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Life history of common dolphins (*Delphinus delphis*) in Aotearoa New Zealand

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Abstract

Common dolphins (*Delphinus delphis*) are a globally distributed species and have been extensively studied in the Northern Hemisphere, predominantly through strandings and fisheries bycatch. Within Aotearoa New Zealand waters, there is a lack of understanding of the life history of common dolphins. In this study, critical parameters of age, growth and reproductive biology from 562 individuals (269 females, 270 males and 23 unsexed individuals) were assessed from stranding and bycatch events around the Aotearoa New Zealand coast. Age was estimated from decalcified thin sections of teeth. Males and females ranged in total body length from 89 to 244 cm and 82 to 233 cm, respectively. The maximum age recorded for males and females was 26 and 29 years, respectively. Physical maturity was determined when asymptotic length was obtained using Gompertz growth models. Males obtained physical maturity at 212.1 cm and 20 years of age and females obtained physical maturity at 198.3 cm and 18 years of age. Sexual size and shape dimorphism was observed for common dolphins, with males being significantly larger than females for 9 (size) and 8 (shape) out of 24 characters measured. Reproductive parameters were assessed in 104 females and 64 males via the gross and histological examination of the gonads. The average age and length at attainment at sexual maturity for males and females was 8.76 years and 198.4 cm, and 7.5 years and 183.5 cm, respectively. Reproductive seasonality was observed in males but not in females. A pregnancy rate of 30% and a calving interval of 3.2 years were determined with gestation, lactation, and resting periods lasting for 12.6–12.8 months, each. Length at birth was estimated at 85.4 cm. Parameters estimated in this study align with global populations though slight variation may indicate population-level differences. The Aotearoa New Zealand population of common dolphins is part of a greater Australasian population that experiences a wide range of anthropogenic impacts. Biological parameters estimated here can now be used as a baseline to monitor any future changes. This thesis has significant implications for the conservation and management of common dolphins in Aotearoa New Zealand waters.

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List of acronyms/abbreviations

AIC	Akaike Information Criterion
ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
APR	Annual pregnancy rate
ASM	Average age at attainment of sexual maturity
CA	*Corpus albicans*
CI	Confidence interval
CL	*Corpus luteum*
CrI	Credible interval
df	Degrees of freedom
DOC	Department of Conservation Te Papa Atawhai
F	Female
GLG	Growth layer group
LSM	Average length at attainment of sexual maturity
M	Male
NZ	New Zealand
NZTCS	New Zealand Threat Classification System
SD	Standard deviation
SE	Standard error
SSD	Sexual size dimorphism
TBL	Total body length
UME	Unusual mortality event

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Chapter 1

Introduction

A common dolphin riding the bow wave of a boat in the Hauraki Gulf, Auckland.

Photograph credit: Wednesday Davis

1.1 Common Dolphin – A Brief Overview of the Species

Common dolphins (*Delphinus delphis*) are a globally distributed and abundant species (Amaral et al. 2012; Evans 1994; Perrin 2018), currently comprising four subspecies; the common dolphin (*D. d. delphis*); the Eastern North Pacific long-beaked common dolphin (*D. d. bairdii*), the Black Sea common dolphin (*D. d. ponticus*), and the Indo-Pacific common dolphin (*D. d. tropicalis*; Society of Marine Mammal Science, Committee on Taxonomy 2022). Prior to this, two species were recognised, the short-beaked (*D. delphis*) and long-beaked (*D. capensis*) common dolphin (Heyning and Perrin 1994; Rosel et al. 1994). This was largely based on morphological and molecular data (Rosel et al. 1994) of the population living along the Californian coast, which did not apply to other regions due to the high levels of intra-specific variation displayed around the world (Natoli et al. 2006). Cunha et al. (2015) proved that the species *D. capensis* was invalid from the genetic data they had collected. Additionally, investigation into skull morphology and variation of common dolphins off South Africa revealed little variation within the species in this region where most specimens in the study belonged to the long-beaked formed (Ngqulana et al. 2019). Under the previous classification, the taxonomic status of common dolphins within Aotearoa New Zealand waters was unclear due to morphometric and genetic uncertainty (Jordan 2012; Jordan et al. 2015; Stockin et al. 2014). Herein, Aotearoa New Zealand common dolphins will be referred to as *D. delphis*.

Common dolphins inhabit waters ranging from tropical to temperate in the Northern and Southern hemispheres (Brereton et al. 2005; Robinson et al. 2010; Stephenson et al. 2020; Stockin et al. 2014). Across both hemispheres, they inhabit both coastal and pelagic waters (Paradell et al. 2019; Vella et al. 2021) and have a high dispersal potential (Barceló et al. 2021; Natoli et al. 2008). Their gregarious nature makes the species notoriously difficult to study long-term in mark-recapture studies (Hupman et al. 2018; Mason et al. 2016; Mevorach et al. 2022; Neumann et al. 2002; Robinson et al. 2010). Despite this, Pawley et al. found that 95% of common dolphins in a particular study have distinct pigmentation (Pawley et al. 2018). Through long-term monitoring, Photo-ID and surveys, habitat usage (Cañadas and Hammond 2008; Danil and Chivers 2006; Giannoulaki et al. 2017), distribution (Caputo et al. 2020; Cockcroft and Peddemors 1990; Dwyer et al. 2016; Filby et al. 2010; Murphy et al. 2013) and abundance (Parra et al. 2021; Saavedra et al. 2018; Santostasi et al. 2016) have been extensively studied. As with their habitat, common dolphin diet can vary spatially and temporally (Ambrose et al. 2013; Brophy et al. 2009; Milani et al. 2021), and has been found to be influenced by prey abundance and availability (Marçalo et al. 2018; Santos et al. 2013).

Common dolphins are the most frequently recorded cetacean in Aotearoa New Zealand waters (Stephenson et al. 2020; Stockin and Orams 2009), the southern limit of distribution for common dolphins (Amaral et al. 2012; Natoli et al. 2006; Stockin et al. 2014). They are observed around the entire coast of Aotearoa New Zealand, as demonstrated by an extensive stranding record that spans the coastline of the North and South Island, and offshore islands such as the Chatham Islands (Chapter 2). The species is most frequently sighted off the east coast of the North Island (Dwyer et al. 2016; Meissner et al. 2015; Neumann 2001a; Neumann et al. 2002; Stockin and Orams 2009; Stockin et al. 2008b). In Aotearoa New Zealand, limited population and distribution estimates are based on opportunistic sightings and reports (Möller et al. 2020; Stephenson et al. 2020; Stockin and Orams 2009). Currently, only actual abundance estimates exist for the Hauraki Gulf and Coromandel (Hamilton et al. 2018; Hupman et al. 2018; Kozmian-Ledward 2014). Photo ID catalogues (Coromandel; Neumann et al. 2002; Neumann and Orams 2006) and density estimates (Hauraki Gulf, Auckland; Dwyer et al. 2016) also exist for these regions. Sightings data is published for the Tasman Sea which gives an additional indication of distribution (Peters and Stockin 2021). Habitat usage and behaviours, especially surrounding tourism, have also been described (Meissner et al. 2015; Neumann 2001b; Neumann and Orams 2005; Neumann and Orams 2003; Stockin et al. 2008a). Common dolphins were shown to alter their behaviour state around tourism vessels (Neumann and Orams 2005) with a shift away from foraging behaviours (Meissner et al. 2015; Stockin et al. 2008). Foraging ecology and stomach contents have been reported for the species in Aotearoa New Zealand waters, with variation observed between immature and mature (Meynier et al. 2008; Peters et al. 2020; Stockin et al. 2022; Stockin et al. 2023). Primary productivity has been shown to affect common dolphin diet within Aotearoa New Zealand waters (Peters et al. 2020), which comprises of a range of cephalopod and fish species and indicates inshore and offshore feeding (Meynier et al. 2008).

1.1.1 Life History

Life history describes how energy is allocated to significant life events such as growth, reproduction and survival (Dantzer et al. 2013; Kaplan and Gangestad 2015; Köhler and Moyà-Solà 2009; Pontzer et al. 2014). Life history traits evolve through intrinsic and extrinsic factors, which in turn influence reproduction and birth and death rates (Nylin and Gotthard 1998; Réale and Festa-Bianchet 2000; Sibly and Brown 2007). Both internal and external factors play an important role in determining an individual's life history (Stearns 1989). Life history parameters such as average age at attainment of sexual maturity and life span can be used to identify certain strategies used by individuals to maximise survival and reproductive success (Allen et al. 2017). Other parameters of interest include age-specific survival, fecundity, first parturition, age at physical maturity and senescence (Purvis and Harvey 1995). Shared traits or parameters can indicate similarities in life history strategies between species, which facilitates categorisation into distinct groups of life history traits (Kraus et al. 2005).

