lo) measured at 91.5 and 102cm, respectively. Due to the lack of clear overlap between unborn and born measurements, length at birth was unable to be calculated in the current study.

3.3 Growth Curve

Data for growth was obtained both from the NZWSDB (*n* = 93) and from cadavers assessed by Massey University (*n* = 45). Maximum total body length (TBL) observed for females (*n* = 51) was 195cm, with 23.1% of females (*n* = 12) exceeding 180cm. Among males (*n* = 73), the highest recorded TBL was 192cm, with 17.8% (*n* = 13) individuals measuring greater than 180cm. Individuals of unknown sex (*n* = 13) exhibited a maximum TBL of 200cm (DOC code 4209, Appendix 3), with four individuals measuring ≥180cm (Figure 3.1).



(a)



(b)

Figure 3.1 (a) Total body length (n = 137) and (b) age (n = 23) frequency distribution for dusky dolphins (*Lagenorhynchus obscurus*) by sex from 1960 to 2023 in New Zealand. Note: aged animals shown here range from 2010 to 2023. Foetuses (n = 5) have been removed from the dataset.

Table 3.1 Mean ($\bar{x}$), standard error (SE), range and sample size (*n*) of weight (kg) and 29 body measurements (cm) collected from female (*n* = 51) and male (*n* = 73) dusky dolphins (*Lagenorhynchus obscurus*) stranded on the Aotearoa New Zealand coast from 1960 to 2023.

	Females				Males			
	Mean	**SE**	**Range**	***n***	**Mean**	**SE**	**Range**	***n***
Weight	58.8	7.64	24.1–74	10	61.3	6.86	7.1–86	14
TBL	158.0	3.87	83–195	51	160.1	3.02	87–192	73
Snout-anus	111.4	2.86	60–131	39	119.2	1.10	103–136	46
Snout-genital slit	103.6	2.88	47–124	37	103.3	1.06	92–117	36
Snout-navel	73.6	3.47	48–94	12	76.8	1.06	72–81	8
Snout-origin flipper	37.9	0.85	24–46	40	2.4	0.44	35–50	47
Snout-origin dorsal fin	85.5	3.17	45–126	42	94.9	2.82	69–150	47
Snout-tip dorsal fin	96.8	3.24	66–109	15	103.3	1.18	99–112	12
Snout-blowhole	24.6	0.78	9–30	34	26.3	0.51	21.5–33	32
Snout- cnr mouth	21.1	1.84	13–25	34	22.4	0.33	17–28.5	38
Genital slit	9.2	0.91	3.2–14.5	14	12.0	0.62	7–16	14
Rostrum	4.1	0.21	2–6	38	4.8	0.20	2–10	40
Cnr mouth-eye	4.3	0.21	3–5.5	17	4.5	0.19	3–6.5	18
Eye-blowhole	15.8	0.41	13–19	17	16.7	0.26	14.5–19	18
Dorsal fin height	18.4	0.53	11–23	38	21.3	0.58	14.5–36	40
Dorsal fin lat base	24.5	0.83	17–29	19	26.0	0.71	21.5–31	19
Fluke width	39.6	1.37	18–52	42	44.7	0.99	12–53	48
Fluke length	13.3	0.42	11–16.5	17	14.6	0.39	13–17.5	15
Fluke notch	2.3	0.13	1.5–3.3	17	2.5	0.19	1–3.5	16
Flipper internal	18.6	1.58	5.5–28.3	15	22.8	1.24	10–28	18
Flipper exterior	31.3	0.73	19.5–38	42	33.8	0.42	25–39	48
Flipper width	9.7	0.24	6–12	38	10.7	0.18	9–12.5	37
Girth eye	62.8	1.09	54–68.5	17	65.9	1.03	58.4–74	17
Girth flippers	89.4	2.71	66–111	19	95.1	1.73	78.8–103.5	18
Axill-girth	89.0	3.95	51–126	20	95.4	2.89	74–120	19
Girth navel	91.9	3.41	69–118	17	99.5	2.30	79–114	16
Girth anus	53.0	1.61	39–64.5	16	59.9	1.68	47–70	17
Blubber dorsal	1.3	0.08	0.5–2	19	1.5	0.15	0.4–3	18
Blubber lateral	1.2	0.09	0.5–2	19	1.1	0.09	0.4–2	18
Blubber ventral	1.2	0.09	0.5–2	19	1.3	0.11	0.4–2	18

Using the Gompertz model, the predicted total body length (TBL) at physical maturity (i.e. asymptotic length) for female and male dusky dolphins was estimated at 170.4 and 171.5cm, respectively (Table 3.2). Figures 3.2 and 3.3 show growth rates for both sexes which were particularly rapid during the first two years. During the first year, female and male dusky dolphins exhibited a growth rate of 43 and 38.7cm, respectively. Beyond the first year, males consistently exhibited faster growth rates than females. For females, the growth rate diminished to less than 1cm per annum after reaching the age of five and continued to decelerate until an asymptotic length of 170.0cm by the age of ten, as shown by the orange line in Figure 3.2. Similarly, male growth rates decreased to less than 1cm per year starting at six years of age, gradually approaching an asymptotic length of 171.5cm, as depicted by the blue line in Figure 3.2.

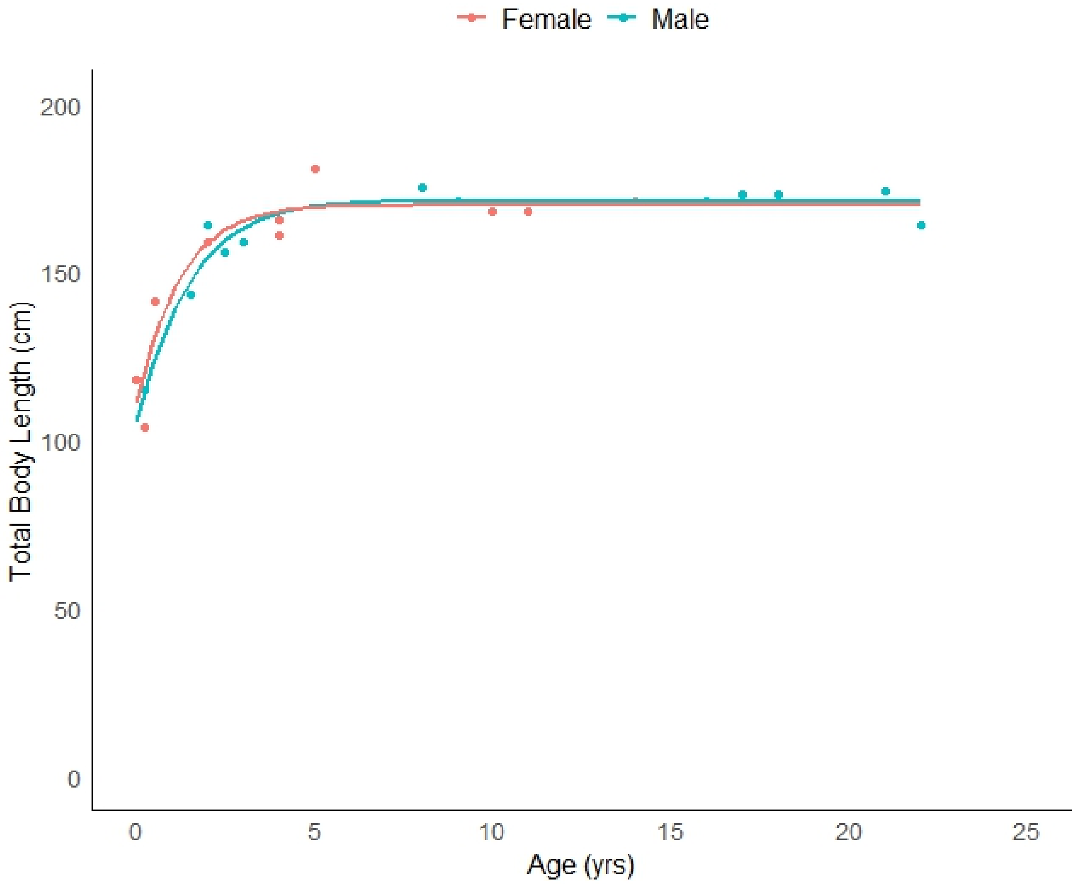


Figure 3.2 Gompertz growth curved fitted to length-at-age data for aged female (*n* = 10) and male (*n* = 12) dusky dolphins (*Lagenorhynchus obscurus*) incidents on the Aotearoa New Zealand coast between 1960 and 2023 - see Table 3.2 for parameter values. Note: Coloured dots represent the length-at-age data, and the solid lines represent the sex-specific growth curves.

Table 3.2 Estimated growth parameters (mean ± *SE*) for Gompertz growth curves (Figure 3.2) from aged male and female dusky dolphins (*Lagenorhynchus obscurus*) incidents on the Aotearoa New Zealand coast between 1960 and 2023.

	L_∞	K	t_0	R^2	n
Female	170.0 ± 4.59	0.91 ± 0.44	-0.94 ± 0.55	0.88	10
Male	171.5 ± 1.88	0.76 ± 0.12	-0.96 ± 0.28	0.93	12

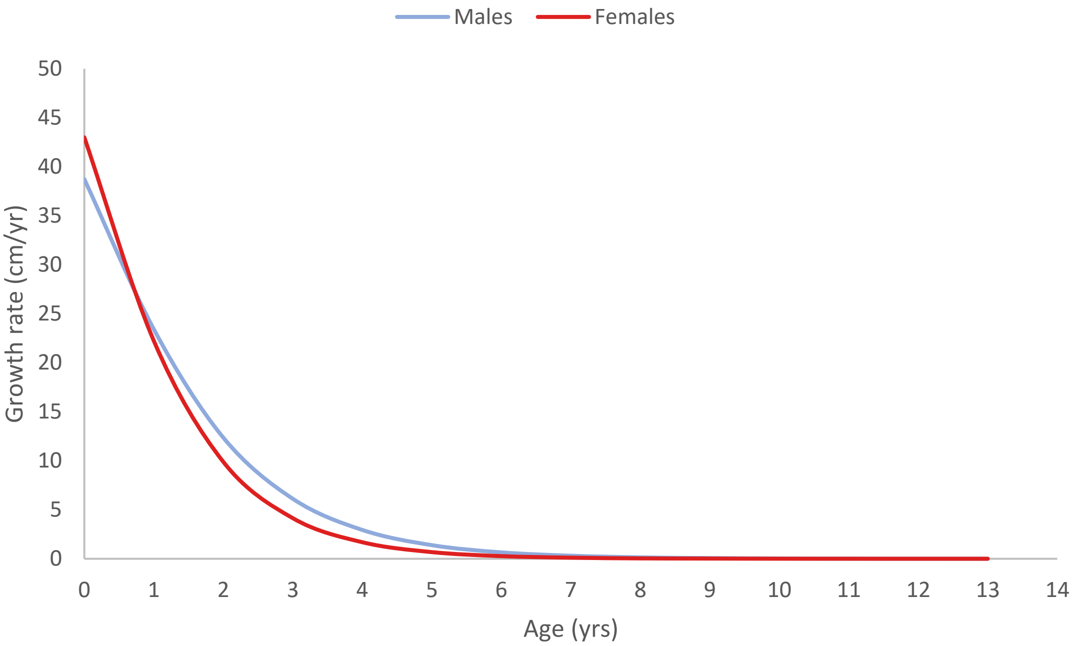


Figure 3.3 Estimated growth rate (cm/year) for Gompertz growth curves (Figure 3.2) from aged male (blue) and female (red) dusky dolphins (*Lagenorhynchus obscurus*) examined from the New Zealand coast between 1960 and 2023.

3.4 Allometry

Allometry was assessed for 73 males and 51 females that were either examined postmortem at Massey University (*n* = 44) or measured in field by the Department of Conservation (*n* = 80). Across 25 external body measurements, negative, positive, and isometric allometry was observed, with no significant (*p*-value <0.05) differences between males and females (Table 3.3). Both sexes displayed isometric allometry in measurements snout to anus and snout to tip of the dorsal fin. Six out of twelve linear measurements exhibited negative allometry in both sexes, including snout to genital slit, snout to dorsal fin origin, snout to blowhole, snout to corner of the mouth, genital slit, and rostrum.

Males exhibited negative allometry for snout to navel and eye to blowhole measurements, while females showed positive allometry in these traits. However, no significant sex differences were found between sexes for these measures (p = 0.63 and p = 0.81, respectively). For snout to origin flipper and corner of the mouth to eye measurements, distinct allometric patterns were noted between sexes. Males showed isometric allometry for snout to origin flipper, while females displayed positive allometry, although no significant difference between sexes was noted (d.f = 90.47, p = 0.52). Females showed negative allometry for corner of the mouth to eye measurements, with males showing isometry although no significant difference between sexes was noted (df = 32.24, p = 0.56).

Both sexes exhibited positive allometry in appendages across four measurements: dorsal fin height, lateral dorsal fin base, fluke width, and fluke notch (Table 3.3). Negative allometry was further observed in the internal flipper measurements for both sexes, while isometric allometry was noted in the external flipper measurements (Table 3.3). Fluke length measurements inferred isometric allometry in males and positive allometry in females, although differences were not significant (t = -0.83, df = 32.19, p = 0.41). Flipper length measurements showed isometric allometry in females and negative allometry in males, though weren't statistically significant between the sexes (t = -0.9, df = 84.57, p = 0.38).

For flipper, axilla, and navel girth, both sexes displayed negative allometry. Girth around the eye showed isometric allometry in males and positive allometry in females (t = 0.33, df = 29.36, p = 0.75), indicating no significant differences. For girth around the anus, despite different allometric patterns of isometric in females, positive in males), no significant differences between sexes were found (t = -0.44, df = 30.96, p = 0.67).

Table 3.3 Allometric growth relationships for 25 external body measurements regressed against total body length (TBL) for physically immature and mature female (F) and male (M) dusky dolphins (*Lagenorhynchus obscurus*) stranded and bycaught on the Aotearoa New Zealand coast between 1960 to 2023. Note: Foetuses (*n* = 5) are excluded.