1.2.2 Life History Trade-offs and Density Dependence

Life history trade-offs occur at and between the genetic, phenotypic and physiological level (Kraus et al. 2005). Resources available to an individual are finite and therefore trade-offs are inevitable (Del Giudice et al. 2015; Husak and Lailvaux 2022). Life history traits are influenced by both intrinsic and extrinsic factors. As these traits are expressed below their maximum capacity, it would suggest that trade-offs have to occur between traits (Stearns 1989). The trade-off between reproductive investment and survival is the most important compromise to occur (Zera and Harshman 2001). As energy is transferred from growth to reproduction once maturity is reached (Purvis and Harvey 1995), individuals can increase their fitness in two ways; either invest in traits that affect the timing of reproduction or the timing of survival (Del Giudice et al. 2015). An early reproductive age enables reproduction to occur sooner, but it also reduces survival rate and life span. Becoming reproductive at a later age allows energy to be invested in growth, and survival is increased along with life span. Other trade-offs also exist (Del Giudice et al. 2015) such as the intra-individual trade-off which occurs between the reproductive effort made by a female in one season and the probability she will survive to the next season. There is also the intergenerational trade-off between a female's reproductive effort and the probability her offspring will survive to the next season (Stearns 1989; Dammhahn et al. 2018). Such trade-offs tend to be negatively correlated with each other, which explains why there can be such a large variability in traits for a natural population (Zera and Harshman 2001). Senescence, as described as a decline in fitness, has recently been shown to have important associated trade-offs and is nearly ubiquitous in the living world (Lemaître et al. 2015; Lemaître et al. 2020). Patterns of aging can show whether growth or reproduction are prioritised in early life i.e., maturing early and reproducing or maturing later and surviving longer (Lemaître et al. 2015; Lemaître et al. 2020). An understanding of how trade-offs are used by species is important as it can indicate the ability of a species to adapt to change (Hao et al. 2021).

Density dependence refers to changes in birth and death rates of a population as a result of changes in population density. This is typically observed as increasing growth rates at low density and decreasing growth rates at high density (Hohn et al. 2007). Over time population size is altered, and as a response, life history parameters such as birthing intervals, ovulation, size and age at sexual maturity, and survivorship change (Fowler 1981). The impacts of density dependence on a species are largely determined by life history (Dantzer et al. 2013; Hohn et al. 2007; Sinclair 2003). Additionally, vulnerability to extinction has been linked to population density and life history parameters (González-Suárez and Revilla 2013; Pearson et al. 2014). For many mammalian species, their specific life history traits do not allow for quick adaptations to a changing environment. Understanding a species' life history, and the trade-offs that occur, will allow for better predictions of how a species will respond to rapidly changing environments (Snell-Rood et al. 2015).

1.2.3 Mammalian Life History

Mammalian life history typically occurs on a ‘slow-fast’ continuum. Development and growth rates among mammals are hugely disparate due to the variation of characteristics such as body size, life expectancy, and reproductive parameters (Clapham 1996; Réale et al. 2009; Sacher and Staffeldt 1974; Stockley and Parker 2002). Such factors, especially body size, are an important predictor of whether species are categorised as having ‘fast’ or ‘slow’ life histories (Del Giudice et al. 2015; Dobson and Oli 2007; Healy et al. 2019). Fast mammals grow rapidly, are smaller in size, and are more productive due to shorter gestation and lactation periods, early maturation, and large litters of small offspring. They also tend to have shorter life spans. In comparison, slow mammals are larger, have longer life spans, and are slower growing. They also have longer gestation and lactation periods, later maturation and produce few, large offspring (Dobson and Oli 2007). Life history can also influence how susceptible certain species are to cancer (Boddy et al. 2020).

Body size is an important determinant when placing species on the fast-slow continuum (Clapham 1996; Kraus et al. 2005; Sibly and Brown 2007). Life history traits tend to show predictable variation within a taxonomic class (Kraus et al. 2005; Réale et al. 2009). In placental mammals, they also scale allometrically with adult body size (Purvis and Harvey 1995). Kraus (2005) suggests that body size, or other strongly correlated variables such as brain size or metabolic rate, are the target of selection. Other life history parameters then vary with these main parameters such as body size. Mortality rate is also strongly related to body size, making it another important determining factor (Kraus et al. 2005).

As new information emerges, current understanding of the fast-slow continuum improves. This continuum is still very relevant and explains much of life history variation. When accounting for body mass and phylogenetic relatedness, 71% of life history strategies can be explained by the continuum (Healy et al. 2019). Despite this, it does not explain all variation in life history traits and strategies (Del Giudice et al. 2015; Wright et al. 2019). Density dependent selection is a newer aspect of the continuum that has been shown to influence life history. This describes how life history variation can also be explained by population density and how it interacts with eco-evolutionary dynamics (Wright et al. 2019). Environmental variation can affect population density across time and space, which in turn creates variation on the fast-slow continuum (Wright et al. 2019). Additionally, a second axis to the continuum has been identified by Healy et al. (2019), which describes how age-specific mortality and reproduction are spread across an individual’s lifetime (Healy et al. 2019).

1.2.4 Mammalian Life History Trade-offs and Density Dependence

Life history traits ultimately aim to improve fitness, either via improving reproduction or improving growth. This trade-off is determined by the life history strategy implemented by the species. More adaptive, smaller mammals tend to increase reproductive rates to improve fitness (Speakman 2008). In larger, slower-adapting mammals, extended periods of growth and negative senescence challenge the idea that improving reproduction is the best way to improve fitness (Mumby et al. 2015). Whether increasing reproductive rates or increasing growth, both 'choices' come with trade-offs.

Pressures such as sibling rivalry and parent-offspring conflict will influence life history (Stockley and Parker 2002). Young mammals are either precocial or altricial. Precocial young become independent immediately or quickly after birth whereas altricial young are dependent on parental care (Temrin and Tullberg 1995). Reproductive parameters associated with altricial individuals are increased foetal growth and shortened gestation periods due to increased pressures of sibling rivalry (Stockley and Parker 2002). Contrastingly, precocial species tend to give birth to single offspring which extends the gestation period as there is no threat of sibling rivalry (Stockley and Parker 2002). Personality is another life history parameter that occurs with trade-offs (Dhellemmes et al. 2021). Studies conducted on rams (*Ovis aries*) and grey mouse lemurs (*Microcebus murinus*) found that boldness varied between age and sex (Dammhahn 2012; Réale et al. 2009). In rams, aggressiveness was linked to increased reproductive success at a young age but at the cost of a reduced life span (Réale et al. 2009). This is in comparison to findings in grey mouse lemurs where younger males had lower fecundity and were less bold compared to older males, but younger individuals had higher future fitness and reproductive success (Dammhahn 2012). The trade-off between current and future reproduction is a major challenge faced by all species and has led to a greater understanding of senescence and how pervasive it is in wild mammalian populations (Del Giudice et al. 2015; Gaillard et al. 2017). This is also important for understanding how species will react to changing environments and their potential adaptability, especially in the context of a changing climate (Pacifici et al. 2020 Suraci et al. 2021).

Density dependence impacts important life history traits and improving reproduction or improving survivorship are the two main responses by species to a changing environment. 'Fast' mammals improve reproduction, through changes in their behaviour and physiology such as decreasing gestation length and altering post-natal growth (Dantzer et al. 2013). 'Slow' mammals however tend to improve survivorship through adaptations such as migration and fat accumulation (Sinclair 2003). Despite both 'types' of mammals being able to adapt to environmental changes, fast species can adapt quicker than slow species and this makes slow species more at risk of extinction. When considering terrestrial mammals, size plays an important role in determining how a species responds to anthropogenic impacts where smaller and faster reproducing species are better able to survive in a human-dominated environment (Suraci et al. 2021). Additionally, larger body size has been correlated with range losses in terrestrial species whereas smaller body size and higher reproductive rates have been associated with range expansions (Pacifici et al. 2020).

Many large mammals, such as primates and marine mammals, have low reproductive rates due to the evolution of their ‘slow’ life histories. Energy-rich environments are required for large mammals due to their metabolism, which requires a constant high energy supply (Köhler and Moyà-Solà 2009). Evolutionary process has resulted in the allocation of most of their energy towards growth or, in the case of primates, the development and maintenance of large brains, rather than reproduction (Pontzer et al. 2014). Such characteristics have resulted in their slow life histories and have made them extremely vulnerable to density-dependent changes and therefore, extinction. However, body size is not the only predictor of extinction. Extinctions of megafauna in the Late Quaternary were not directly related to body size (Johnson 2002). Instead, species with low reproductive rates (less than one offspring per female per year) were at high risk of extinction, regardless of body size.

1.2.5 Marine Mammal Life History

Life history is more challenging to study in partially or fully aquatic species compared to their terrestrial counterparts (Mann and Karniski 2017; Pomeroy 2011). Data can be difficult to obtain, especially long-term datasets, which are required to assess change over time (Lanyon and Burgess 2014). Marine mammal groups that were commercially harvested, such as mysticetes and pinnipeds, are more well researched and understood in comparison to those that were not targeted i.e., odontocetes (Magera et al. 2013). Nowadays, long-term mark-recapture studies and non-invasive sampling and research techniques are used to assess a wider number of species, with some more accessible than others (Hohn et al. 2007; Pomeroy 2011).

Known fundamental life history characteristics of marine mammals include long-life spans and extensive energy investment into producing large, precocial young (González-Suárez and Revilla 2013; Lanyon and Burgess 2014; Lewison et al. 2004). Marine mammals can invest heavily in reproduction when the marine environment has abundant, reliable, high-quality resources readily available (Sibly and Brown 2007). Growth rates and longevity of marine mammals are highly linked to their reproductive parameters, increased brain size, cognition, and social behaviours (Street et al. 2017). Variability in growth and reproductive parameters are determined by differences in size, behaviour and lifestyle between species. Historically, marine mammal life history data were obtained through commercial interests and exploitation (Kasuya and Marsh 1984; Perrin and Henderson 1984).

Pinnipeds and polar bears (*Ursus maritimus*) have a semi-aquatic lifestyle of marine feeding and terrestrial breeding (Cassini 1999). Pinniped mating systems are mainly polygynous, where males defend territories and associated females. Their breeding seasons are short, seasonal and synchronous (Pomeroy 2011). Female pinnipeds can delay the implantation of the fertilised egg for a flexible period of time after mating. This period is controlled by both the external environment and the nutritional condition of the female (Boyd 1991; Pomeroy 2011). Gestation periods of pinnipeds vary between 10 months in Aotearoa New Zealand fur seals (*Arctocephalus forsteri*, McKenzie et al. 2005) and up to 15 months in walruses (*Odobenus rosmarus*, Kastelein et al. 2015). For female New Zealand sea lions (*Phocarctos hookeri*), physical maturity (90% asymptotic body length) is reached at ca. 4 years (Childerhouse et al. 2010). This is similar to female polar bears which reach 97% asymptotic body length by ca. 4.5 years whereas males reach physical maturity at ca. 5 years. Growth is sexually dimorphic in polar bears, with males weighing over double the weight of females, which is thought to be the result of sexual selection (Derocher et al. 2010). Female polar bears are seasonal breeders, are pregnant for around 60 days and tend to have cubs every two to three years (Pomeroy 2011).

Sirenians and sea otters (*Enhydra lutris*) are fully aquatic and inhabit coastal areas, which makes these groups relatively accessible for life history studies. Sirenian reproduction is thought to be condition dependent as not all males produce spermatozoa continuously (Marsh et al. 1984a; Marsh et al. 1984b). Marsh et al. (1984a;b) found over half of the mature males sampled were infertile, possibly due to periods of sexual inactivity. Gestation periods for manatees (*Trichechus* sp.) and dugongs (*Dugong dugon*) vary between 12 and 14 months, with lactation lasting for up to 15 years (Pomeroy, 2011). In comparison, sea otters gestate for around six to seven months and lactate for between five and six months (Monson et al. 2000).

Cetaceans are also fully aquatic but inhabit a wide range of riverine, coastal and oceanic areas, making them the most challenging marine mammals to study (Campbell et al. 2022). The lack of accessibility inhibits understanding of their reproductive biology (Feyrer et al. 2020). Cetacean mating systems are either polygynous or polyandrous, and male-male competition is prevalent (Pomeroy 2011). Gestation periods vary between 10 and 16 months in odontocetes (toothed whales) and 10 and 17 months in mysticetes (baleen whales) (Reidenberg and Laitman 2002). Compared to other marine mammal taxa, gestation periods are extended in cetaceans as newborns can see, hear, swim and vocalise immediately after birth. Mysticetes are usually weaned within a year (Christiansen et al. 2014; Lockyer 1984) whereas lactation can occur over months to years with odontocetes (Brodie 1969). Lactose, the sugar found in milk, has been detected in the stomachs of sperm whales (*Physeter* *macrocephalus*) of up to 13 years of age (Fedak et al. 2002). Ovarian characteristics also differ between infra-orders. Odontocetes display distinct bias in ovarian activity with a tendency to use the left ovary more than the right compared to mysticetes, which appear to use both ovaries equally (Lockyer 1987; Pomeroy 2011; Slijper 1949).

Reproductive traits across marine mammal groups have evolved to maximise fitness and increase survivability e.g., large body size, long life span and slower growth. This has also made them extremely sensitive to human-induced mortality as they are unable to adjust to rapid, dramatic changes in the environment (Hutchings et al. 2012; Mannocci et al. 2012). Major anthropogenic impacts to marine mammals include fisheries bycatch, ship strike, direct take and harvest, marine debris, entanglement, pollution, and tourism (Bearzi 2017; Derville et al. 2023; Desforges et al. 2016; Dunlop et al. 2021; Padula et al. 2023; Peltier et al. 2016; Pierce et al. 2008; Redfern et al. 2013; Reeves et al. 2013; Roe 2007; Waugh and Monamy 2016; Zantis et al. 2023). According to the IUCN Red List, over a quarter of marine mammal species are threatened with extinction (Davidson et al. 2012). Additionally, up to 40% of marine mammal species have insufficient data to provide an accurate threat status. Therefore, the likely number of threatened marine mammal species is much greater than currently estimated (Davidson et al. 2012). An in-depth understanding of life history including growth, reproduction and longevity is paramount for effective conservation management. Such traits directly determine the long-term survivability of a population or species (Chilvers et al. 2010; Huang et al. 2008; Myrick Jr et al. 1983; Plön et al. 2020).

1.2.6 Marine Mammal Density Dependence

Losses to marine mammal populations are especially detrimental due to their ‘slow’ life history traits such as slow growth and low resilience (Williams et al. 2013). Long-term studies are critical for detection of density dependent responses in the form of changes to life history traits (Mann and Karniski 2017). ‘At risk’ populations can be identified using specific traits as classifying factors, e.g., slow rate of increase, large body size, low fecundity, specialised habitat requirements, isolated populations, and small population size (Brashares 2003; Lanyon and Burgess 2014; Sinclair 2003; Stearns 1992). More than 650,000 marine mammal deaths are caused by fisheries bycatch annually (Davidson et al. 2012; Read 2008). Fisheries-related mortalities are one of the main drivers of low density in cetacean populations (Lewison et al. 2004; Moore et al. 2013; Read 2008), which in many cases are far below productive and natural levels (Fowler 1981; Lanyon and Burgess 2014). With ongoing anthropogenic threats to many marine mammal species, life history must be understood to allow for effective conservation management (Young et al. 2006).

1.2.7 Common Dolphin Life History

Life history knowledge in common dolphins has predominantly originated from Northern Hemisphere populations via fisheries-related mortalities and stranding events (e.g. Danil and Chivers 2007; Murphy and Rogan 2006; Murphy et al. 2009; Westgate and Read 2007). The life history parameters of Southern Hemisphere populations are relatively poorly understood, with only a few studies of the species existing (Grandi et al. 2022; Ngqulana et al. 2017; Siciliano et al. 2007), predominantly for African and South American populations.

Age and Growth

Age and growth have been widely studied in common dolphin populations globally, with the maximum body length reported as 252 cm for females (Read et al. 2019) and 250 cm for males (Murphy et al. 2013) in the eastern North Atlantic. In the eastern tropical Pacific, the largest female recorded a body length of 213 cm (Danil and Chivers 2007). Smaller maximum lengths are also observed off the coast of California (North Pacific Ocean) with the largest male measuring 201 cm from aerial surveys (Leander et al. 2021). The oldest aged female common dolphin exceeds 30 years (Danil and Chivers 2007; Murphy et al. 2010; Westgate and Read 2007). For males, maximum age ranges from 25 and 29 years in the Northern Hemisphere populations (Murphy and Rogan 2006; Read et al. 2019; Westgate 2005). Similarities of maximum age across numerous studies would suggest that 30 years is around the maximum age for the species in the wild (Murphy et al. 2014).