Measurement	Female Equation	SE (*b*)	*n*	r^2	b	Male Equation	SE (*b*)	*n*	r^2	b	F vs M
Snout-anus	$y= 0.548x^{0.96}$	0.02	39	0.97	b=1	$y=0.764x^{0.92}$	0.04	55	0.92	b=1	F = M
Snout-genital slit	$y= 1.472x^{0.77}$	0.05	37	0.89	b<1	$y=0.925x^{0.91}$	0.04	45	0.92	b<1	F = M
Snout-navel	$y= 1.131x^{0.91}$	0.09	12	0.90	b<1	$y=0.347x^{1.10}$	0.04	11	0.98	b>1	F = M
Snout-origin flipper	$y= 0.972x^{1.12}$	0.10	40	0.78	b>1	$y=1.430x^{1.10}$	0.07	58	0.79	b=1	F = M
Snout-origin dorsal fin	$y= 2.779x^{0.51}$	0.10	42	0.38	b<1	$y=3.022x^{0.46}$	0.08	57	0.40	b<1	F = M
Snout-tip dorsal fin	$y= 0.281x^{1.05}$	0.07	15	0.95	b=1	$y= 0.399x^{1.02}$	0.07	16	0.94	b=1	F = M
Snout-blowhole	$y= 3.201x^{0.58}$	0.10	34	0.52	b<1	$y=2.534x^{0.8}$	0.08	42	0.68	b<1	F = M
Snout-cnr mouth	$y= 2.543x^{0.82}$	0.13	35	0.53	b<1	$y= 2.541x^{0.83}$	0.08	48	0.68	b<1	F = M
Genital slit	$y= 4.062x^{0.42}$	0.11	14	0.52	b<1	$y= 3.995x^{0.44}$	0.08	23	0.56	b<1	F = M
Rostrum	$y= 4.506x^{0.39}$	0.06	38	0.57	b<1	$y= 4.517x^{0.36}$	0.08	50	0.29	b<1	F = M
Cnr mouth-eye	$y= 4.462x^{0.41}$	0.15	17	0.29	b<1	$y= 5.162x^{-0.06}$	0.20	21	0.05	b=1	F = M
Eye-blowhole	$y= 3.031x^{0.74}$	0.30	17	0.24	b<1	$y= 1.928x^{1.13}$	0.16	22	0.7	b>1	F = M
Dorsal fin height	$y= 2.883x^{0.75}$	0.08	38	0.68	b>1	$y= 3.38x^{0.57}$	0.07	50	0.59	b>1	F = M
Dorsal fin lat base	$y= 2.769x^{0.72}$	0.12	19	0.65	b>1	$y= 2.910x^{0.68}$	0.10	22	0.7	b>1	F = M
Fluke width	$y= 2.53x^{0.69}$	0.05	42	0.81	b>1	$y= 3.41x^{0.45}$	0.05	58	0.54	b>1	F = M
Fluke length	$y= 3.375x^{0.65}$	0.25	17	0.27	b>1	$y= 2.701x^{-0.9}$	0.14	18	0.7	b=1	F = M
Fluke notch	$y= 4.821x^{0.29}$	0.14	17	0.17	b>1	$y= 4.978x^{0.109}$	0.1	19	0.01	b>1	F = M
Flipper internal	$y= 3.751x^{0.42}$	0.11	15	0.49	b<1	$y= 4.246x^{0.26}$	0.12	26	0.13	b<1	F = M
Flipper exterior	$y= 1.846x^{0.93}$	0.12	42	0.6	b=1	$y= 1.824x^{0.94}$	0.07	60	0.74	b=1	F = M
Flipper width	$y= 2.944x^{0.93}$	0.07	38	0.81	b=1	$y= 3.218x^{0.8}$	0.08	49	0.67	b<1	F = M
Girth eye	$y= -2.144x^{1.74}$	0.26	17	0.73	b>1	$y= 0.704x^{1.05}$	0.12	21	0.8	b=1	F = M
Girth flippers	$y= 1.477x^{0.8}$	0.16	19	0.57	b<1	$y= 1.484x^{-0.8}$	0.08	22	0.82	b<1	F = M
Axill-girth	$y= 1.423x^{0.81}$	0.10	20	0.76	b<1	$y= 1.934x^{0.7}$	0.11	23	0.62	b<1	F = M
Girth navel	$y= 1.893x^{0.70}$	0.17	17	0.5	b<1	$y= 2.182x^{0.64}$	0.07	20	0.82	b<1	F = M
Girth anus	$y= 1.385x^{0.93}$	0.20	16	0.57	b=1	$y= 2.409x^{0.66}$	0.08	21	0.78	b>1	F = M

Growth patterns have been determined in the form of $y = ax^b$, where x = TBL (cm); y = measurement (cm); b = growth coefficient; a = intercept. SE = standard error for growth coefficient; *n* = sample size; r^2 = correlation coefficient; F vs. M, comparison of slopes between sexes with TBL as the independent variable. For an explanation of the measurement codes, see Figure 2.1

3.5 Sexual Dimorphism

Sexual dimorphism was analysed across 29 measurements of physically mature female (*n* = 22) and male (*n* = 32) dusky dolphins measuring greater than the asymptotic lengths of 170cm and 171cm (calculated in section 3.3), respectively (Table 3.4). To assess potential differences between the sexes, ANOVA, ANCOVA, Linear Discriminant Function Analysis (LDFA) and sexual dimorphism index (SDI) were performed, as described in Section 2.7.

On average, females displayed greater length in just over half (*n* = 15) measurements, whereas males were larger than females in just under half (*n* = 14) of the measurements. However, significant differences between the sexes were noted only in the snout to genital slit length (Table 3.4), with females significantly larger by an average of 9.5cm (F = 40.6, p = 6.78e-07, SDI = -0.08, LDFA = -0.24). This is reflected in the mean values for this measurement where females had an average of 115.8cm (SE = 16.18, range = 110–124cm, *n* =13), compared to males with 106.3cm (SE = 13.09, range = 101–112cm, *n* = 17). However, no evidence of sexual size or shape dimorphism in the appendage, girth, or blubber thickness measurements were detected (see Table 3.4; Appendix Table 1).

Table 3.4 Mean (x̄), standard error (SE), range and sample size (*n*) of 26 external body measurements, with results of Welch's ANOVAs and ANCOVAs comparing data collected from physically mature female (*n* = 22) and male (*n* = 32) dusky dolphins *(Lagenorhynchus obscurus)* stranded and bycaught on the Aotearoa New Zealand coast between 1960 and 2023.

Measurement	Females				Males						
	Mean (cm)	SE	Range (cm)	*n*	Mean (cm)	SE	Range (cm)	*n*	ANOVA	ANCOVA	LDFA
TBL	179.51	1.70	170–195	22	177.83	1.11	171–192	32			-0.06
Snout-anus	125.07	16.47	118.5–131	14	120.83	12.85	103–134	23			-0.05
Snout-genital slit	115.75	16.18	110–124	13	106.26	13.09	101–112	17	***		-0.24
Snout-navel	82.75	16.40	76–94	4	78.50	12.96	76–81	5			
Snout-origin flipper	41.87	5.53	37–46	14	41.98	3.82	36–50	24			0.12
Snout-origin dorsal fin	93.98	9.59	71–117	25	93.98	8.47	71–117	25			0.02
Snout-tip dorsal fin	104.70	20.10	99–109	5	103.92	16.84	99–112	6			
Snout-blowhole	26.54	3.77	21–30	13	26.68	3.63	21.5–31	14			-0.06
Snout-cnr mouth	22.17	3.28	18–24.5	12	22.71	2.81	20–28	17			-0.02
Genital slit	13.50	2.75	12–14.5	3	12.14	2.00	7–16	7			
Rostrum	5.02	0.68	4–6	14	4.44	0.39	3–6	18			-0.07
Cnr mouth-eye	4.48	0.94	3.7–5.3	5	4.39	0.68	3–5	9			
Eye-blowhole	16.82	3.23	15.5–18	5	16.67	2.54	16–18	9			
Dorsal fin height	20.87	2.77	12–23	14	21.45	2.68	17–26	17			0.11
Dorsal fin lat base	27.00	5.03	25–29	6	27.20	4.09	22–31	10			
Fluke width	46.16	5.30	40–51	16	46.60	4.00	35–53	25			0.05
Fluke length	14.60	1.59	13.5–15.5	5	15.38	2.41	13–17.5	8			
Fluke notch	2.62	0.52	2–3.3	5	2.53	0.42	1–3.5	8			
Flipper internal	26.27	5.36	22.5–28.3	3	21.83	3.60	10–28	8			
Flipper exterior	34.83	4.00	30.2–38	16	34.43	3.14	25–39	24			-0.22
Flipper width	10.86	1.44	10–12	14	11.05	1.41	9–12.5	16			0.90
Girth eye	67.24	12.90	65–68.5	5	67.17	10.26	61–74	9			
Girth flippers	98.08	17.93	89–107	6	97.18	14.51	85.8–103.5	10			

Axill-girth	101.00	17.74	88–126	8	106.33	17.30	89–120	6
Girth navel	102.20	10.73	80–118	5	100.88	15.76	88–114	8
Girth anus	58.00	11.48	54.5–64.5	4	61.61	9.46	47–70	9
Blubber dorsal	1.35	0.25	1.2–1.7	6	1.61	0.27	0.4–3	9
Blubber lateral	1.08	0.20	0.9–1.4	6	1.22	0.20	0.4–2	9
Blubber ventral	1.22	0.23	0.9–1.6	6	1.33	0.22	0.4–2	9

***$P<0.001$. For an explanation of the measurement codes, see Figure 2.1.

3.6 Reproduction

3.6.1 Age and Length at Attainment of Sexual Maturity

3.6.1.1 Females

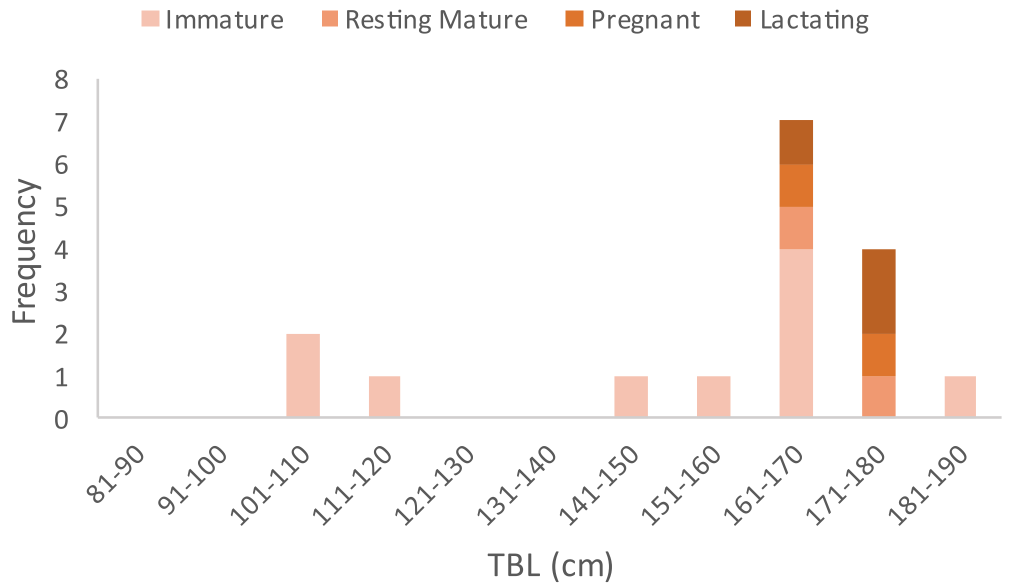
Of the female cadavers examined by Massey University between 1997 and 2023 (*n* = 17), seven were classified as immature, and four were classified as mature (Figure 3.4a) with age ranging from 0 to 14 years (n = 10; Figure 3.4b) using histology. Unfortunately, the remaining four individuals could not be histologically assessed due to tissue not being available. However, the maturity status of the four individual (WS99-15Lo) was determined at gross examination as one immature (WS99-15Lo), two lactating (WS97-54Lo & WS99-12Lo), and one resting mature (WS97-21Lo). Sexually immature dolphins ranged from 102 to 181cm (*n* = 10) and 0 to 5 years (n = 7). Sexually mature individuals ranged from 166 to 175.7cm (*n* = 7) and 10 to 14 years (*n* = 3). Of the mature sample, two females (KS11-41Lo & KS23-18Lo) were pregnant, three were lactating (KS14-40Lo, WS99-12Lo & WS97-54Lo), and two females were resting mature (KS11-51Lo & WS97-21Lo).

Ovarian characteristics are shown in Table 3.6 (*n* = 17). Combined ovarian weight increased from birth until the approximate length of sexual maturity of 167.5cm (Figure 3.5a). Immature ovaries (*n* = 10) were smooth and pale in colour, with lengths ranging from 22.0 to 35.6mm (mean = 27.6 ±13.44, *n* = 7) and 18.8 to 38.8mm (mean = 29.2 ±14.8, *n* = 7) for left and right ovaries, respectively. Weights ranged from 0.3 to 1.4g (mean = 0.9g ±0.5, *n* = 7) and 0.3 to 1.5g (mean = 0.8 ±0.5, *n* = 7) for left and right ovaries, respectively. Left ovary widths and depths ranged from 6.9 to 15.0mm (mean = 11.09 ±5.6, *n* = 7) and 4.1 to 8.3mm (mean = 5.83 ±3.1, *n* = 7), respectively. Right ovary width and depth ranged from 6.8 to 11.3mm (mean = 8.8 ±4.2, *n* = 7) and 4.4 to 8.5mm (mean = 6.3 ±3.2, *n* = 7), respectively.

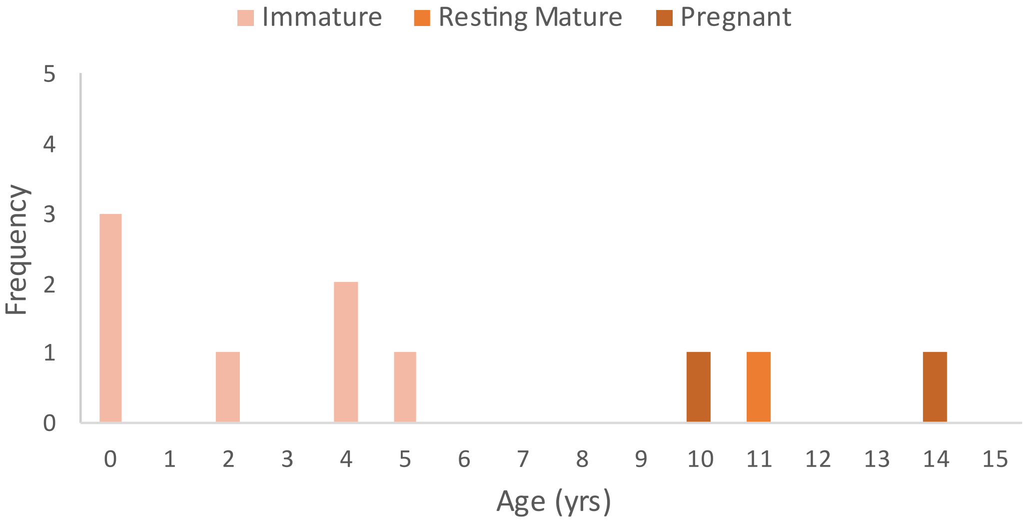
Mature ovaries (*n* = 7) were ochre in colour and pitted in texture, with lengths ranging from 21.3 to 28.2mm (mean = 43.0 ±21.3, *n* = 4) and 31.9 to 40.7mm (mean = 35.0 ±16.0, *n* = 4) for left and right ovaries, respectively. Weights ranged from 3.9 to 11.6g (mean = 7.3 ±4.6, *n* = 4) and 1.3 to 3.3g (mean = 2.2 ±1.2, *n* = 4) for left and right ovaries, respectively. Left ovaries recorded widths and depths ranging from 11.3 to 28.3mm (mean = 20.16 ±11.1, *n* = 4) and 6.8 to 18.9mm (mean = 14.0 ±7.8, *n* = 4), respectively. Right ovaries reported widths and depths ranging from 10.9 to 21.7mm (mean = 15.8 ±8.4, *n* = 4) and 7.0 to 9.9mm (mean = 8.7 ±0.6, *n* = 4), respectively.