Physical maturity has been assessed in the species, with the largest individuals obtaining physical maturity at 221.5 cm and 202.2 cm for males and females, respectively, in the western North Atlantic (Westgate 2005). In the eastern North Atlantic, physical maturity was obtained at ca. 216 cm for males and 194.7 cm for females (Murphy and Rogan 2006). Females reach asymptotic length at 197.2 cm in the eastern tropical Pacific (Danil and Chivers 2007) and 179.4 cm in the North Pacific (Ferrero and Walker 1995). Off southeastern Brazil, asymptotic length for the species was 215.9 cm and occurred at ca. 5–6 years of age (Siciliano et al. 2007). Due to a limited sample size for this study, sex specific asymptotic lengths and growth curves were not able to be calculated.

Allometry has also been examined in a few regions for the species such as in the eastern North Atlantic and off South Africa (Murphy and Rogan 2006; Ngqulana et al. 2017). Negative, isometric, and positive allometry was observed in the two populations for certain morphometric measurements. Sexual dimorphism has been observed for the species with males being larger than females in body length and several other morphometric measurements in both the eastern and western North Atlantic (Murphy et al. 2005; Murphy and Rogan 2006; Westgate 2005), and off South

Africa (Ngqulana et al. 2017). This is likely a reflection of the mating system in place in these populations and for the species globally, where sexual selection is occurring with males competing for access to females via pathways such as sperm competition (Mesnick and Ralls 2018). This is thought to be a result of intra-specific competition and establishing dominance among males (Lewis 1991; Murphy et al. 2005; Neumann et al. 2002; Ngqulana et al. 2017).

Length-at-birth was calculated at between 87 and 88 cm for the eastern tropical Pacific (Danil and Chivers 2007). In the eastern North Atlantic, 93 cm was reported as the length-at-birth (Murphy et al. 2009). The western North Atlantic estimated length-at-birth as 92.7 cm (Westgate and Read 2007).

Male reproduction

Male reproductive biology has been studied in several Northern Hemisphere populations. In the eastern North Atlantic, on average sexual maturity is attained at 204 cm (Read et al. 2019). This aligns with males in the eastern tropical Pacific where sexual maturity is estimated to be attained at an average length of 202 cm (Oliver 1973). In the western North Atlantic, males are reported to attain sexual maturity at ca. 215 cm (Westgate 2005). In contrast, males from the North Pacific attain sexual maturity at ca. 182 cm (Ferrero and Walker 1995). Immature and mature males in the western South Atlantic overlap between 184 and 209 cm (Grandi et al. 2022). In the eastern North Atlantic (Irish and French dataset), males attain sexual maturity at 11.86 years (Murphy et al. 2005), in North-West Spain at 10.5 years (Read et al. 2019), and at ca. 10.5 years in the North Pacific (Ferrero and Walker 1995). In the western North Atlantic, sexual maturity is attained at 9.45 years (Westgate and Read 2007). In Argentine waters, immature and mature males overlap in age between 6 and 9 years (Grandi et al. 2022). Due to a small sample size, estimates were not obtained for the western South Atlantic.

Female reproduction

Female reproductive biology has also been assessed in common dolphin populations globally. Females in the eastern tropical Pacific attain sexual maturity at 186.5 cm (Danil and Chivers 2007) and in the eastern North Atlantic at ca. 188 cm (Murphy et al. 2009). In the western North Atlantic, females attain sexual maturity at approximately 200 cm, which is over 10 cm larger than any other population (Westgate and Read 2007). In the southwestern Atlantic, off the coast of Argentina, an overlap between immature and mature female total body length (TBL) was noted, with the largest immature female measuring 191 cm and the smallest mature female measuring 178 cm (Grandi et al. 2022). In contrast, the estimated length at sexual maturity (LSM) for female common dolphins in the North Pacific is at least 10 cm less than any other population for which estimates exist (ca. 172 cm, Ferrero and Walker 1995). Females in the North Atlantic are estimated to obtain sexual maturity at 8.22 years (Murphy et al. 2009) and 8.3 years (Westgate and Read 2007) for the eastern and western populations, respectively. In the North Pacific and eastern tropical Pacific, the estimated age at sexual maturity (ASM) is 8 years and 7.9 years, respectively (Ferrero and Walker 1995; Danil and Chivers 2007). In the southwestern Atlantic, the oldest immature female and youngest mature female sampled were 6 years and 7 years, respectively (Grandi et al. 2022).

Gestation periods for international populations of common dolphins range between 10 and 12 months for the North Pacific (Ferrero and Walker 1995), North Atlantic (Westgate and Read 2007; Murphy et al. 2009), and eastern tropical Pacific (Danil and Chivers 2007). Lactation periods range from 10.35 months for the eastern North Atlantic population (Murphy et al. 2009) to 16.5 months for the eastern tropical Pacific population (Danil and Chivers 2007). The resting periods have a much greater variation with females in the eastern tropical Pacific resting for just 2.8 months (Danil and Chivers 2007) compared to females in the eastern North Atlantic who rest for 20.7 months (Murphy 2004; Murphy et al. 2009). Annual pregnancy rate (APR) estimates for the eastern and western North Atlantic populations were 26% and 28%, respectively (Westgate and Read 2007; Murphy et al. 2009). In the temperate eastern North Pacific, a birth rate of 13% was reported by converting the estimated proportion of calves assuming a 1:1 male:female sex ratio in the population (Chivers et al. 2016). This is much lower than a previous study in the region where the APR was recorded as 28% using steroid hormones to assess pregnancy (Kellar et al. 2006; Kellar et al. 2014). In the eastern tropical Pacific, a higher APR of 47% has been recorded using the same methodology as used in this study (Danil and Chivers 2007). Calving interval for the eastern North Atlantic is estimated as 3.79 years (Murphy et al. 2009).

1.3 Threats and Management

The IUCN Red List of Threatened Species has most recently classified common dolphins as ‘Least Concern’ due to their widespread and abundant occurrence (Braulik et al. 2021). In contrast, international literature (Murphy et al. 2021; Murphy et al. 2013; Piroddi et al. 2011; Vella et al. 2021) notes that several subpopulations are vulnerable and declining (Bearzi et al. 2020; Bearzi et al. 2003). Within Aotearoa New Zealand, common dolphins are the only resident species to lack a species-specific management plan (Stockin 2008; Suisted and Neale 2004) and are classified as ‘Not Threatened’ by the Aotearoa New Zealand Threat Classification System (NZTCS, Townsend et al. 2008), predominantly due to data paucity (Baker et al. 2019). However, the apparent wider global population stability versus the vulnerability of the subpopulations indicates that a robust population viability assessment of the Aotearoa New Zealand population is required. Population Viability Analysis

(PVA) assesses the vulnerability and recovery potential of a population/species (Ashe et al. 2021; Lacy 1993; Manlik et al. 2016; Verborgh et al. 2021; Wade et al. 2012). To do this, life history knowledge and wider population biology estimates are required (Fisheries New Zealand 2022).

Human-induced impacts on common dolphin populations have been extensively documented, including pollution (Borrell et al. 2001; Hernandez-Gonzalez et al. 2018; Murphy et al. 2018; Pierce et al. 2008), tourism (Cecchetti et al. 2018; Filby et al. 2013), habitat degradation (Mussi et al. 2021; Piroddi et al. 2011), and fisheries interaction and bycatch (Fernández-Contreras et al. 2010; Mannocci et al. 2012; Murphy et al. 2021; Peltier et al. 2021; Peltier et al. 2016; Read 2016; Saavedra et al. 2018). Fisheries bycatch has been an issue for common dolphins, and other small delphinids, for decades (Geijer and Read 2013). In the eastern North Atlantic, bycatch over a 10-year period peaked in 1999 with an estimated 2,101 common dolphins caught (Brophy et al. 2009). In 2003 and 2004, a tuna-pelagic trawl fishery bycaught 128 individuals annually (Brophy et al. 2009; Northridge 2006). A later assessment reported over 1000 common dolphins were bycaught annually in the same region (Mannocci et al. 2012). During February and March of 2017, an Unusual Mortality Event (UME) occurred along the French Atlantic coasts that caused a large number (*n* = 793) of cetaceans to strand, with common dolphins comprising 84% of the strandings (Peltier et al. 2020). Using reverse drift modelling, a total of 3,690 common dolphins were estimated to have died in fishing gear in the Bay of Biscay during this period (Peltier et al. 2020). After identifying two main events where 483 common dolphins stranded, 297 examined individuals showed evidence of death by fishing gear (Peltier et al. 2020). Additionally, since 2011, 17 UMEs related to bycatch have occurred (Peltier et al. 2021).

In the Australasian region, fisheries bycatch is also a major issue for common dolphins (Abraham and Berkenbusch 2019a; Abraham et al. 2021; Barceló et al. 2021; Thompson et al. 2013; Tulloch et al. 2020). A genomic assessment of common dolphins within Aotearoa New Zealand and Australian waters has revealed that a wider, Australasian population exists (Barceló et al. 2021). As high levels of bycatch of common dolphins exist across Aotearoa New Zealand and Australia (Banks et al. 2018; Hamer et al. 2008; Parra et al. 2021; Tulloch et al. 2020), the absence of biological knowledge and reproductive parameters is of concern.

In Australia, common dolphins are one of the most frequently bycaught cetaceans with over 400 capture events recorded since 1990, not including state-based fisheries (Tulloch et al. 2020). Historically, high levels of common dolphin bycatch have been reported in the South Australian region, i.e., an estimated 1,728 common dolphins were encircled in nets and 377 killed over a 7-month period within a sardine fishery (Bilgmann et al. 2014; Hamer et al. 2008). With the introduction of a Code of Practice, fatal interactions have decreased by >97% (Hamer et al. 2008; Mackay and Goldsworthy 2017; Tulloch et al. 2020). Despite this, there are still concerns that dolphin bycatch is unsustainable due to uneven observer coverage and underreporting in the absence of observers (Goldsworthy et al. 2019; Tulloch et al. 2020).

Common dolphins are the most at-risk species from commercial fisheries in Aotearoa New Zealand (Abraham et al. 2017; Mackenzie et al. 2022; Ministry for Primary Industries 2016) as well as the most frequently bycaught cetacean in commercial trawl fisheries on the west coast of the North Island (Du Fresne et al. 2007; Thompson et al. 2013). Between 1995 and 2011, 119 common dolphin captures were reported for this region alone (Thompson et al. 2013), and when expanding the period to between 1992 and 2018, this increased to 218 individuals (Abraham and Berkenbusch 2019a). Annual potential fatalities for all Aotearoa New Zealand fisheries for 2012–13 and 2014–15 were estimated at 230.4 individuals (Abraham et al. 2017; Fisheries New Zealand 2022). The Aquatic Environment and Biodiversity Annual Review (AEBAR) 2021 reported no accidental captures of common dolphins were recorded by observers between 2016 and 2020 despite almost 100% observer coverage (Du Fresne et al. 2007; Thompson et al. 2013). However, observer coverage is highly inconsistent across other regions and is usually very low in several key fisheries (0.5–3%; Fisheries New Zealand 2022; Thompson et al. 2013), meaning that bycatch rates are likely underrepresented (Stockin and Orams 2009). Additionally, Stockin et al. (2009) documented that 28% of carcasses examined post-mortem evidenced signs of net entanglement. Bycatch is also self-reported in some instances by fisheries within Aotearoa New Zealand (Ministry for Primary Industries 2022). This data has been made available by the Ministry for Primary Industries (MPI), the Department of Conservation (DOC) and Dragonfly Science. A total of 34 common dolphins were bycaught between 2019 and 2022 (Ministry for Primary Industries 2022), as self-reported by fisheries within Aotearoa New Zealand. Trawl fisheries had the greatest number of bycaught individuals ($n = 23$) during the 2019–2022 period, followed by set nets and seine (both respectively $n = 4$), and longline fisheries (surface: $n = 1$ and bottom: $n = 2$).

Along with fisheries being a major anthropogenic threat to the species within Aotearoa New Zealand waters (Abraham and Berkenbusch 2019a, 2019b), other threats include tourism (Fumagalli et al. 2021; Meissner et al. 2015; Neumann and Orams 2005; Neumann and Orams 2006; Stockin et al. 2008a), vessel collisions (Martinez and Stockin 2013; Stockin et al. 2009), and pollution (Stockin et al. 2007; Stockin et al. 2021a; Stockin et al. 2021b).

The consequences of known cumulative pressures (fisheries bycatch, pollutants, tourism etc.) in addition to yet unknown biological parameters have been observed in common dolphin populations in the Northern Hemisphere with devastating effects (Ashe et al. 2021). For example, the Mediterranean subpopulation of common dolphins experienced a huge population decline due to overfishing and habitat degradation. The species is now classified as endangered when historically, they have been abundant in the area (Bearzi et al. 2008; Piroddi et al. 2011; Vella et al. 2021). Life history knowledge is important and timely as this is required to measure conservation indicators such as population viability analyses and maximum rate of increase (Boyce 1992; Tezanos-Pinto et al. 2013; Wade 1998).

1.4 Thesis Rationale / Aims / Objectives

Life history parameters are critical for determining the vulnerability and recovery potential of a population/species through assessments such as Population Viability Analysis (PVA; Lacy 1993; Manlik et al. 2016; Verborgh et al. 2021; Wade et al. 2012). Common dolphins are a species widely impacted by several anthropogenic impacts, as previously outlined. The wider Australasian population lacks basic biological knowledge, especially that concerning growth and reproduction, which is critical for important baseline data. Life history data will allow the assessment and identification of any changes that may be occurring in the population and allow for PVA (Boyce 1992; Brook et al. 2000; Thompson et al. 2000) to be performed.

Accordingly, this thesis aims to provide first insights into the life history of common dolphins in Aotearoa New Zealand waters. Specifically, my objectives are to:

Objective 1: Assess age structure, growth rates, allometry and sexual dimorphism of common dolphins in Aotearoa New Zealand waters.

Objective 2: Estimate the reproductive parameters in male common dolphins in Aotearoa New Zealand waters.

Objective 3: Describe the reproductive parameters in female common dolphins in Aotearoa New Zealand waters.

1.5 Thesis Structure

This thesis is organised into five chapters that comprise of three data chapters, an overall introduction chapter and a final discussion chapter. These data chapters have been written in publication format that have been either published (Chapters 3 and 4) or, are currently under peer review (Chapter 2).

In Chapter 1, I provide an overview of the study species, the rationale of the thesis, and a broad literature review that delves into life history and the importance of understanding this knowledge.

Chapter 2 represents the first data chapter that addresses age, length at birth, growth, and sexual dimorphism of common dolphins. Here, I specifically examine sex-specific growth rates, allometry, age structure, and sexual dimorphism.

Chapter 3 addresses male reproductive parameters of common dolphins. Here, I detail indicators of sexual maturity, average age and length at attainment of sexual maturity, and reproductive seasonality.

Chapter 4 investigates female reproductive parameters of common dolphins. Specifically, I estimate the average age and length at attainment of sexual maturity, reproductive phases (gestation, lactation and resting periods), foetal growth rate, ovulation rate, annual pregnancy rate, and calving interval. Ovarian characteristics and reproductive seasonality are further assessed.

Chapter 5 synthesizes the key findings of this thesis in the context of conservation and management. I discuss the conservation implications of this research, study limitations and future research objectives for common dolphins in Aotearoa New Zealand waters.

Chapter 2

Age, growth and sexual dimorphism of common dolphins (*Delphinus delphis*) in Aotearoa New Zealand waters

Two common dolphins underwater in the Hauraki Gulf, Auckland.

Photograph credit: Wednesday Davis

This chapter is a reformatted version of the following manuscript:

Palmer EI, Stockin KA, Murphy S, Perrott MR, Smith ANH, Betty EL (in prep). Age, growth and sexual dimorphism of common dolphins (*Delphinus delphis*) in Aotearoa New Zealand waters.

2.1 Abstract

Stranding events provide a valuable source of biological information. Despite common dolphins having an extensive stranding record along Aotearoa New Zealand's coastline, knowledge of age, growth and sexual dimorphism does not exist for the species. This study presents biological parameters related to age and growth of common dolphins in Aotearoa New Zealand waters. Teeth and body measurements were obtained post-mortem from 269 females, 270 males and 23 unsexed individuals involved in stranding and bycatch events around the coastline of Aotearoa New Zealand between 1979 and 2020. Age or minimum age (yrs) was determined via growth layer groups (GLGs) in the dentine of decalcified thin sections of teeth. Females ranged in body length from 82 to 233 cm (modal length class 191 to 200 cm) and males from 89 to 244 cm (modal length class 211 to 220cm), respectively. Maximum ages of 29 and 26 years were determined for females (n = 110) and males (n = 83), respectively. Length-at-birth was estimated at 85.4 cm using a logistic regression model (both sexes combined). The Gompertz growth model was applied to both females and males and indicated rapid, early growth followed by a second phase of slower growth. Asymptotic lengths were estimated at 198.3 cm for females and 212.1 cm for males, which corresponded to 18 and 20 years of age, respectively. Sexual size and shape dimorphism was evident in the population. Males were significantly larger than females for 11 out of 24 external measurements, and sexual shape dimorphism was detected in 12 out of 24 characters measured. A sexual size dimorphism ratio of 1.07 was calculated from mean lengths of 207.9 cm and 222.3 cm in physically mature females and males, respectively. Biological parameters align with global populations, and it is recommended that these data are used as a baseline to monitor future population changes for Aotearoa New Zealand common dolphins.