Combined *corpus albican* (CA) count recorded for sexually mature females ranged from one to 12 (*n* = 4). CA scars were observed on both ovaries in sexually mature individuals (Table 3.5), with lengths ranging from 1.79 to 5.6mm (mean = 5.63 ±2.3, *n* = 23). On average, the left ovary had 5.3 (± 2.08) CAs whereas, the right ovary had 2 (±1.8). However, the amount of CA scars between the left and right ovaries did not vary (t = 1.07, p = 0.17, df = 5), although the sample size was limited. Of the three CL's observed, two were noted on the left ovaries and one on the right ovary. The average length, width, and diameter of the CLs were 24.43mm (±11.03), 25.13mm (±3.97), and 17.53mm (±2.68), respectively (*n* = 3).

An observed overlap between immature and mature females measuring 160 to 180cm in TBL was noted (Figure 3.4a, 3.5a). Length of sexual maturity (LSM) using the SOFI method was 167.5cm (95% CI = 166.0 – 168.98, *n* = 11). Due to a lack of overlap for age and maturity status, the age at sexual maturity (ASM) was unable to be determined (Figure 3.4b). However, the smallest sexually mature female (KS14-40Lo) measured 175.7cm and was lactating, with a total of 11 CAs. The youngest sexually mature female (KS23-18Lo) was estimated to be 10 years old with a TBL of 168cm and pregnant (Figure 3.4b, 3.5b). The largest sexually immature female (KS18-40Lo) appears somewhat of an outlier, measuring 181cm and estimated to be between five and six years old (Figure 3.4b, 3.5b). The oldest sexually mature female (KS11-41Lo) was estimated to be 14 years old with a TBL of 171cm and was pregnant with 12 CAs on the ovaries (Figure 3.4b, 3.5b; Table 3.5).



(a)



(b)

Figure 3.4 Maturity stage at (a) TBL (*n* = 17) and (b) age (*n* = 10) for female dusky dolphins (*Lagenorhynchus obscurus*) examined from the New Zealand coast between 1997 and 2023. Note: excluding foetuses (*n* = 2).

Table 3.5 Mean (±SE), range and sample size (*n*) for total body length (TBL), age and ovarian characteristics of all reproductive groups of female dusky dolphins (*Lagenorhynchus obscurus*) examined from Aotearoa New Zealand waters (1997-2023). Note: excluding foetuses (*n* = 3).

Stage	***n***	**TBL (cm)**	**Age (yrs)**	**Weight (g)**		**Length (mm)**		**Width (mm)**		**Depth (mm)**		**Corpora count (CAs +CLs)**		**CL present**	
				Left	**Right**	**Left**	**Right**	**Left**	**Right**	**Left**	**Right**	**Left**	**Right**	**L**	**R**
Immature	10	145.9 (±54.4) 102–181 (*n* = 10)	2.25 (±1.4) 0–5 (*n* = 7)	0.9 (±0.5) 0.3–1.4 (*n* = 7)	0.8 (±0.5) 0.3–1.5 (*n* = 7)	27.6 (±13.4) 22.0–35.6 (*n* = 7)	29.2 (±14.77) 20.3–38.8 (*n* = 7)	11.1 (±5.6) 6.9–15 (*n* = 7)	8.8 (±4.2) 6.8–11.3 (*n* = 7)	5.8 (±3.1) 4.1–8.3 (*n* = 7)	6.3 (±3.2) 3.5–8.5 (*n* = 7)	0	0	0	0
Pregnant	2	169.5 (±36.9) 168–171 (*n* = 2)	12 (±4.9) 10–14 (*n* = 2)	10.5 (±1.1) 9.4–11.6 (*n* = 2)	1.9 (±1.2) 1.3–2.6 (*n* = 2)	50.6 (±0.2) 50.5–50.8 (*n* = 2)	32.8 (±1.0) 31.9–33.8 (*n* =2)	26.0 (±2.3) 23.8–28.3 (*n* = 2)	14.9 (±4.0) 10.9–18.9 (*n* = 2)	18.2 (±0.8) 17.4–18.9 (*n* = 2)	7.8 (±0.8) 7.0–8.6 (*n* = 2)	3.8 (±8.0) 0–12 (*n* = 2)	0	2	0
Lactating	3	171.6 (±45.4) 166–175.7 (*n* = 3)	n/a	3.9 (±2.8) (*n* = 1)	1.8 (±1.3) (*n* = 1)	42.5 (±30.1) (*n* = 1)	40.7 (±28.8) (*n* = 1)	17.3 (±12.2) (*n* = 1)	11.7 (±8.3) (*n* = 1)	13.0 (±9.2) (*n* = 1)	9.4 (±6.6) (*n* = 1)	15.3 (±4.8) 5–11 (*n* = 3)	0	0	1
Resting mature	2	171 (±31.8) 168–174 (*n* = 2)	11 (*n* = 1)	4.2 (±3.0) (*n* =1)	3.3 (±2.3) (*n* = 1)	28.2 (±19.9) (*n* = 1)	33.7 (±23.8) (*n* = 1)	11.3 (±8.0) (*n* = 1)	21.7 (±15.4) (*n* = 1)	6.8 (±4.8) (*n* = 1)	9.9 (±7.0) (*n* = 1)	1 (±1.5) 0–3 (*n* = 2)	4 (±4.8) 1–11 (*n* = 2)	0	0

All mature	7	170.8 (±56.4) 166–175.7 (*n* = 7)	11.6 (±4.16) 10–14 (*n* = 3)	7.3 (±4.6) 3.9–11.6 (*n* =4)	2.2 (±1.2) 1.3–3.3 (*n* = 4)	43.0 (±21.3) 28.2–50.8 (*n* = 4)	35.00 (±16.0) 31.9–40.7 (*n* = 4)	20.2 (±11.1) 11.3–28.3 (*n* = 4)	15.8 (±8.4) 10.9–21.7 (*n* = 4)	14.0 (±7.8) 6.8–18.9 (*n* = 4)	8.7 (±0.6) 7.0–9.9 (*n* = 4)	5.3 (±2.1) 0–12 (*n* = 6)	2.4 (±1.8) 0–11 (*n* = 6)	2	1
Total	17	156.1 (±57.3) 102–181 (*n* = 17)	5.1 (±1.4) 0–14 (*n* = 10)	3.2 (±1.2) 0.3–11.6 (*n* = 11)	1.3 (±0.3) 0.3–3.3 (*n* = 11)	33.2 (±3.1) 22.0–50.8 (*n* = 11)	31.3 (±15.2) 20.3–40.7 (*n* = 11)	14.4 (±2.0) 6.9–28.3 (*n* = 11)	11.4 (±6.6) 6.8–21.7 (*n* = 11)	8.8 (±1.6) 4.1–18.9 (*n* = 11)	7.2 (±0.5) 4.4–9.9 (*n* = 11)	1.1 (±2.9) 0–12 (*n* = 16)	0.4 (±0.7) 0–11 (*n* = 14)	2	1

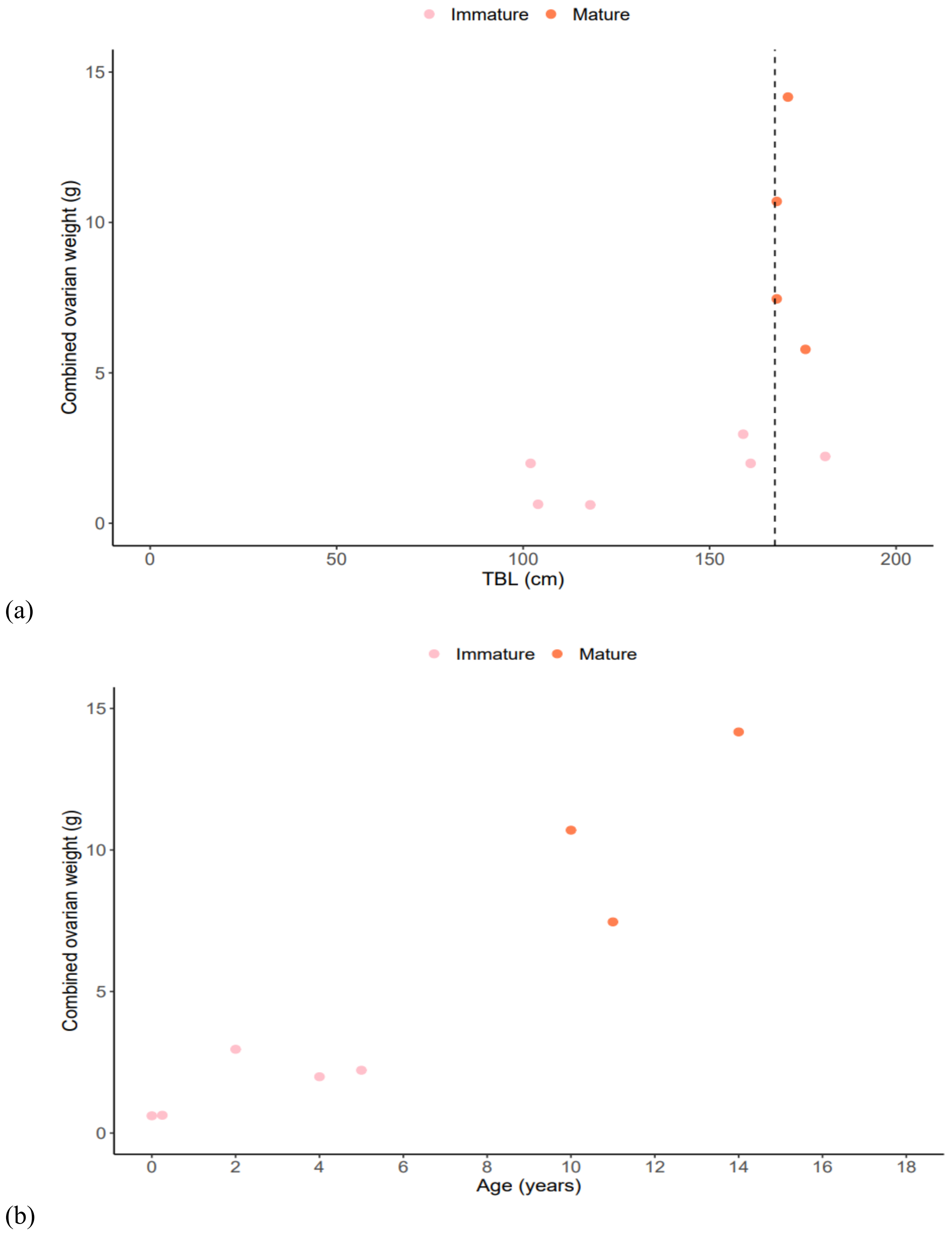


Figure 3.5 Combined ovarian weight vs (a) total body length (TBL; *n* = 10) and (b) age (*n* = 8) for female dusky dolphins (*Lagenorhynchus obscurus*) stranded and bycaught on the Aotearoa New Zealand coast between 1997 and 2023. The dashed line indicated the best estimate of average length (167.5cm) at attainment of sexual maturity.

3.6.1.2 Males

Of the male cadavers examined by Massey University between 1997 and 2020 (*n* = 20), nine were classified as immature (including one late pubescent), and five were classified as mature (Figure 3.6a; Table 3.6). Unfortunately, the remaining six individuals could not be histologically assessed due to decomposition or tissue availability. However, the maturity status of three of those six individuals (WS99-13Lo, WS04-06Lo & WB02-11Lo) was determined as immature at gross examination (WS99-13Lo & WS04-06Lo) and one as presumed mature (WB02-11Lo) based on gross development of testis and evidence of semen on cross section. The maturity status of the remaining three (WS97-53Lo, WS97-57Lo & WS02-29Lo) were unknown since TBL and gonadal characteristics overlapped the late pubescent and mature categories (Figure 3.6a, Table 3.6). TBL, age and testicular variables (testes weight, testes length, testes depth, index of testicular development, and mean seminiferous tubule diameter) for immature, pubescent and mature male dusky dolphins are summarized in Table 3.6.

Sexually immature individuals (excluding pubertal) ranged from 91.5 to 175.5cm (*n* = 10) in length and from 0.25 to 9 years (*n* = 7; Figure 3.7a, b, Table 3.6). Immature testes ranged from 63 to 330mm (mean = 124.9 ±30.1, *n* = 8) and 64 to 330mm (mean = 129.9 ±29.0, *n* = 9) for left and right testis, respectively. Weights (excluding epididymis) of immature testes ranged from 2.45 to 180g (mean = 42.6 ±20.2, *n* = 9) and 2.77 to 180g (mean = 43.8 ±20.2, *n* = 10) for left and right testes, respectively. The smallest immature male had a TBL of 91.5cm, with left and right testes weights (excluding the epididymis) of 2.45g and 2.77g, respectively.

The largest immature male (TBL 175.5cm, KS18-02Lo) also had the largest immature testes (300mm and 330mm, respectively for left and right testes), with left and right testes weight excluding the epididymis of 160g and 180g, respectively. Histologically, immature testes were characterized by seminiferous tubules that were compactly organized and surrounded by a substantial volume of interstitial tissue (Figure 3.8a, b). These tubules were relatively narrow, with tubule diameters ranging from 42.3 to 109.5µm (mean = 65.2 ±20.2, *n* = 8). Within these structures, there was an absence of spermatocytes, spermatids, or spermatozoa. The seminiferous tubules were lined by a basement membrane, which encapsulated one or two layers of cells consisting of supportive Sertoli cells and spermatogonia (germinal cells). These cells were engaged in mitotic activity and were meticulously organized around the periphery of the tubules.

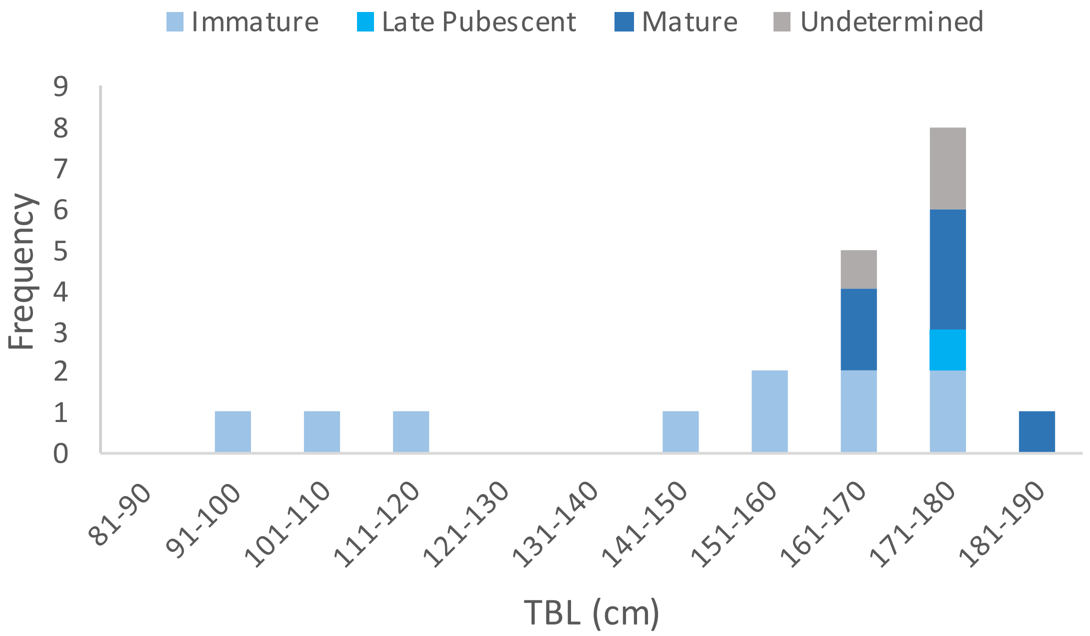
The individual classified as late pubescent (KS10-22Lo) had a TBL of 173cm and was estimated to be 18 years old. Pubescent testes (*n* = 1, Figure 3.7, Figure 3.8c, d; Table 3.6) had lengths of 265.5mm and 290mm for left and right testis, respectively. Left and right testis weights, excluding epididymis were 225g and 230g, respectively. The seminiferous tubules of the pubescent testes recorded an average size of 117.8µm. Spermatogonia and spermatocytes were present, with a reduction in the interstitial tissue and Sertoli cells when compared to immature testes. The spermatogonia and spermatocytes showed distinct zonation, with the spermatogonia actively undergoing meiosis to produce spermatocytes. Some spermatids were present in a few tubules, although no spermatozoa were present.

Sexually mature individuals ranged from 164 to 182cm (*n* = 4) and from 16 to 21 years (*n* = 3; Figure 3.6, Table 3.6). Mature testes (Figure 3.8e, f; Table 3.6, *n* = 5), recorded left and right lengths which ranged from 308 to 445mm (mean = 405.6 ±172.8, *n* = 5) and 318 to 460mm (mean = 415.4 ±174.7, *n* = 5), respectively. Weights (excluding epididymis) of mature testes ranged from 235 to 2642g (mean = 1688.9 ±1002.2, *n* = 5) and 220 to 2659g (mean = 1705.1 ±1015.5, *n* = 5) for left and right testis, respectively.

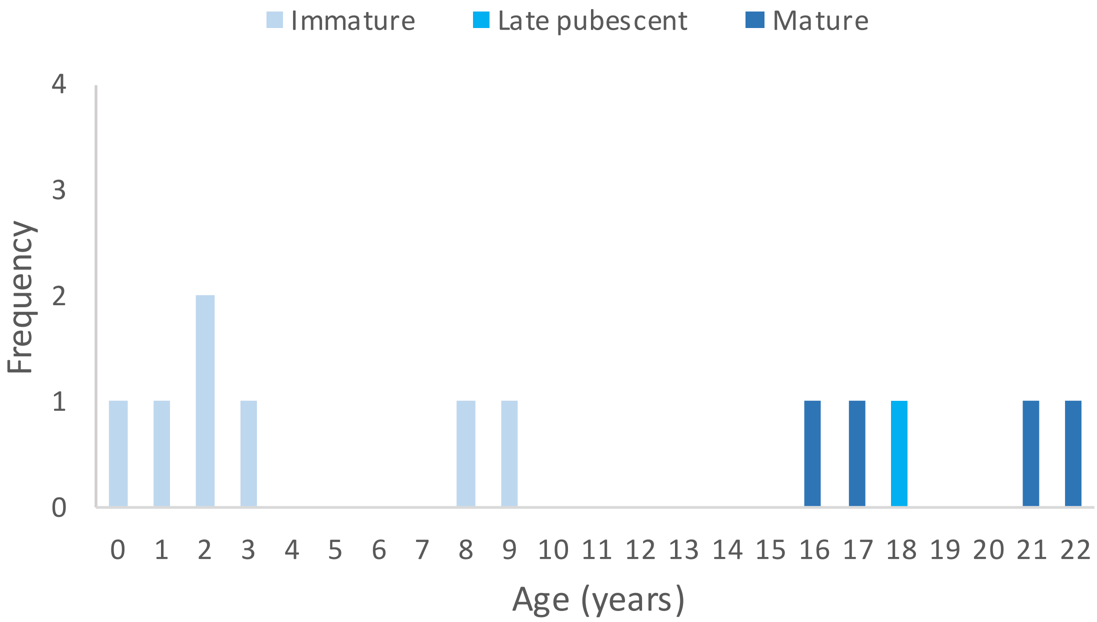
The mature individual with the smallest testes reported a TBL of 173cm, with testes weights (excluding epididymis) of 235 and 220g for the left and right testis, respectively. The smallest mature individual recorded a TBL of 164cm, with testes weights (excluding epididymis) of 1748 and 1763g for the left and right testes, respectively. The individual with the largest mature testes had a TBL of 171cm, with the left and right testes weights (excluding epididymis) of 2642 and 2659g, respectively. Mature testes contained large seminiferous tubules with a diameter range of 138.6 to 271.3µm (mean = 203.2 ±79.6, *n* = 5). All cell types involved in spermatogenesis were present, with spermatocytes, spermatids and spermatozoa observed in high proportions. Low proportions of interstitial tissue, Sertoli cells and spermatogonia were observed.

Individuals of undetermined maturity (Table 3.6, *n* = 3), recorded left and right testis lengths that ranged from 200 to 280mm (mean = 226.7 ±22.1, *n* = 3) and 180 to 280mm (mean = 220.0 ±19.2, *n* = 3), respectively. Only one individual of undetermined maturity had testes weights recorded, with mean weights of 152.0g (±107.5SE) and 115g (±81.3SE), for left and right testis, respectively.

An observed overlap in TBL between immature (including pubescent) and mature males measuring 165 to 175.5cm, resulting in an estimated length of sexual maturity (LSM) of 170cm (95% CI = 170.3 – 170.6cm). However, due to a lack in overlap for age and maturity status, the age at sexual maturity (ASM) was unable to be determined (Figure 3.6b). The smallest sexually mature male (KS18-35Lo) measured 164cm in TBL and had an estimated age of 22 years. The youngest sexually mature male was estimated to be 16 years old, with a TBL of 171cm. The largest sexually immature male (KS18-02Lo), measured 175.5cm in TBL and was estimated as 8 years old. The oldest sexually immature male (KS10-22Lo), which was late pubertal, measured 173.0cm in TBL and was estimated to be 18 years old, though pathological findings from the histopathology report would suggest this individual to be an outlier.



(a)



(b)

Figure 3.6 Maturity stage at (a) TBL (*n* = 20) and (b) age (*n* = 12) for male dusky dolphins (*Lagenorhynchus obscurus*) stranded and bycaught on the Aotearoa New Zealand coast between 1997 and 2020. Note: excluding foetuses (*n* = 3).

Table 3.6 Mean (±*SE*), range and sample size (*n*) obtained for each variable (TBL, age, testes weight, testes length, testes width, an index of testicular development [index], and seminiferous tubule diameter) at each stage of sexual maturation (immature, late pubescent, mature) for male dusky dolphins (*Lagenorhynchus obscurus*) examined in the study (1997–2020). Note: excluding foetuses (*n* = 3).

	Immature	**Late Pubescent**	**Mature**	**Undetermined**	**All**
TBL (cm)					
$\bar{X}$	144.0	173.0	172.3	170.0	157.9
SE	±40.5		±51.1	±43.4	±59.2
Range	91.5–175.5		164–182	167–172	91.5–182
n	10	1	6	3	20
Age (years)					
$\bar{X}$	3.75	18.0	19.0	n/a	10.0
SE	± 2.7		± 4.1		±8.3
Range	0.25–9		16–22		0.25–22
n	7	1	4		12
Left testis weight + epi (g)					
$\bar{X}$	52.4	305.0	1882.4	260.0	653.0
SE	± 72.8		±1091.5	±183.9	±963.6
Range	3.18–190		310–2866		3.18–2866
n	9	1	5	1	16
Right testis weight + epi (g)					
$\bar{X}$	53.8	300.0	1890.5	239.0	619.4
SE	± 24.0		±432.9	±169.0	±948.5
Range	3.84–209		295–2868		3.84–2868
n	10	1	5	1	17
Left testis weight - epi (g)					
$\bar{X}$	42.6	225.0	1688.9	152.0	575.3
SE	± 20.2		±1002.2	±107.5	±875.8

Range	2.45–160		235–2642		2.45–2642
n	9	1	5	1	16
Right testis weight - epi (g)					
$\bar{X}$	43.8	230.0	1705.1	115.0	547.6
SE	± 20.2		±1015.5	±81.3	±867.2
Range	2.77–180		220–2659		2.77–2659
n	10	1	5	1	17
Left testis length (mm)					
$\bar{X}$	124.9	265.5	405.6	226.7	233.7
SE	±30.1		±172.8	±22.1	±161.0
Range	63–300		308–445	200–280	63–445
n	8	1	5	3	17
Right testis length (mm)					
$\bar{X}$	129.9	290	415.4	220.0	233.1
SE	±29.0		±174.7	±19.2	±163.0
Range	64–330		318–460	180–280	64–460
n	9	1	5	3	18
Left testis width (mm)					
$\bar{X}$	26.4	56	99.8	51.7	54.2
SE	±7.4		±12.4	±17.5	±41.9
Range	9–68		51–118	45–60	9–118
n	8	1	5	3	17
Right testis width (mm)					
$\bar{X}$	26.0	54	96.3	48.3	48.1
SE	±6.2		±50.3	±18.6	±38.5

Range	9–60		49–121	40–60	9–121
n	9	1	4	3	17
Left testis depth (mm)					
$\bar{X}$	12.0	n/a	57.2	42.5	32.5
SE	±2.0		±23.0	±24.7	±27.2
Range	5–21		21–100	40–45	5–100
n	7		5	2	14
Right Testis depth (mm)					
$\bar{X}$	12.9	n/a	56.8	40.0	30.5
SE	±2.4		±25.0	±23.09	±25.4
Range	6–23		22–90	40	6–90
n	7		4	2	13
Seminiferous tubule diameter (µm)					
$\bar{X}$	65.2	117.8	203.2	n/a	118.2
SE	±20.2		±79.6		±30.1
Range	42.3–109.5		138.6–271.3		42.3–271.3
n	8	1	5		14
Log_index (g/mm)					
$\bar{X}$	1.8	1.0	0.9	1.1	1.4
SE	±0.7		±0.4	±0.8	±0.8
Range	1.07–3.03		0.79–1.05		0.79–3.03
n	9	1	5	1	15

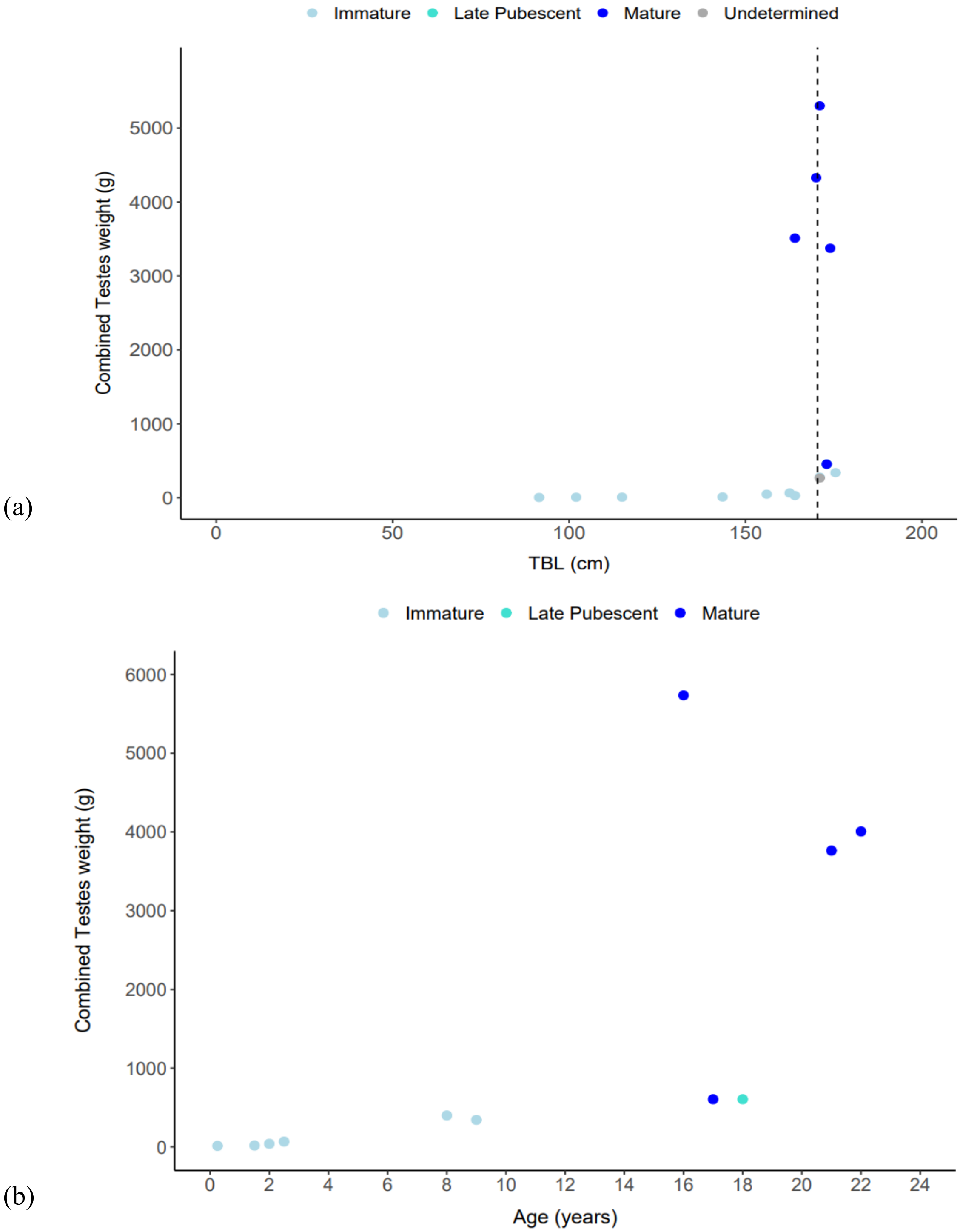


Figure 3.7 Combined testicular weight vs (a) total body length (TBL; *n* = 20) and (b) age (*n* = 11) for male dusky dolphins (*Lagenorhynchus obscurus*) stranded and bycaught on the Aotearoa New Zealand coast between 1997 and 2020. The dashed line indicates the best estimate of average length (170.0cm) at attainment of sexual maturity. Note: One individual (KS11-03Lo, aged 3) is excluded due to a missing testis from a shark bite.