2.2 Introduction

Knowledge of age and growth rates is critical for life history studies (De Magalhaes and Costa 2009; Oli and Dobson 2003; Pacifici et al. 2013) and provides insights into birth and death rates, reproductive output, sex ratio, age structure, growth rates, allometry, and sexual dimorphism. Understanding allometric relationships and age allows assessment of temporal changes in growth rates as well as age profiles within conservation units (Stolen et al. 2002). Sexual dimorphism can indicate the mating system and social structure of a species (Murphy and Rogan 2006; Ngqulana et al. 2017; Tolley et al. 1995), as well as provide insights into behaviour and social interactions (Dixson and Anderson 2004; Leander et al. 2021; Mesnick and Ralls 2018). Such information is essential for effective management and conservation of a population or species (Brophy et al. 2009; Murphy and Rogan 2006). Data deficient populations/species (those that lack life history data) tend to have an elevated risk of extinction due to changes going unnoticed (Magera et al. 2013; Parsons 2016). Historic exploitation through commercial whaling has resulted in age and growth being well understood for many large mysticete species (Clapham and Baker 2018; Lockyer 2007). For small delphinids, much of our knowledge of age and growth has originated from strandings and bycatch mortalities (Amano et al. 2014; Betty et al. 2022; Meager and Sumpton 2016).

Knowledge of age, growth and sexual dimorphism in common dolphins (*Delphinus delphis*) has predominantly originated from Northern Hemisphere populations via fisheries-related mortalities and stranding events (Danil and Chivers 2007; Murphy and Rogan 2006; Westgate 2005; Westgate and Read 2007). Growth models, including the Gompertz growth curve (Fitzhugh Jr 1976; Gompertz 1825; Laird 1966), have previously been applied to assess age and growth for the species (Murphy and Rogan 2006; Read et al. 2019; Siciliano et al. 2007). In the Southern Hemisphere much less is known, with only a few studies conducted on common dolphin age and growth to date (Grandi et al. 2022; Ngqulana et al. 2017; Plön et al. 2012; Siciliano et al. 2007).

Parameters of age, growth and sexual dimorphism are currently unknown for common dolphins within Aotearoa New Zealand waters. This is of concern given that this common dolphin population is subject to several anthropogenic impacts, including fisheries bycatch (Abraham et al. 2017; Du Fresne et al. 2007; Thompson et al. 2013), and baseline biological parameters are required to undertake population viability analyses (Ashe et al. 2021; Cervin et al. 2020). The requirement for such understanding is only exacerbated by the potential for cumulative anthropogenic effects across a population's known range (Karczmarski et al. 2017; Murray et al. 2021; Sinclair et al. 2020). Common dolphins within Aotearoa New Zealand waters are part of a wider Australasian population (East and South Coast of Australia) as revealed in a recent genomic assessment (Barceló et al. 2021). The species is heavily impacted by fisheries across the Tasman Sea (Abraham and Berkenbusch 2017; Bilgmann et al. 2014; Parra et al. 2021; Stockin and Orams 2009; Thompson et al. 2013). Such cumulative fisheries-related mortalities raise concerns about the sustainability of the wider population (Barceló et al. 2021), an issue also observed in the Mediterranean Sea sub-population (Bearzi et al. 2003; Piroddi et al. 2011; Vella et al. 2021). In this context, knowledge of population structure, age structure and growth is now more important than ever for common dolphins in the Australasian region.

2.2.1 Study aims and objectives

Here, age, growth and sexual dimorphism were investigated for Aotearoa New Zealand common dolphins from data collected post-mortem from stranded and by-caught individuals between 1979 and 2020. This study presents critical demographic parameters for this population of common dolphins, specifically: (1) length at birth, (2) sex-specific growth rates, (3) allometric relationships, and (4) sexual size and shape dimorphism.

2.3 Materials and Methods

2.3.1 Data collection

A total of 562 individuals (269 females, 270 males and 23 unsexed individuals) were used to examine age, growth and sexual dimorphism. Dolphins were either stranded along the Aotearoa New Zealand coastline or bycaught in fisheries around Aotearoa New Zealand between 1979 and 2020 (Figure 2.1). Decomposition state was noted for each individual (*fresh*, *mild*, and *moderate*) as per Stockin et al. (2007). Due to the nature of opportunistic sampling, as is the case from stranding events, not every individual has all measurements and associated location data. Therefore, sample sizes may vary between measurements, calculations and figures.

2.3.2 Age estimation

Age was estimated for 209 individuals (115 females, 86 males and 8 individuals of unknown sex). Age estimation was performed by counting growth layer groups (GLGs) in the dentine of thin, decalcified, stained sections of teeth (Murphy et al. 2014; Myrick Jr et al. 1983; Lockyer 1995). One GLG is considered to represent one year of life for common dolphins (Gurevich et al. 1980). Tooth preparation methods for this study were adapted from Lockyer (1995). At post-mortem, between five and ten of the least worn/curved teeth were extracted from each animal and stored in 70% ethanol. Teeth were then adequately fixed in formalin and decalcified in 10% formic acid, with the endpoint of calcium removal determined by a chemical method. A predetermined volume of used formic acid was adjusted to neutral pH using ammonia solution. If no precipitation was noted, an equal amount of saturated calcium oxalate to that of the formic acid was added. Precipitation of any kind indicated that decalcification was incomplete and immersion in formic acid continued.

Decalcified teeth were rinsed in water for several hours (usually overnight). Teeth were mounted using OCT compound (Tissue-tek® Sakura) onto a specimen holder and frozen to -20°C in a Leica Jung CM1800 cryotome. Teeth were then sectioned at 12–18 µm thickness along the longitudinal axis, i.e. 'the dolphin cut'. The most central sections through the pulp cavity were selected. These were placed in pre-frozen cassettes and immediately transferred into 0.2–0.5% Toluidine blue (pH 8.4), the staining solution, for approximately 6 minutes at room temperature. The sections were then rinsed in water to remove excess stain. The rinsed sections were positioned on superfrost plus slides (Menzel Glaser) and blotted to remove excess liquid before mounting using Entellan resinous medium (ProScitech).

Sections were examined using a binocular microscope (10x – 40x). All readings and age estimates were initially made 'blind' i.e., without prior knowledge of biological information about the individual. Each section was examined twice by at least two of three experienced readers and best age estimates or age ranges were subsequently compared. In the case of any disagreement (i.e., a discrepancy greater than one GLG), at least two readers re-read the section with knowledge of the prior estimate. If no agreement was reached, another section was selected and read by at least two readers until a final estimate was determined (Murphy et al. 2014; Westgate and Read 2007). Individuals that could not be reliably aged (i.e., due to tooth wear or damage) were excluded from further analysis. A neonate was identified if the neonatal line was not present or just forming in the dentine of the tooth.

2.3.3 Length at birth

The probability of birth (p) as a function of TBL was modelled using Bayesian logistic regression with 'HOF' parameterisation (Huisman et al. 1993), as follows:

$$y_i \sim \text{Bernoulli}(p_i)$$

$$\log\left(\frac{p_i}{1-p_i}\right) = \omega(x_i - l_{50})$$

where i indexes individuals, y_i is either 0 (unborn) or 1 (born), x_i gives the lengths of individuals. There are two model parameters; ω is a rate parameter and l_{50} is the length at which the probability of birth is 50% i.e., the median length-at-birth.