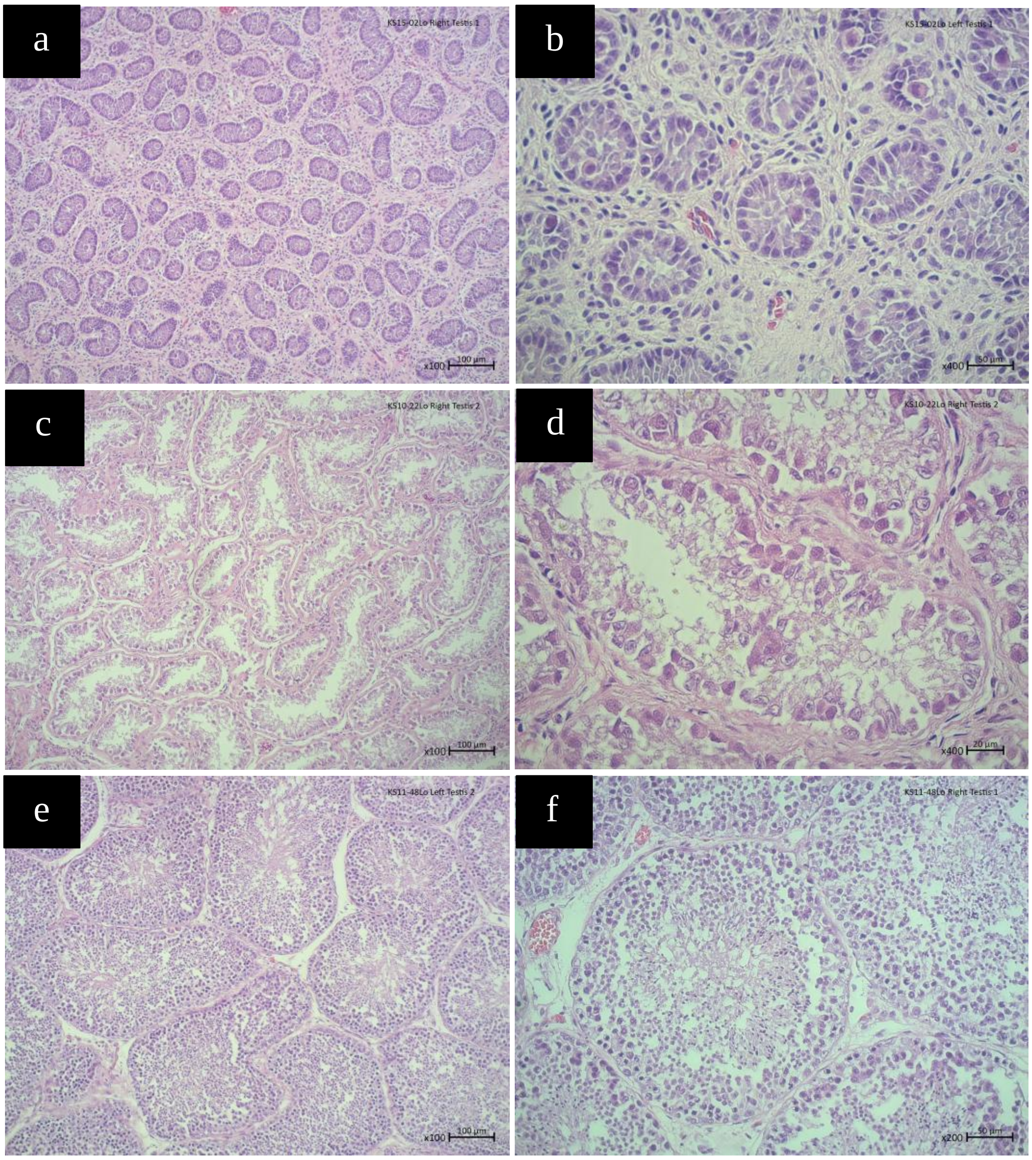


Figure 3.8 Histology of immature, pubescent, and mature dusky dolphin (*Lagenorhynchus obscurus*) testes examined from Aotearoa New Zealand waters (1997 – 2023). **(**a) KS15-02Lo; immature, TBL 115cm, combined testes weight 12.55g, mean seminiferous tubule diameter 46.79µm at 100x magnification, sale bar is 100µm, and (b) KS15-02Lo at 400x magnification, scale bar is 20µm. (c) KS10-22Lo; late pubescent, TBL 173cm, combined testes weight 605g, mean seminiferous tubule diameter 117.84µm at 100x magnification, scale bar is 100µm, and (d) KS10-22Lo, at 400x magnification, scale bar is 20µm. (e) KS11-48Lo; mature, TBL 171cm, combined testes weight 5734g, mean seminiferous tubule diameter 271.26µm, at 100x magnification, scale bar is 100µm, and (f) KS11-48Lo, at 200x magnification, scale bar is 50µm.

Chapter 4 Discussion

Photo credit: Jared Kreiss

4.1 Gestation & Length at birth

The observed variation in gestation periods and birth lengths among species within the Lagenorhynchus genus reflects a complex interplay of ecological and physiological factors. The Peruvian population of dusky dolphins has the longest observed gestation period, averaging 12.9 months (Van Waerebeek & Read, 1994), which contributes to the larger birth sizes in this region. This gestation period is notably longer compared to the South African population, where gestation is estimated at 10 to 11 months, and the New Zealand population, which averages 11.4 months (Best & Meÿer, 2010; Cipriano, 1992; Van Waerebeek & Read, 1994). The extended gestation in Peru allows for more time for foetal development and growth in utero, resulting in larger lengths at birth.

Similar patterns are observed in the wider *Lagenorhynchu*s genus. Specifically, the Pacific white-sided dolphin (*L. obliquidens*) has a gestation period of about 12 months, similar to the dusky dolphins in South Africa and New Zealand, and gives birth to calves with an average length of ~91.8 cm (Best & Meÿer, 2010; Cipriano, 1992; Ferrero & Walker, 1996). White-beaked dolphin (*L. albirostris*) and the Atlantic white-sided dolphin (*L. actus*), are distantly related to dusky dolphins and are found in the coldest waters of the *Lagenorhynchus* genus. These species inhabit the subarctic and temperate waters of the North Atlantic and Arctic Oceans. Both species have gestation periods ranging from 10 to 12 months and give birth to calves with lengths between 110 and 120 cm (Alstrup et al., 2024; Cipriano, 2018; Galatius et al., 2013; Kinze, 2009; Perrin & Reilly, 1984). In colder environments, the slower metabolic rates in pregnant females may lead to longer gestation periods, allowing for greater foetal development to ensure that offspring are sufficiently developed at birth (Cipriano, 2018; Davis, 2019; Eskelinen et al., 2020; Galatius et al., 2013). Additionally, the variability and quality of nutritional resources in these environments can influence foetal growth, with longer gestation periods serving as an adaptive strategy to ensure offspring are born larger and better equipped to survive in harsh conditions (IJsseldijk et al., 2021).

Despite the significance of gestation periods in determining birth lengths, accurately estimating length at birth in dusky dolphins can be challenging. Length at birth could not be calculated in the present study due to a lack of overlap in body length between foetuses and neonates. Foetuses in this study ranged from 25.5 to 81 cm, while the smallest known neonates measured 91.5 and 102 cm. Additionally, six individuals ranging from 83 to 95 cm could not be confidently differentiated between foetus or neonate owing to a lack of postmortem access for assessment. Previous research on the New Zealand population detailed five individuals with milk in their stomachs at total body lengths ranging from 97 to 120 cm (Cipriano, 1992; Würsig, 2007). The smallest three individuals measured between 97 and 102 cm, with two displaying neonatal characteristics such as floppy dorsal fins and foetal folds (Cipriano, 1992; Würsig, 2007).

Length at birth in dusky dolphin populations have demonstrated significant variation, indicating that different international populations exhibit distinct growth patterns. Specifically, different environmental factors, nutritional resources, and local environmental conditions can influence length at birth. The South African population gives birth to the smallest newborns, with length at birth estimated at 86.6 cm, calculated from the average length of 29 neonates that stranded during the birthing season from January to early April (Best & Meÿer, 2010). Meanwhile, neonates in the South African population ranged in body length from 72 to 91 cm (n = 29 neonates; Best & Meÿer, 2010). In contrast, the Peruvian population exhibits an average birth length of 91.4 cm (Van Waerebeek & Read, 1994; range = 80.5 to 104.5 cm; n = 32 foetuses, n = 42 neonates). The mean body length at birth for the Peruvian population was calculated using the arithmetic mean of two methods: the first used the mean of the foetuses and neonates, estimating a length of 92.1 cm. The second involved a linear technique using a smooth polynomial, which estimated a length of 90.7 cm.

However, inherent biases exist in the methods applied across these studies. For example, the South African study primarily relied on measurements of neonates collected from January to April, with the birth season spanning from January to March. Consequently, the mean length at birth calculated may not accurately reflect the size at birth, as it includes neonates measured later in the season who might be larger due to rapid postnatal growth. Similarly, the use of a linear technique with a smooth polynomial in the Peruvian study assumes a continuous and consistent growth pattern, which may not accurately reflect the actual variability in growth rates among individuals (Van Waerebeek & Read, 1994).

4.2 Growth and Attainment of Physical Maturity

In my study, dusky dolphins reach asymptotic length at approximately 170cm (*n* = 22) for females and 171.5cm (*n* = 32) for males, respectively. These findings align with the earlier asymptotic maximum size range reported by Cipriano (1992), which indicated that males and females reach asymptotic length between 170 to 180cm in New Zealand (*n* = 12, sexes pooled). How this compares internationally however, is unclear since the asymptotic lengths for neither Peruvian and South African dusky dolphins is currently known.

For New Zealand dusky dolphins, growth rates for both sexes are particularly rapid during the first two years. In the initial year, female dusky dolphins exhibit a growth rate of 43cm (0.118cm/day), which exceeds the 38.7cm (0.106 cm/day) growth rate observed in males. Beyond the first year, males consistently exhibit faster growth rates than females. For females, the growth rate diminishes to less than 1cm per annum after reaching the age of five and continues to decelerate until it stabilizes at an asymptotic length of 170.0cm by the age of ten. Similarly, male growth rates decrease to less than 1cm per year starting at six years of age, gradually approaching an asymptotic length of 171.5cm, by age twelve. The difference in growth patterns between sexes may be influenced by varying life history strategies and energy allocations for reproduction and survival.

There is no available information on the growth rates during the first year of life for wider populations of dusky dolphins, making it difficult to compare New Zealand data internationally. However, foetal growth rate has been estimated for the South African and Peruvian populations. In South Africa, sizes of foetuses, neonates, and calves were combined and plotted against their respective dates of occurrence using a Bartlett's best-fit regression, which indicated a period of linear foetal growth at a rate of 0.321cm/day, over 8.9 months (Best & Meÿer, 2010). For the Peruvian population, a linear regression model was used to estimate a foetal growth rate of 0.261cm/day, up to parturition (Van Waerebeek & Read, 1994).

Previous estimates for the New Zealand population indicate an average maximum body length of between 170 to 180cm for both males and females (Cipriano, 1992; *n* = 12, sexes pooled), with a maximum of 186cm reported for one male. However, data reported here indicate females (*n* = 51) and males (*n* = 73) reach maximum body lengths of 192 and 195cm, respectively. These measurements place New Zealand dusky dolphins between the current maximum body lengths reported for South Arican and Peruvian populations. Dusky dolphins in South Africa reach maximum body lengths of approximately 190 to 191cm for both males (*n* = 51) and females (*n* = 53) (Cipriano 1992). The Peruvian population is estimated to be 8 to 10cm larger than populations in South Africa and New Zealand, with the maximum total body lengths observed in the Peruvian population being 205 and 210cm for females and males, respectively (Cipriano, 1992).

Body length is influenced by age class, and therefore, age distributions of specimens may not have been comparable across regions or be representative within each population. For example, maximum ages of dusky dolphins in New Zealand assessed as part of this study were 22 years and 14 years for females and males, respectively. Cipriano (1992) estimated one male in the New Zealand population to reached at between 35 to 36 years (NM1661), while another male was estimated to at between 26 to 30 years old (84MW12). Additionally, one female (84MW15) was estimated to have lived between 22 and 24 years (Cipriano, 1992). South African and Peruvian populations display similar age ranges, with the oldest documented age in the South African population at ~ 21 years, though notably this was a captive individual (Best, 1976). In the Peruvian population, the maximum age recorded for males is 11.5 years, while females have been documented to live between 15 and 22 years (Cipriano & Webber, 2010; Manzanilla-Naim, 2011). The age distributions indicate a comparable lifespan among the populations, though whether these ranges reflect maximum age of dusky dolphins in all three regions remains unclear.

Body size is a critical determinant of individual survival and reproductive success, significantly influencing the life history strategies of populations and species (Adamczak et al., 2023; Calder, 2001). McNab's rule suggests that variation in growth rates is influenced by the availability resources in an environment (Adamczak et al., 2023; McNab, 2010). Similarly, Bergmann's rule suggests that populations in colder climates tend to exhibit larger body sizes compared to those in warmer climates. This phenomenon is attributed to the need for larger body masses to better retain heat and maintain stable internal temperatures in colder environments (Adamczak et al., 2023; Blackburn et al., 1999; Torres-Romero et al., 2016). For dusky dolphins, growth rates and body lengths are influenced by resource availability, water temperature, and the effects of different ocean currents on each population.

Dusky dolphins in New Zealand span a latitude of 36° to 52°S, surrounding the South Island and along the eastern coast of the North Island New Zealand. These areas are characterised by various oceanic currents that influence water temperatures and nutrient availability (Hitt et al., 2022; Law et al., 2018; Sutton & Bowen, 2019). Such nutrient-rich and cooler waters (9° to 22°) may result in the New Zealand dusky dolphins being larger than the South African (10° to 26°) counterparts, although smaller than reported off Peru (14° to 20°). The South African population of dusky dolphins inhabits the warmest waters, influenced by the Agulhas Current. This warm environment supports a diverse marine ecosystem but offers less nutrient availability than Peru’s Humboldt Current (Adamczak et al., 2023; Asdar et al., 2022; Beal et al., 2011; Biastoch et al., 2024; Chevallier et al., 2021; Gutiérrez et al., 2016; McNab, 2010). The higher water temperatures in South Africa can increase metabolic rates in dusky dolphins, leading to greater energy requirements for growth and maintenance, potentially contributing to their smaller body sizes compared to other regions (Augustyn et al., 2017; Gruber et al., 2011; Hutchings et al., 2009; Kainge et al., 2020; Lingen et al., 2006). In contrast, the nutrient-rich Humboldt Current in Peru supports a productive ecosystem with abundant prey, enabling Peruvian dusky dolphins to grow at accelerated rates and achieve larger body sizes (Chevallier et al., 2021; Gutiérrez et al., 2016; Llapapasca et al., 2018; Montecino & Lange, 2009; Pietri et al., 2021).

4.3 Allometry

No differences between the sexes in overall growth were observed, with males and females growing at comparable rates. However, despite this lack of difference, the sexes exhibited distinct allometric patterns in various body measurements. Specifically, male dusky dolphins examined here exhibited negative allometry for linear measurements such as snout to navel and eye to blowhole, while females showed positive allometry in these measurements. This indicates such body parts grow at a slower rate relative to total body size in males compared to females. When considering appendage measurements, both males and females display positive allometry for dorsal fin height, lateral dorsal fin base, fluke width, and fluke notch. However, for fluke length and flipper length, males show negative allometry, whereas females exhibit either positive or isometric allometry. This suggests that males in New Zealand experience slower growth of these appendages compared to their body size, while females demonstrate more variable patterns. In respect to girth, New Zealand dusky dolphins demonstrate negative allometry around the flippers, axilla, and navel. In contrast, girth measurements around the eye and anus exhibit isometric or positive allometry. These findings highlight variable scaling patterns in girth measurements for the New Zealand population, with some areas growing more proportionally to body size while others do not.

In contrast, the Peruvian population of dusky dolphins, while exhibiting significant differences in growth rates between sexes, show more uniform allometric patterns compared to the New

Zealand population. Significant differences in growth rates for Peruvian dusky dolphins were evident including snout to gape and eye to blowhole (with p-values < 0.01), indicating notable variations in growth slopes. Similarly, fluke length and flipper length showed significant differences (p-values <0.05), suggesting divergent growth patterns between males and females in the Peruvian population.

For linear measurements, Peruvian dusky dolphins demonstrated consistent negative allometry for anterior body measurements, such as snout to corner of mouth, snout to eye, snout to blowhole, and snout to origin flipper, across both sexes (Best & Meyer., 2010; Van Waerebeek., 1993). This uniform negative allometry in the Peruvian population contrasts with the variable allometric patterns observed in the New Zealand population. For the Peruvian dolphins, significant differences have been noted between the sexes for several measurements, indicating distinct growth patterns (Van Waerebeek & Read, 1994). In contrast, measurements from the New Zealand population did not show significant differences between males and females, suggesting more uniform growth trends across sexes. For appendage measurements, the Peruvian dolphins display positive allometry for dorsal fin height, lateral dorsal fin base, fluke width, and fluke notch, aligning with the positive allometry observed in New Zealand for these traits. However, the Peruvian population shows negative allometry for fluke length and flipper length, while New Zealand dolphins show more variability: males with negative allometry and females with either positive or isometric allometry.

In terms of girth measurements, the New Zealand population shows greater variability compared to the Peruvian population. For example, New Zealand dolphins exhibit negative allometry for flipper, axilla, and navel girth, while showing isometric or positive allometry for eye and anus girth. In contrast, the Peruvian population maintains isometric allometry around the axilla, between the axilla and anterior insertion of the dorsal fin, at the anterior insertion of the dorsal fin, and at the posterior of the dorsal fin. Overall, Peruvian dolphins demonstrate a more consistent scaling relationship across measurements compared to the more variable patterns seen in New Zealand. This variability in the New Zealand population could potentially represent a lack of standardization in measurements taken by the Department of Conservation (DOC), which may have caused inconsistency in the recording of girth measurements. An alternative explanation relates to ecological niches, food availability, or social structures that influence dusky dolphin growth and development in each region. Developmental plasticity, or the ability of an organism to alter its development in response to environmental conditions, may also contribute to these variations (Nijhout & McKenna, 2019). In New Zealand, the observed variability could be driven by more complex or region-specific factors, such as localized environmental conditions or distinct social behaviours, that shape growth patterns differently (Tombak et al., 2024). Environmental factors like temperature, food availability, and habitat stability contribute significantly to these selective pressures, leading to different allometric patterns across populations (Killen et al., 2010; Sun et al., 2019; Thompson, 2019; Yin et al., 2017). In contrast, the more consistent allometric patterns observed in the Peruvian population suggest that different selective pressures or environmental conditions are influencing growth patterns. This consistency could indicate a more stable or uniform environment, where selective pressures, such as predation risks, prey availability, or habitat characteristics, are exerting a steady influence on growth and development. The uniformity in growth patterns may reflect adaptive responses to a relatively constant set of environmental factors, leading to predictable allometric outcomes across the population.

4.4 Sexual Dimorphism

This study revealed no evidence of sexual size or shape dimorphism in the appendage, girth, or blubber thickness of New Zealand dusky dolphins. In contrast to the current findings, previous research on New Zealand dusky dolphins indicated marginal sexual size and shape dimorphism in the dorsal fin. Specifically, males (n = 21) were observed to have larger dorsal fins than their female counterparts (n = 12), characterised by a broader base and greater surface area (Cipriano, 1992; Cipriano & Webber, 2010; Van Waerebeek, 1993). However, the current study aligns with the South African population which similarly identified no difference between the sexes. In contrast, the Peruvian population exhibits differences in six body measurements, with males greater in girth at the anus, maximum flipper width, base length of dorsal fin, depth of flukes, and females greater in snout to anus and snout to genital slit measurements (Best & Meyer, 2010; Van Waerebeek, 1993). This observed difference in snout to genital slit length in the Peruvian population concurs with findings from the New Zealand population.

Sexual monomorphism in species, where males and females exhibit similar sizes and appearances, can be influenced by a variety of ecological, social, and evolutionary factors. In dusky dolphins, monomorphism may arise due to both sexes occupying the same ecological niches and using the same resources, minimising selective pressures for divergence in size or appearance (Orbach, 2019). Sperm competition plays a significant role in polyandrous mating systems, such as that displayed by dusky dolphins, where males invest more time and energy into reproductive organ development rather than traits associated with physical dominance (Degrati et al., 2019; Markowitz, 2004; Orbach, 2019; Vinterstare et al., 2023). This reduces the selection pressure linked with male-male competition, supporting monomorphism (Dunham & Rudolf, 2009). When predation pressures affect both sexes equally, it can result in the development of similar survival traits in male and females (Ishikawa et al., 2018). These traits may include camouflage, speed, and agility, as both sexes adapt to the same environmental challenges to increase their chances of survival (Marshall & Pyenson, 2019; Martin & Hammerschlag, 2012; Pembury Smith & Ruxton, 2020). Stable environments can also affect monomorphism in species. Specifically, in environments where resources and conditions do not fluctuate widely, monomorphism may be favourable, as different traits are not required to adapt to varying conditions (Berns, 2013; Li & Kokko, 2021).

4.5 Gonad Characteristics

4.5.1 Females

In sexually immature dusky dolphins examined here, ovarian lengths and weights ranged from 22.0 to 35.6mm and 0.3 to 1.5g (*n* = 10), respectively. For sexually mature individuals, ovarian lengths and weights ranged from 28.2 to 40.7mm (*n* = 4) and 1.3 to 11.6g (*n* = 7), respectively. The combined corpora count for New Zealand dusky dolphins in my study ranged from 0 to 12, with a mean of 5.3 (±2.1 SE, n = 6) on the left ovary and 2.4 (±1.8 SE, n = 6) on the right ovary. The only previous data for the New Zealand population originates from Cipriano (1992), who reported on a single pregnant female with left and right ovaries measuring 14.8 and 1.6g in weight, respectively. Meanwhile Crespo (1997), reported on population of dusky dolphins off the coast of Patagonia, in which 18 females (8 mature) were examined. Among the mature individuals in that study, 4 were pregnant, 3 were resting, and 1 was lactating. Notably, none of the females were simultaneously pregnant and lactating. All *corpora* were observed on the left ovary, with the mean diameter of CAs and CLs being 7.12 and 24.5mm, respectively (Crespo, 1997). This average CL diameter (24.5mm) is larger than the average diameter of 17.5mm (± 2.68) reported for CLs in the current study (*n* = 3). The difference in ovarian measurements and characteristics observed between populations and studies may simply represent stage (term) of pregnancy in which measurements were taken. Such limited data underscores the need for further research to understand ovarian characteristics and reproductive health in dusky dolphins.

Knowledge of ovarian characteristics is also limited for other members of the *Lagenorhynchus* genus. An immature Peale's dolphin (*L. australis*) had ovaries with a combined weight of 109g, with the left ovary measuring 36 x 19 x 6mm in length, width and depth, respectively, and the right ovary measuring 38 x 14 x 6mm, respectively (Claver et al., 1993), *n* = 1). Mature Peale's dolphins exhibit larger ovarian dimensions, with combined weights ranging from 110 to 115g and length between 46 to 55mm (Claver et al., 1993; *n* = 2). A preliminary report on two pregnant Peale's dolphins, noted one female with a CL on the left ovary, but no CAs on either ovary, suggesting a first pregnancy, and another individual with 15 CAs on the left ovary and two on the right (Claver et al., 1993; *n* = 2). Comparatively, in Pacific white-sided dolphins mature ovarian weights of between 4.8 and 21.8g have been reported (Ferrero & Walker, 1996; *n* = 10). In comparison, the average CA count for three white-beaked dolphins was 14.67. Specifically, the first white-beaked dolphin exhibited nine and seven CAs on the left and right ovaries, respectively, while the second dolphin displayed nine and six CAs on the left and right ovaries, respectively. A third dolphin reported four and nine on the left and right ovary, respectively (Galatius et al., 2013; *n* = 3).

As supported by the data, the number of corpora varies greatly between species. However, the extent of variation between populations of dusky dolphins is unknown. Ovarian asymmetry has been observed in several species including common dolphin (Danil & Chivers, 2007; Kemper et al., 2014; Palmer et al., 2022), as well as long-finned pilot whales (*Globicephala melas edwardii*, Betty 2019). Studies on various mammalian species, including pinnipeds like Cape fur seals (*Arctocephalus pusillus pusillus*) and terrestrial mammals such as rodents and carnivores, have also shown ovarian asymmetry, suggesting this phenomenom may be more widespread than previously thought (Dominguez et al., 2003; Odendaal et al., 2002). While asymmetry exists for many species, there has been no conclusive explanation to why this occurs in odontocetes. While limited knowledge on the ovarian characteristics of the *Lagenorhynchus* genus exists, this study supports the suggestion ovarian asymmetry occurs in the genus, via left ovary dominance evident.

4.5.2 Males

Testes of sexually immature New Zealand dusky dolphins ranged in length from 63 to 300mm (mean = 124.9mm, ±30.1, *n* = 8) and 64 to 330mm (mean = 115.8, ±29.0, *n* = 9) for left and right testis and weighed 3.18 to 190g (mean = 52.4g ±72.8, *n* = 9) and 3.84 to 209g (mean = 53.8g, ±24.0, *n* = 10), respectively. The late-stage pubescent individual (KS10-22Lo) recorded a left and right testes lengths of 265.5 and 290mm weights of 305.0 and 300.0g, respectively. Histopathological assessment of testicular tissue for this individual revealed testicular torsion with mild lipofuscinosis (Massey University, unpublished data), a condition which can induce significant implications for reproduction and overall testicular health (Brunk & Terman, 2002; Singh et al., 2012).

Testes of mature dusky dolphins exhibited a length range of 308 to 445mm (mean = 405.6mm ± 172.8, *n* = 5) and 318 to 460mm (mean = 415.4mm ± 174.7, *n* = 5) for left and right testis, respectively. Weights (testis and epididymis) ranged from 310 to 2866g (mean = 1882.4, ±1091.5, *n* = 5) 295 to 2868g (mean = 1890.5, ±432.9, *n* = 5) for left and right, respectively. However, as dusky dolphins exhibit reproductive seasonality (Markowitz et al., 2023), bias in the data is possible due to variations in testicular size and weight throughout the year. Unfortunately, due to the small sample size of this study, reproductive seasonality was unable to be assessed.

Previous research on the New Zealand population, which included just three immature males, reported a narrower weight range for testes: left testes (including epididymis) ranging from 12 to 27.4g and right testes (including epididymis) from 12.9 to 26.7g (Cipriano, 1992; *n* = 3). Cipriano (1992) also reported that a subadult male with semen in the epididymis had left and right testes weights of 637g and 663g, respectively. The weight range for mature males in this study exceeds the ranges reported by Cipriano (1992), which were 277.4 to 2,143g and 252.5 to 2,085g for left and testes, respectively (*n* = 9).

The heaviest testes weights reported for immature males in the Peruvian population were 300g and 310g for the left and right testes, respectively (Van Waerebeek & Read, 1994). My findings align with those reported for the Peruvian population, where the mean lengths of immature testes were 230mm for the left and 240mm for the right, falling within the range observed in the New Zealand population (Van Waerebeek & Read, 1994; *n* = 38). Dusky dolphins from Peru show a larger range in the mass and length of mature testes (with epididymides attached), given the much larger sample size this is expected, with ranges as follows: left testis 53 to 5,120 g (mean = 1,464g; *n* = 125) and 12.3 to 58.5cm (*n* = 132); right testis 53 to 4,930g (mean = 1,486g; *n* = 125) and 135 to 580mm (*n* = 133) (Van Waerebeek & Read, 1994). Best & Meÿer (2010) reported that individuals in South Africa with TBLs less than 163cm had combined testes weights (excluding epididymis) of less than 80g (*n* = 18). In contrast, individuals with a TBL greater than 176cm demonstrated combined testes weights exceeding 500g (excluding epididymis), with two individuals reporting combined testes weights over 2500g (*n* = 8).

Connor et al., (2000) predict that odontocete species with large testes relative to body size are more likely to engage in sperm competition and exhibit promiscuous behaviour. The large testis size observed in this study along with the high levels of promiscuity documented in field observations (Markowitz et al., 2010; Orbach et al., 2014) supports this hypothesis for New Zealand dusky dolphins. The polygynandrous mating system of dusky dolphins involves frequent mating, necessitating that males produce and store large quantities of sperm to succeed in reproduction, as promiscuous females may have sperm from multiple males in their reproductive tract (Orbach, 2019; Roldan, 2019). In such a system, males with larger testes and higher sperm production would gain significant reproductive advantage (Dines et al., 2015; Parker et al., 2013).

4.6 Attainment of Sexual Maturity

Sexually immature females in the New Zealand population show a TBL range of 78 to 181cm, exceeding the TBLs of immature female dusky dolphins examined in South Africa and Peru. For instance, in Peru, immature females measure between 127 to 179.5cm (*n* = 8), with the largest females measuring 174, 177, and 179.5cm (Cipriano & Webber, 2010; Manzanilla-Naim, 2011). Meanwhile, in the South African population, immature females range from less than 160 to 176cm (Best & Meÿer, 2010; *n* = 20).

For sexually mature females assessed in this study, TBL ranged from 166 to 175.5cm, which is comparable to mature females in South Africa, where mature individuals ranged from 168 to >185cm (*n* = 15). The Peruvian population exhibit similar body length range, from 173 to 193cm (*n* = 18), with minimal overlap with the mature females in this study (Cipriano & Webber, 2010; Manzanilla-Naim, 2011).

Sexually immature males in my study ranged from 91.5 to 175.5cm, aligning with immature individuals observed in the Peruvian population, with two immature males from Peru measured

141 and 172cm (Cipriano & Webber, 2010; Manzanilla-Naim, 2011). The range of immature males is greater in New Zealand compared to the South African, where immature males range from less than 160cm to 176cm (Best & Meÿer, 2010; *n* = 27). New Zealand mature males range from 164 to 182cm, which aligns with the lengths that mature individuals in the South African population, which range from 166 to over 185cm (Best & Meÿer, 2010; *n* = 10). In Peru, mature males range from 176 to 206cm, with the largest reaching 210cm (Van Waerebeek, 1993b; *n* = 12) (Cipriano & Webber, 2010; Manzanilla-Naim, 2011).

In New Zealand, female and male dusky dolphins attain sexual maturity at a body length of 167.5cm (CI = 166.0 – 168.98, *n* = 17) and 170.0cm (CI = 170.3–170.6, *n* = 20), respectively. In South Africa, female dusky dolphins reach sexual maturity at lengths between 170 to 175cm (Best & Meÿer, 2010; *n* = 16), while males show a broader range, maturing at lengths between 166 to 176cm (Best & Meÿer, 2010; *n* = 37). In contrast, the Peruvian population exhibits a more consistent LSM between the sexes, with males and females maturing at approximately 175cm (Van Waerebeek, 1993; *n* = 394, sexes pooled). Notably, New Zealand dusky dolphins differ, with females reaching sexual maturity at a lower total body length compared to the Peruvian population. Additionally, New Zealand males reach sexual maturity at a lower TBL than those in Peru, although their LSM is consistent with the broad range reported for South African males.