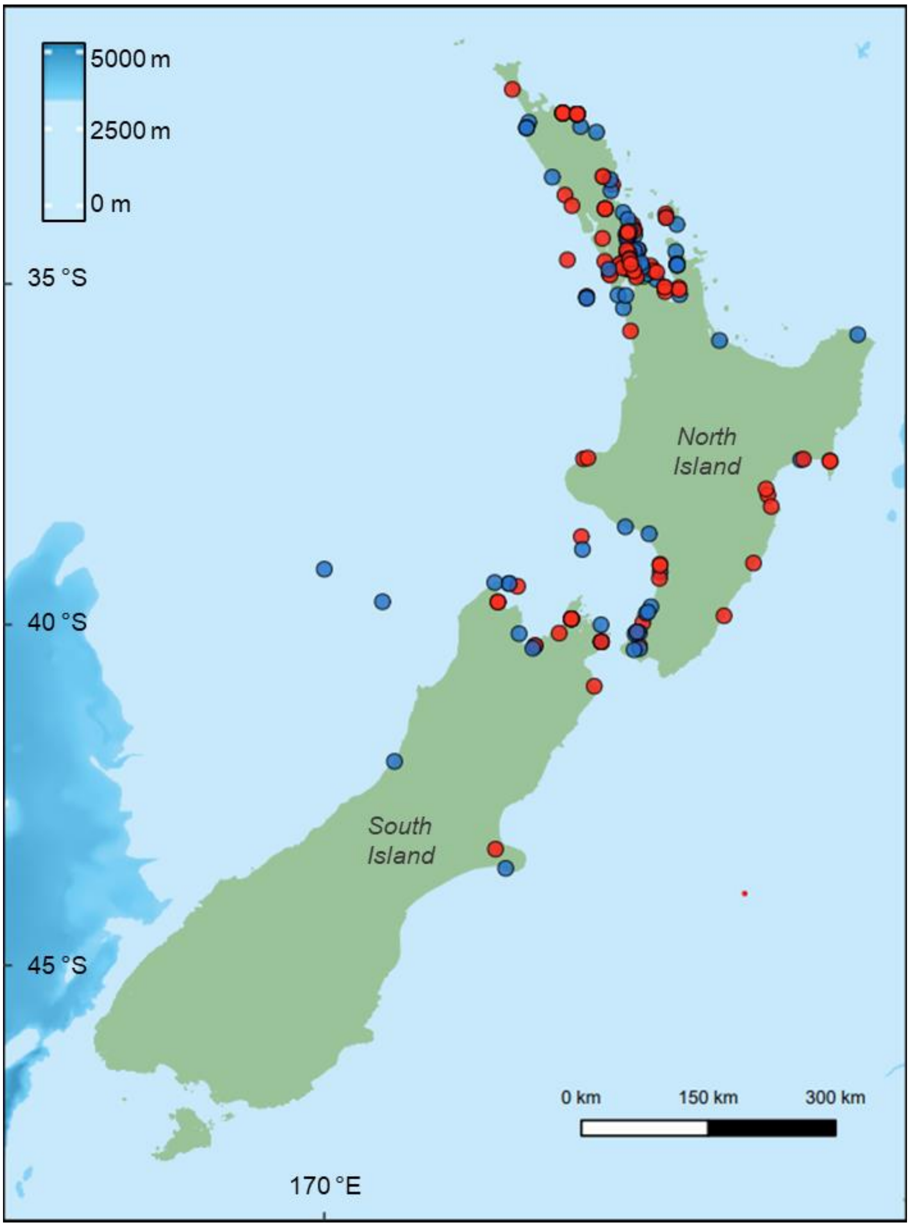


Figure 2.1. Location of common dolphin (*Delphinus delphis*) stranding (coastal) and bycatch (offshore) events around Aotearoa New Zealand (1990-2020), for which location, age and TBL is known for this study. Females (*n* = 167) are represented by red circles and males (*n* = 153) by blue circles.

Bayesian models were fitted using Stan (Stan Development Team 2021) for modelling in R (R Development Core Team 2021). After prior predictive simulation (Figure 2B in Appendices), weakly informative priors were chosen for the two parameters, l_{50} ~ N(90,20), ω ~ N^{+} (0,1). Only positive values of the slope were considered as the assumption is that, on average, 'born' dolphins have a longer TBL than 'unborn' dolphins. The dataset of this model included all foetuses and postnatal dolphins ≤160 cm (*n* = 103) for which TBL was available. Foetuses were defined as any dolphin found in the uterus of the female at post-mortem. This dataset comprised of 13 unborn (n_0) and 90 born dolphins (n_1). To mitigate any potential effects of the unbalanced sample on estimates (Salas-Eljatib et al. 2018), weights were assigned to each case. These cases were from group k according to the sample size of the group n_k, relative to the overall sample size n, using $w_k = \sqrt{0.5/(\frac{nk}{n})}$. For the weights w_i to have an average of 1, the vector of weights w_i were normalised.

Two models were fit, the fully-weighted model and the square-root weighted model. These models were compared using model weights and Leave-One-Out diagnostics (LOO; with Pareto-smoothed importance sampling and refitting models for 103 observations with Pareto k > 0.7; 'loo' package in R; Vehtari et al. 2017). The partially weighted model, taking the square root of the sample size difference, was a better fit and so was used. For the logistic regression, the mean and 95% interval were the mean and highest posterior density interval from the posterior distribution of the median length-at-birth (i.e., the length at which the probability of birth is 50%).

Due to the small sample size of foetuses (n = 19, with only 3 female foetuses), sex differences for length at birth were not calculated. Two additional statistics, the mean overlap and mean neonatal length, were calculated to allow comparisons to other common dolphin populations. The mean overlap is the mean of overlapping foetal and calf body lengths, which includes the smallest non-overlapping calf and the largest overlapping foetus (Börjesson and Read 2003). The mean neonatal length is the mean body length of neonates/calves that did not possess a neonatal line in the tooth or had the neonatal line forming (with no additional postnatal dentine), and were subsequently aged as 0 years and classified as newborn (Murphy et al. 2009).

2.3.4 Growth models

Several growth models were used to predict age and length at physical maturity for female and male common dolphins. The age-length data was checked against records and any anomalies were removed. The growth models were fitted to this curated, verified dataset. The Gompertz growth model was first fitted to the age-length data as it has been commonly used for common dolphins and other cetacean species (Fitzhugh Jr 1976; Laird 1966; Murphy et al. 2009; Read et al. 2019). The 'nlme' package (Pinheiro et al. 2017) was used with a self-starting function ('SSgompertz') in R (R Development Core Team 2021).

The equation for the Gompertz growth model is as follows:

$$L_t = A^{[-b^{-kt}]}$$

where L_t is total body length (TBL) at age (t), A is the asymptotic value, b is the constant of integration, and k is the growth rate constant.

The ‘FlexParamCurve’ package in R (R Development Core Team 2021) was used to fit other parametric curves (growth curves) to the age-length data (Oswald 2018; Oswald et al. 2012). Within the package, the function ‘pn.mod.compare’ was used for model selection as it determines what model with what parameters are best suited to the age-length data. The Richards model is a standard four parameter Richards curve and the Double-Richards model is a six parameter model that requires two-second curve parameters (Oswald 2018).

The models are based on the FlexParamCurve equation which is the subtraction of one Richards curve from the other (Oswald 2018) and is as follows:

$$y = \frac{A}{\left[1 + m^{(-k(x-i))}\right]\frac{1}{m}} + \frac{A'}{\left[1 + m'^{(-k'(x-i'))}\right]\frac{1}{m'}}$$

where A is the asymptotic length of the first positive curve, k is the growth rate constant (rate parameter of the first phase of growth), i is the point of infliction, and m is the shape parameter of the first phase of growth. In the second half of the equation all parameters with an apostrophe by it, e.g. A’, refer to the same values as described for the first phase of growth, but instead for the second phase of growth.

Using this equation, the Richards model used the first half of the equation i.e., $y = \frac{A}{\left[1+m^{(-k(x-i))}\right]\frac{1}{m}}$ and the Double-Richards curve used the full equation.

Individuals were considered physically mature if their TBL was equal to or greater than the asymptotic value generated by the equations. Using the different packages in R, growth curve parameters were estimated for each of the models and the most appropriate model was selected using the Akaike Information Criterion (AIC; Akaike 1998).

2.3.5 Allometry

Allometry was assessed following Murphy and Rogan (2006) and Betty et al. (2022). Allometric measurements were recorded post-mortem either in the lab or field and were adapted from Betty et al. (2022) and Murphy and Rogan (2006). These are depicted in Figure 2.2.

To reduce inter-observer error, transcription error, and outliers, regression plot analysis was carried out. All measurements (morphological data) were transformed on a logarithmic scale [$\mathrm{Log}_{10}(x)$] and each measurement was plotted against TBL for males and females, separately. Any data that were more than three standard deviations away from the fitted line were omitted from the dataset.