Previous research on New Zealand dusky dolphins reported a marginally lower range of body length for sexual maturity of 160 to 165cm (Cipriano, 1992; *n* = 21, sexes pooled). This may be due to a small sample size of mature individuals (females *n* = 4, males *n* = 9). The current estimates for sexual maturity of 167.5cm for females and 170.4cm for males in New Zealand, with the maturing range for females being 166 to 181cm (*n* = 8) and 164 to 175.5cm (*n* = 9) for males, respectively. The current estimates lie between earlier New Zealand findings (Ciprian, 1992) and the ranges reported for both the South African (Best & Meÿer, 2010) and Peruvian (Van Waerebeek, 1993) populations, with up to 10cm variation both within and between populations.

Due to a lack of overlap in age between immature and mature individuals for both sexes in the present study, it was not possible to calculate ASM for either females or males in the New Zealand population. However, the literature suggests dusky dolphins off Peru reach sexual maturity between 4.3 to 5 years for females and between 3.8 to 4.7 years for males (Van Waerebeek & Würsig, 2018). Previously, Cipriano (1992) suggested the New Zealand population reaches sexual maturity later than the Peruvian population, attaining sexual maturity around 7 to 8 years of age, for both sexes. In this study, sexually immature females ranged from 0 to 5 years, while sexually mature females ranged from 10 to 14 years. Sexually immature New Zealand males in the present study range from 0.25 to 18 years, including one late pubescent individual at 18 years of age (KS10-22Lo), while sexually mature males from this study range from 16 to 22 years old. KS10-22Lo was aged 18 years old, outlier and demonstrated testicular torsion with mild lipofuscinosis which can affect reproductive capabilities (Brunk & Terman, 2002; R. Singh et al., 2012). Nonetheless, New Zealand dusky dolphins may potentially mature later in comparison to their Peruvian counterparts, though limited sample sizes for the New Zealand population currently make it challenging to compare between populations. Additionally, the age at which sexual maturity is attained has not been determined for the South African population yet.

Attainment of physical and sexual maturity are intrinsically linked and can vary between populations due to several factors. Environmental conditions such as resource availability and quality, play a critical role; populations with abundant and high-quality food sources tend to reach sexual maturity and asymptotic lengths faster than those facing limited resources (Adamczak et al., 2023; Hantak et al., 2021; Kelt et al., 2019; Lehodey et al., 2006; Liu & Fu, 2017; Pineda-Munoz et al., 2016). Social dynamics and competition within populations can impact growth rates; populations with less competition for resources or lower predation pressure may have a faster growth rate (Chasco et al., 2017; Kelt et al., 2019; Tarjuelo et al., 2022). Additionally, water temperature can affect growth rates, species in colder waters often need to grow quickly and for longer periods to effectively thermoregulate and survive in their environment (Adamczak et al., 2023; Hantak et al., 2021; Liwanag, 2010; Rutishauser et al., 2004). Environmental stressors such as pollution or habitat degradation can have a negative impact on growth rates, which may result in delayed attainment of physical and sexual maturity (Hantak et al., 2021; Kebke et al., 2022; Murphy et al., 2020).

These factors contribute to the differences in life history characteristics observed between populations of the same species, with varying environmental conditions playing a significant role. For example, harbour seals (*Phoca vitulina*) in colder regions, such as Alaska and the northern North Atlantic, grow more slowly and mature later than those in warmer environments, such as Californian and Western Europe, due to increased energetic demands for thermoregulation and seasonal fluctuations in prey availability (Blanchet et al., 2021; Ferguson et al., 2025; Harding et al., 2018; Teilmann & Galatius, 2018). Northern populations also tend to have larger body sizes and lower reproductive rates, while southern populations, experiencing more stable prey availability and reduced thermoregulatory costs, grow faster, mature earlier, and reproduce more frequently. Such variations underscore the impact of local ecological factors, such as temperature and resource availability, on shaping growth, maturation, and reproductive strategies within species (Blanchet et al., 2021; Ferguson et al., 2025; Harding et al., 2018; Teilmann & Galatius, 2018). Similar examples can be found across other groups as well such as seals, sea otters and birds (Davis, 2019; Song et al., 2016).

The influence of stress and contaminants on reproductive success and the attainment of sexual maturity has been demonstrated in several species, including common dolphin, spinner dolphins (*Stenella longirostris*), North Atlantic right whales (*Eubalaena glacialis*), and killer whale (*Orcinus orca*) (Beineke et al., 2010; Derous et al., 2020; Harwood, 2001; IJsseldijk et al., 2021; Kebke et al., 2022; Lacy et al., 2017; Martineau, 2007; Murphy et al., 2018b; Law, et al., 2018; Reeves et al., 2001). Chronic stress from environmental pressures (e.g., resource availability, social dynamics, or human activities) often results in elevated cortisol levels (Sanganyado et al., 2021; Sanganyado & Liu, 2022), which can interfere with reproductive cycles, potentially delaying the onset of oestrus, reducing fertility and conception rates, and increasing the likelihood of spontaneous abortion (Betty, 2019; Casano-Bally, 2023; IJsseldijk et al., 2021; Munson et al., 1998; Murphy et al., 2020; Palmer et al., 2022, 2023; Sanganyado & Liu, 2022).

Contaminants, such as persistent organic pollutants (POPs) including polychlorinated biphenyls (PCBs) and dichlorodiphenyltrichloroethane (DDT), also play a crucial role in reproductive health. In females, exposure to these contaminants can disrupt reproductive hormones (Hohn et al., 2007; Murphy et al., 2010; Murphy et al., 2018a; Law, et al., 2018), while in males, it can suppress testosterone production, which is essential for sperm production (Williams et al., 2021). This suppression can delay testicular development and overall maturation, leading to decreased sperm production and quality, ultimately affecting fertility (Lacy et al., 2017; Sanganyado et al., 2021; Sanganyado & Liu, 2022; Williams et al., 2021). In addition, stress can affect lactation, potentially decreasing both the quantity and quality of milk available to calves, which can impair their growth and development (Murphy et al., 2010). Environmental disturbances or changes in prey availability may exacerbate these stress-related energy deficits, further compromising reproductive health and delaying sexual maturity (Kebke et al., 2022; Yang et al., 2021).

4.7 Reproductive Strategies

Body size and condition are important factors that influence reproductive success in both males and females (Castrillon & Bengtson Nash, 2020). In cetaceans such as harbour porpoises (*Phocoena phocoena*), dusky dolphins and spinner dolphins, smaller body size in males may enhance manoeuvrability and speed which is advantageous in the context of sperm competition when competing for a female (Chivers & Danil, 2023; Connor, Read, et al., 2000; Kesselring et al., 2019; Markowitz et al., 2023; Markowitz et al., 2010). However, since males produce and store large quantities of sperm, the real competition occurs post copulation. The sperm of multiple males competes within the female's reproductive tract to fertilize the eggs (Durrant, 2019; Orbach et al., 2014; Parker et al., 2013; Roldan, 2019). Investing in testicular development rather than body length or sexual dimorphism allows males with larger testes to produce more sperm, leading to higher fertilization success (Dines et al., 2015; Mesnick & Ralls, 2018). As males age, their reproductive effort increases due to the energy expenditure associated with multiple mates (Foley et al., 2018). Immature males prioritize growth over building endogenous reserves, while sexually mature males can invest more time and energy into building reserves and engaging in breeding activities (Foley et al., 2018; Yoccoz et al., 2002).

For females, body condition is equally critical. Adequate body reserves are necessary to support pregnancy and lactation, which are energetically demanding processes (Christiansen et al., 2014). Females with better body condition are more likely to successfully carry a pregnancy to term and provide adequate nutrition to their calves through lactation. In the context of dusky dolphins' polygynandrous mating system, females mate with multiple males, increasing genetic diversity among their offspring. This strategy can be advantageous in unpredictable environments, as it maximises the chances of offspring survival (Markowitz, 2004; Markowitz et al., 2010; Orbach, 2019; Orbach et al., 2015; Pearson et al., 2017; Würsig et al., 2023).

In New Zealand dusky dolphins, there is an observed increase in testicular weight that coincides with the birthing season, typically from October to January (Markowitz et al., 2023). Similarly, in Peruvian dusky dolphins, testis weight increases in August, peaks in September to October, and then subsequently decreases in November, synchronising with the timing of ovulation and conception in this population (Van Waerebeek & Read, 1994). This increase in testicular weight is likely related to the breeding season, as males prepare for breeding by producing more sperm, increasing their reproductive success. Seasonality in females ensures that calves are born during a time when environmental conditions are most favourable for their survival and growth (Varpe, 2017). The alignment of reproductive activities for both sexes alongside optimal environmental conditions maximises the chances of successful reproduction and calf survival, which are essential for the sustainability of the population.

4.8 Study Limitations

While this thesis offers important insights to the growth and reproduction of dusky dolphins, it is not without limitation. For instance, data for this thesis originated from stranded and bycaught dusky dolphins, which represents several points worthy of consideration. The opportunistic nature of sampling introduces temporal and spatial biases, as the availability of cadavers from stranded or bycaught dolphins varies both temporally and spatially (Lanyon & Burgess, 2014). Such variability can result in data gaps, and therefore affect the representativeness of the population, particularly in understanding seasonal and regional differences in growth and reproductive patterns, including reproductive seasonality.

The use of stranded animals further gives rise to the limitation in the state of preservation, as samples from decomposed carcasses can lead to inaccurate measurements. This issue has been managed by decomposition scaling at postmortem at Massey University or by photographs and comments reported by the DOC officer. To mitigate the issue, individuals beyond moderate decomposition were excluded from this study. Additionally, the use of stranded animals often results in a positive bias towards individuals with underlying health or disease conditions (Ijsseldijk et al., 2020). The quality of samples collected from stranded individuals can further be compromised by exposure to air, sun, and water, which can deteriorate tissue quality and affect the determination of sexual maturity, as gonadal samples are particularly prone to rapid decomposition (Ijsseldijk et al., 2020; Yarmolenko et al., 2011). Transporting carcasses may further impact tissue quality (Ijsseldijk et al., 2020).

A key limitation in this study is the inability to calculate life history measurements such as age at physical and sexual maturity, as well as length at birth, due to insufficient samples data of foetuses, neonates, and individuals across some reproductive stages. The lack of smaller individuals (<150cm) is a notable gap in the data set, limiting this study’s ability to calculate length at birth and construct accurate growth models. Although the dataset spans ages from 0 to 22, the small data set and considerable number of unsampled age groups, limits the accuracy of growth models and estimates of asymptotic length. Including more data from a diverse range of ages and body lengths would significantly improve the models and provide a clearer understanding of the growth patterns and life stages of New Zealand dusky dolphins.

This study faces a particular gap in understanding the reproductive and developmental stages of pubescent males, older immature, and young mature females. For pubescent males, there is substantial research on testicular development in delphinids (Atkinson, 2024; Murphy et al., 2005b; Palmer et al., 2023). However, a lack of information detailing pubertal testicular development during the transition to adulthood in dusky dolphins remains notable. Such data is essential for accurately estimating the age at sexual maturity and understanding the reproductive development of male dusky dolphins.

Similarly, data on females, specifically those in the critical reproductive age range of five to ten years, in my study was insufficient. This age range is crucial for assessing reproductive parameters, including the frequency of pregnancies and the overall reproductive health of the population. Additionally, differentiating between ovarian scars from ovulation or pregnancy is vital for making definitive conclusions about reproductive patterns and overall population dynamics. Due to the temporal and spatial limitations of the available data, reproductive seasonality could not be ascertained in my study. The opportunistic nature of sampling and the limited number of individuals in various reproductive stages prevented the analysis of seasonal variations in reproductive patterns.

Beyond the caveats of opportunistic sampling (Dalili, 2019; Shaheen et al., 2019; Viola et al., 2024), methodological considerations also need mention. For example, the methodology of aging through growth layer groups in teeth poses challenges. GLGs in teeth are incremental layers that start accumulating annually after birth, forming because of the cyclical deposition of dentin and cementum layers within the tooth (Hohn, 2009; Read et al., 2018). Except for the anterior and posterior underdeveloped teeth, any normal developed tooth can provide an accurate estimation of age (Betty, 2019; Hohn, 2009). Challenges such as tooth wear, curvature and staining, can compromise age estimates (Waugh et al., 2018). To mitigate these issues, this study implemented practices around tooth selection and standardised methods, including blind reading and assessments by multiple experienced readers, enhancing the reliability of the ages.

Similarly, ovarian scar reabsorption in cetaceans introduces further considerations. Ovarian scars (CAs), form after ovulation when the CL regresses (Dabin et al., 2008; Mikhalev, 2019). Over time, these scars may be reabsorbed by the ovarian tissue, making the assessment of reproductive history and other life history characteristics more difficult to analyse (Dabin et al., 2008). The reabsorption of scars can lead to an underestimation of the number of past ovulations or pregnancies, impacting the ability to accurately determine age at sexual maturity (Inbaraj et al., 2021). Furthermore, ovarian scar reabsorption can make it challenging to estimate length at sexual maturity, as the number of reproductive events help inform this analysis.

While such sampling and methodological limitations exist, protocols and procedures have been established to minimize their impact. For example, the dataset used in this study spans more than half a century and offers a valuable baseline for future research. A comprehensive approach is critical for developing effective conservation strategies, as it facilitates a better understanding of reproductive health, and population responses to environmental changes. Such efforts are essential for the sustainable management and preservation of dusky dolphin populations in Aotearoa New Zealand.

4.9 Future Research

Despite the scientific knowledge contributions made by this thesis, significant knowledge gaps remain for dusky dolphins in Aotearoa New Zealand. Addressing these gaps is essential for gaining a comprehensive understanding of growth and reproductive since such parameters are intrinsically liked to survivorship and population-level impacts. Longitudinal studies and increased sample sizes will enhance the reliability of age and size estimates for both sexes, which would enable a more reliable estimate of life history traits of dusky dolphins.

Birth length serves as a fundamental baseline for tracking growth rates and development. Targeting sampling of near-term foetuses and newborns would enable greater understanding on the early life stages of dusky dolphins which is pivotal for assessing the length of birth for dusky dolphins in Aotearoa New Zealand waters. Additionally, detailed data on females across all maturity statuses, with a particular focus on those aged five to ten years of age, are required to gain better understanding on the developmental stages leading to sexual maturity. This information is not only vital for understanding individual reproductive strategies but also for predicting future population trends. For male dusky dolphins, there is a similar need, particularly concerning pubescent and mature individuals. Understanding the age and size at which males reach sexual maturity is essential for assessing their role in reproduction and competition. Further investigation into the reproductive development of pubescent males, including hormonal and physical changes, is recommended to differentiate between stages of maturity.

An extended dataset that encompasses a broader range of individuals across various lengths and ages would also enable further research into the age at attainment of physical maturity. Accessing more cadavers to be able to age further individuals and reduce the number of unknown sex animals would further facilitate age-related growth patterns and age at attainment of physical maturity. To refine and update previous assessments, further research should focus on longitudinal studies to monitor reproductive behaviours and timing throughout the year, gather data on mating and calving seasons, and identify any seasonal variations in reproductive success. Additionally, detailed studies on aspects of the reproductive cycle, such as the resting period and calving interval, are needed. This information is crucial for predicting reproductive success and its impacts on population dynamics.

4.10 Conclusion

This study provides important insights into the age, growth, and sexual dimorphism of dusky dolphins in Aotearoa New Zealand waters. Here I have described growth and attainment of physical maturity, allometry and sexual dimorphism, gonadal characteristics, attainment of sexual maturity, and reproductive strategies. While these findings provide a foundation for understanding how local populations compare to those in other regions, critical information such as length at birth and comprehensive data on individuals from all ages remain unknown. This gap hinders our ability to fully understand the growth and reproductive patterns of this species both within New Zealand and beyond. Despite these limitations, this study establishes baseline parameters that are crucial for detecting population trends, guiding further scientific research and conservation efforts.

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Appendices

Appendix 1 Analysis of sexual dimorphism in 29 external measurements of physically mature female (*n* = 22) and male (*n* = 32) dusky dolphins (*Lagenorhynchus obscurus*) stranded and bycaught on the Aotearoa New Zealand coast from 1960 and 2023: based on Welch's ANOVA test results and means from Table 3.4.

Measurement	F vs M	Difference between sexes (cm)	F-value	P-value	Size Dimorphism Index (SDI)
TBL	F > M	1.681	0.75	0.39	-0.01
Snout-anus	F > M	4.241	3.93	0.055	-0.03
Snout-genital slit	F > M	9.489	40.60	6.78e-07	-0.08
Snout-navel	F > M	4.250	1.37	0.28	-0.05
Snout-origin flipper	F < M	0.108	0.01	0.92	0.00
Snout-origin dorsal fin	F > M	4.783	0.67	0.42	0.00
Snout-tip dorsal fin	F > M	0.783	0.08	0.78	-0.01
Snout-blowhole	F < M	0.140	0.01	0.91	0.01
Snout- cnr mouth	F < M	0.539	0.64	0.43	0.02
Genital slit	F > M	1.136	0.51	0.5	-0.10
Rostrum	F > M	0.271	0.37	0.55	-0.05
Cnr mouth-eye	F > M	0.451	1.29	0.28	-0.09
Eye-blowhole	F > M	0.153	0.08	0.79	-0.01
Dorsal fin height	F < M	0.576	0.54	0.47	0.03
Dorsal fin lat base	F < M	0.200	0.02	0.89	0.01
Fluke width	F < M	0.444	0.12	0.74	0.01
Fluke length	F < M	0.775	0.97	0.97	0.05
Fluke notch	F > M	0.095	0.05	0.83	0.04
Flipper internal	F > M	4.442	1.05	0.33	-0.17
Flipper exterior	F > M	0.392	0.19	0.67	-0.01
Flipper width	F < M	0.193	0.40	0.53	0.02
Girth eye	F > M	0.073	0.001	0.97	0.00
Girth flippers	F < M	1.097	0.11	0.74	0.01
Axill-girth	F < M	5.333	0.79	0.39	0.05

Girth navel	F > M	1.325	0.04	0.84	-0.01
Girth anus	F < M	3.611	0.89	0.37	0.06
Blubber dorsal	F < M	0.261	0.58	0.46	0.19
Blubber lateral	F < M	0.139	0.43	0.52	0.13
Blubber ventral	F < M	0.117	0.24	0.63	0.10

Appendix 2 Dusky dolphins (*Lagenorhynchus obscurus*) used in morphometric and life history analyses that were stranded and bycaught on the Aotearoa New Zealand coast from 1960 and 2023, ordered by total body length (TBL), including DOC ID, Massey Animal ID, Sex, Sexual Maturity (F = Foetus, I = Immature, LP = Late Pubescent, M = Mature), Age (Years), TBL (cm), Date, and Location.

DOC ID	**Massey Animal ID**	**Sex**	**Sexual Maturity**	**Age (years)**	**TBL (cm)**	**Date**	**Location**
	KS23-18LoA	Male	F		25.5	8/04/2023	Pohara beach, Golden bay
	KS11-41LoA	Male	F		52.5	26/08/2011	Marlborough, South Island
	KS23-63Lo	Female	F		77.5	28/11/2023	Golden Bay, Tasman District
	WS01-32Lo	Male	F		78	2/11/2000	Ocean View Beach, Kaikorai
	KS23-64Lo	Female	F		81	10/11/2023	Katigi beach, Otago
3349		Female			83	5/11/2002	Karitane beach, Otago
2832		Male			87	21/11/2007	Kaikoura, Canterbury
3345		Unknown			88	2/11/2002	Nugget Point, Otago
1386		Female			90	4/11/1990	Purakanui Inlet, Dunedin
3497	KS14-48Lo	Male	I		91.5	1/11/2014	Rabbit Island, Nelson
2455		Male			93	21/11/2003	Ngaio Bay, Motueka
3869		Male			95	18/10/2017	Kina Beach, Tasman
	WS04-06Lo	Male			102	30/01/2004	Moeraki, Otago
	KS23-68Lo	Female			102	29/11/2023	Mangakuri Beach, Hawkes Bay
592		Male			104	2/11/1975	Awatoto beach, Napier
4031	KS19-01Lo	Female	I	0.25	104	20/01/2019	Kaikoura esplanade

1698		Female			105	1/09/1994	Kaikoura, Canterbury
1750		Male			108	1/01/1995	Kaikoura, Canterbury
4306		Male			108	7/01/2008	Fox River, West Coast
	KS15-02Lo	Male	I	0.25	115	5/01/2015	Kaikoura, Canterbury
4030	KS19-02Lo	Female	I	0	118	8/01/2019	Oaro Beach, Kaikoura
	WB98-04Lo	Female			118		
2670		Unknown			119	27/02/2006	Kaikoura, Canterbury
2093		Unknown			120	26/08/1999	Nelson Estuary, Nelson Haven
	WB98-31Lo	Female			120		
620		Male			121	1/09/1976	Tongoio beach, Napier
361		Female			128	11/05/1964	Paekakariki Beach, Wellington
2442		Unknown			133	20/10/2003	Motueka Sand Spit, Tasman
2466		Male			134	2/01/2004	Goose Bay, Kaikoura
3344		Female			134	12/10/2007	Surat Bay, Otago
3763		Male			137	22/09/2016	Rabbit Island, Nelson
4209		Unknown			140	19/02/2021	Goose Bay, Kaikoura
3044	KS10-24Lo	Female	I	0.5	141.6	15/07/2010	Owaka Heads, Otago
1935	WS97-08Lo	Female			142	20/04/1997	South Bay Kaikoura
3278	KS12-07Lo	Male	I	1.5	143.5	24/06/2012	Pelorus Sound, Marlborough
923		Unknown			144	1/09/1983	South Beach, Greymouth
2099		Female			145	22/09/1999	Motueka Sand Spit, Tasman

4286		Female			146	25/11/2021	Snout Point, Waikawa Bay
4337	KS22-39Lo	Male			146	19/04/2022	Orore Point, Otago
1375		Unknown			150	27/09/1990	Portobello, Otago
2406		Female			154	13/03/2003	South Bay, Kaikoura
1216		Male			156	8/10/1988	Portobello, Dunedin
2790		Female			156	26/05/2007	Wellington Harbour
4146	KS20-19Lo	Male	I	2.5	156	10/07/2020	Kaikoura, Canterbury
4234		Male			156	4/05/2021	Boulder Bank Scenic Reserve, Nelson
12		Female			157	27/09/1999	Motueka, Nelson
2523		Female			157	12/09/2004	Motueka, Nelson
4268	KS21-34Lo	Male			158	19/09/2021	Porirua Harbour, Wellington
	KS11-03Lo	Male	I	3	159	28/01/2011	Kaikoura, Canterbury
4259	KS20-27Lo	Female	I	2	159	23/09/2020	Marahau Sandspit, Tasman
1897		Male			160	4/10/1996	Ruby Bay, Tasman
2173		Unknown			160	21/08/2000	Waimea Inlet, Nelson
2559		Male			160	23/12/2004	Oaro, Kaikoura
2883		Unknown			160	7/07/2008	Pelorous Sound, Marlborough Sounds
3368		Male			160	27/07/2012	Golden Bay, Tasman District
2453		Male			161	15/11/2003	Goose Bay, Kaikoura
2671		Male			161	01/03/2006	Tukurua, Golden Bay
4095	KS18-24Lo	Female	I	4	161	10/07/2018	Pohara, Golden Bay

	WS99-13Lo	Male			162.5	16/07/1999	Parapara Inlet, Tasman
	WB01-11Lo	Female	I		162.5	7/02/2000	Kaikoura, Canterbury
2302		Male			163	1/03/2002	Kaikoura, Canterbury
3703		Male			163	8/04/2016	Pohara, Golden Bay
	WS99-15Lo	Female	I		164	20/07/1999	Ruakaka Bay, Queen Charlotte Sounds
3973	KS18-35Lo	Male	M	22	164	27/10/2018	Ruby Bay, Tasman
4097	KS19-33Lo	Male	I	2	164	3/10/2019	Tahunanui, Nelson
1949	WS97-52Lo	Male	M		164.5	29/08/1997	Jimmy Armers Beach, Kaikoura
	WS97-09Lo	Female			165	3/04/1997	Pohara Beach, Golden Bay
1949	WS97-51Lo	Male			165	29/08/1997	Jimmy Armers Beach, Kaikoura
3004	KS09-40Lo	Female	M		165	7/10/2009	Boulder Bank, Nelson
4268	KS21-49Lo	Male			165	18/09/2021	Porirua Harbour, Wellington
3105	KS10-23Lo	Female	I	4	165.5	16/07/2010	Te Waewae Bay, Blue Cliffs
537	NM1661 (Cipriano, 1992)	Male			166	13/06/1973	Pukerua Bay, Wellington
1515		Male			166	10/10/1992	Karitane Wharf, Dunedin
1949	WS97-54Lo	Female			166	29/08/1997	Jimmy Armers Beach, Kaikoura
1952	WS97-57Lo	Male			167	3/09/1997	Jimmy Armers Beach, Kaikoura
2814		Female			167	16/08/2007	Nelson Haven, Motueka
3977		Male			167	23/11/2018	North Richmond Bay, Pelorus Sound

709	NM1815 (Cipriano, 1992)	Male			168	1/06/1978	Nelson Haven, Motueka
3529	KS11-51Lo	Female	M	11	168	26/11/2011	Portobello Bay, Otago Harbour
	KS23-18Lo	Female	M	10	168	8/04/2023	Pohara Beach, Golden Bay
709	NM1816 (Cipriano, 1992)	Male			170	1/06/1978	Nelson Haven, Motueka
2098		Female			170	7/01/1999	South Bay, Kaikoura
2098		Male			170	17/09/1999	Porirua Harbour, Wellington
	WB01-12Lo	Female			170	17/01/2001	Kaikora, Caanterbury
	WB02-11Lo	Male	M		170	30/01/2002	Wairoa, Hawkes Bay
2908		Female			170	3/10/2008	Maruhau, near Motueka
3762	KS16-28Lo	Male			170	17/10/2016	Raspberry Bay, Mahau Sound
709	NM1817 (Cipriano, 1992)	Male			171	1/06/1978	Nelson Haven, Motueka
831		Male			171	8/08/1981	Paekakariki, Wellington
2101		Male			171	27/09/1999	Tahuna, Nelson
2333	WS02-29Lo	Male			171	19/05/2002	Brooklands Lagoon, Canterbury
3167	KS11-41Lo	Female	M	14	171	25/08/2011	Marlborough, South Island
3192	KS11-48Lo	Male	M	16	171	10/11/2011	Portobello, Otago
4032	KS19-15Lo	Male	I	9	171	9/04/2019	Caroline Bay, Timaru
669		Male			172	19/10/1977	Waerongomai Beach, Welligton
1949	WS97-53Lo	Male			172	29/08/1997	Jimmy Armers Beach, Kaikoura

2216		Male			172	18/01/2001	Boulder Bank, Nelson
2459		Female			172	13/12/2003	Okiwi Bay, Marlborough
	WS99-12Lo	Female	M		173	12/07/1999	Ruakaka Bay, Picton
3043	KS10-22Lo	Male	LP	18	173	13/07/2010	Otago, South Island
3667	KS15-22Lo	Male	M	17	173	14/08/2015	Kaikoura, Canterbury
1102		Male			174	26/08/1987	Katikara Stream, Taranaki
1953	WS97-21Lo	Female	M		174	8/09/1997	Monaco Peninsula, Stoke Nelson
3277	KS12-22Lo	Male	M	21	174	5/10/2012	Kotiata, Wanganui
1066		Female			175	20/12/1986	Chatham Island
1066		Male			175	20/12/1986	Chatham Island
3892	KS18-02Lo	Male	I	8	175.5	20/01/2018	Rabbit Island, Nelson
	KS14-40Lo	Female	M		175.7	12/08/2014	Motueka Sandspit, Tasman
363	NM1531 (Cipriano, 1992)	Male			176	29/06/1964	Ohiroa Bay, Wellington
1430		Male			176	15/09/1991	Moeraki Boulders, Otago
2104	KS99-01Lo	Female			176	21/10/1999	Long Point Dunedin
	WB01-01Lo	Male			176	7/08/2000	Paekakariki, Wellington
1700		Male			178	6/09/1994	Kaikoura, Canterbury
2273		Male			179	22/11/2001	Goose Bay, Kaikoura
343		Unknown			180	16/08/1963	Castlecliff, South Taranaki
362		Female			180	15/05/1964	Paekakariki Beach, Wellington

373		Male			180	1/11/1965	Foxton Beach, Foxton
1066		Unknown			180	20/12/1986	Chatham Island
1780		Unknown			180	14/10/1990	Ringaringa Beach, Southland
1383		Male			180	26/04/1995	Jacks Rd, Greymouth
1899		Female			180	10/10/1996	Ripivo Beach, Northland
2976		Female			180	6/01/2010	Boulder Bank, Nelson
2117		Female			181	21/12/1999	Kaikoura, Canterbury
3942	KS18-40Lo	Female	I	5	181	25/07/2018	Lochmara Bay, Marlborough
1732		Female			182	1/12/1994	Kaikoura, Canterbury
1744		Male			182	19/12/1994	Kaikoura, Canterbury
3277	W12-10Lo	Male	M		182	24/06/2012	Pelorous Sound, Marlborough
784		Female			183.5	25/07/1980	Pukerua Bay, Porirua
832		Male			184	11/08/1981	Strandon Beach, New Plymouth
592		Female			185	2/11/1975	Awatoto Beach, Napier
783	NM1835	Female			185	25/07/1980	Titahi Bay, Porirua
1700		Male			185	6/09/1994	Kaikoura, Canterbury
4282		Male			185	30/10/2021	Napier, Hawkes Bay
2470		Male			186	10/01/2004	Hector Beach, Hector
1700		Male			187	6/09/1994	Kaikoura, Canterbury
2363		Male			188	29/10/2002	Oaro, Kaikoura
2830		Male			188	10/11/2007	King Beach, Motueka

3773		Male		192	5/08/2016	Cissy Bay, Marlborough Sounds
477		Female		195	28/09/1971	Waitangi, Clive
2469		Female		195	7/01/2004	Haumuru Bluff, Kaikoura
4234		Female		195	4/05/2021	Lyall Bay, Wellington
4209		Unknown		200	19/02/2021	Goose Bay, Kaikoura
4429	KS22-78Lo	Unknown	0.25		15/12/2022	Haast Beach, Haast