To analyse the growth patterns and make comparisons between sexes, allometric growth equations for the 14 body measurements were created in the form:

$$y = ax^b$$

where y is the measurement (dependent variable), x is the TBL (independent variable), b is the growth coefficient, and a is the intercept (Schmidt-Nielsen 1993). Following Read and Tolley (1997), negative allometry is indicated when the growth coefficient is significantly smaller than 1, positive allometry is indicated when the growth coefficient is significantly greater than 1, and isometric allometry is indicated when the coefficient is not significantly different from 1. To test the null hypothesis H_0: b = 1, the test statistic (t_s) was calculated as:

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

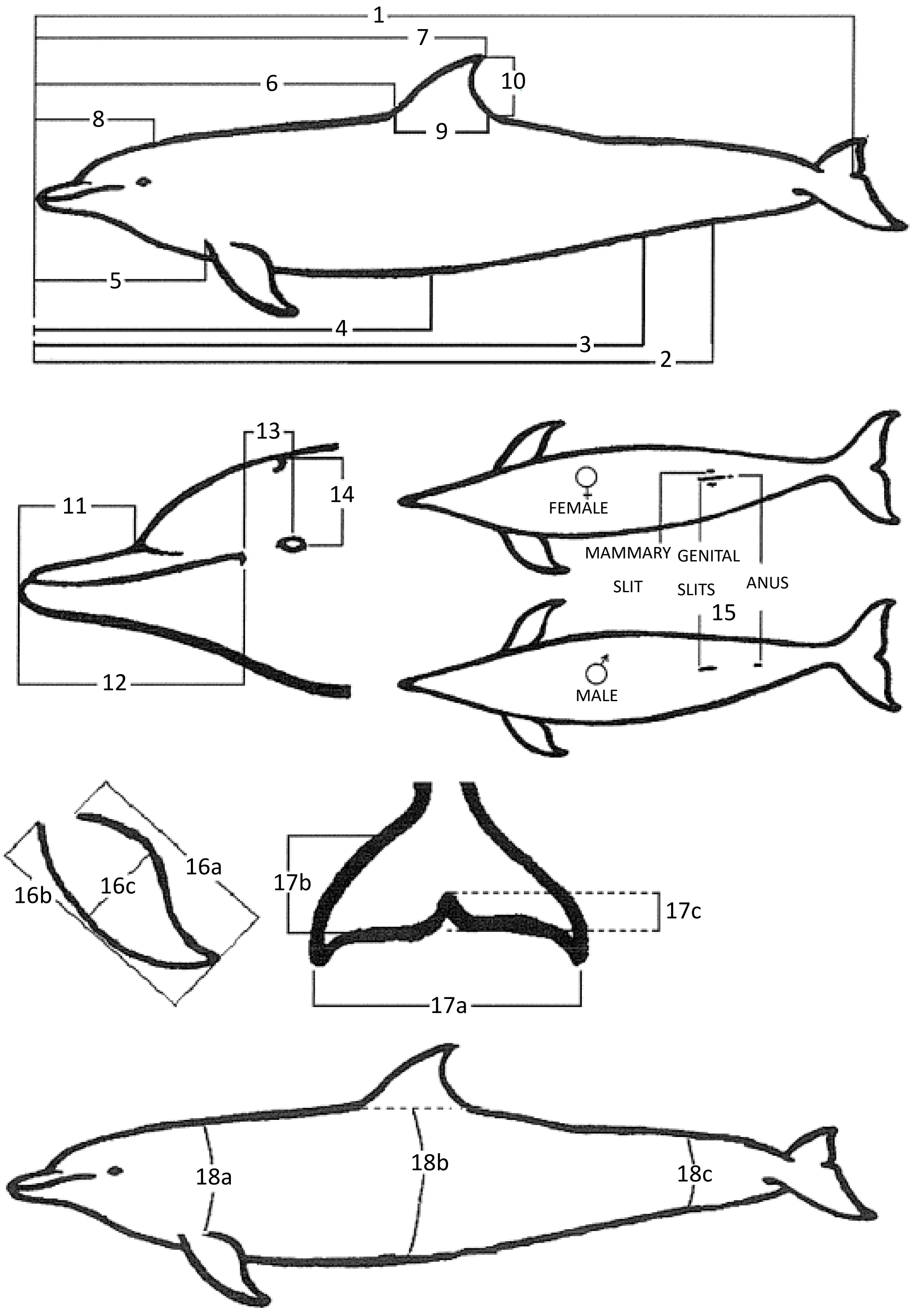
where b = slope, SEb = standard error of slope, df = $n - 2$ and α = 0.05, using Student's t-test tables. To compare growth coefficient values between males and females, comparing slope analysis was performed, where df = $n - 2$ and α = 0.05, using Student's t-test tables. Data were used from all physically immature and mature common dolphins and analysed using R (R Development Core Team 2021). No post-hoc adjustments were made to *P*-values.

2.3.6 Sexual dimorphism

Sexual dimorphism was assessed only in physically mature individuals (defined as TBL ≥ asymptotic length). Following Murphy and Rogan (2006) and Betty et al. (2022), dimorphism was assessed in two ways: analysis of sexual size dimorphism without correcting for body size (considering both size and shape), and analysis of sexual shape dimorphism (accounting for variation in body length). Spearman's rank correlation coefficients were used to analyse relationships between sex and morphometric measurements. All physically mature morphometric data were tested for homogeneity of variance (Levene's test) and normality (Shapiro-Wilk test) before analysis. R was used to analyse all data when investigating sexual dimorphism (R Development Core Team 2021).

Each measurement was analysed separately for males and females by conducting both Welch's univariate analysis of variance (ANOVA) and univariate analysis of covariance (ANCOVA). ANOVA was used to investigate the variation in size and/or shape between males and females. ANCOVA was used to assess sexual variation of body shape only, by removing the effect of dolphin size on individual measurement types. This is done by using TBL as the covariate. As testing suggested a departure of data from normality, all morphological data was transformed on a logarithmic scale [$\text{Log}_{10}(x)$] prior to ANCOVA analysis. As the position of the genital slit differs between females and males, the Snout-genital slit measurement was excluded from ANCOVA analysis. Due to an insufficient sample size ($n < 10$), the Snout-navel measurement was also excluded from ANCOVA measurements. No post hoc adjustments to the *P*-values were made.

If an individual had more than five missing measurements, they were omitted from the dataset used for multivariate analysis. The remaining missing variables were calculated using multiple imputation (linear regression method). The subsequent data set was used to carry out linear discriminant function analysis to investigate sexual dimorphism in body size and shape. There were insufficient sample sizes ($n < 20$) for 10 measurements (Snout-navel, Snout-origin dorsal, Genital slit, Cnr mouth-eye, Eye-blowhole, Dorsal fin lat base, Fluke length, Fluke notch, Girth navel and Girth anus) and so these were omitted from analyses. The Snout-genital slit measurement was also excluded due to the differing position of the genital slit between males and females. Linear discriminant function analysis in R was used to assess the differences in 14 measurements, which included 7 linear measurements, 6 appendage measurements, and 1 girth measurement.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17b
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17a
18a
18b
18c

Figure 2.2. Twenty-four morphometric characters (adapted from Norris 1961) measured from common dolphins (*Delphinus delphis*) stranded and bycaught around the Aotearoa New Zealand coast: (1) total body length (TBL); (2) Tip of upper jaw to anus (Snout-anus); (3) Tip of upper jaw to genital slit (Snout-genital slit); (4) Tip of upper jaw to navel (Snout-navel); (5) Tip of upper jaw to front (forward insertion) of flipper (Snout-origin flipper); (6) Tip of upper jaw to front (posterior insertion) of dorsal fin (Snout-origin dorsal fin); (7) Tip of upper jaw to tip of dorsal fin (Snout-tip dorsal fin); (8) Tip of upper jaw to blowhole (Snout-blowhole); (9) Length of base of dorsal fin (Dorsal fin lat base); (10) Height of dorsal fin (Dorsal fin height); (11) Length of rostrum (Rostrum); (12) Tip of upper jaw to the corner of the mouth (Snout-cnr mouth); (13) Corner of mouth to middle of eye (Cnr mouth-eye); (14) Eye to middle of blowhole (Eye-blowhole); (15) Length of genital slit (Genital slit); (16a) Length of flipper – internal (Flipper internal); (16b) Length of flipper – external (Flipper exterior); (16c) Greatest width of flipper (Flipper width); (17a) Length of fluke (Fluke length); (17b) Greatest width of tail flukes (Fluke width); (17c) Length of fluke notch (Fluke notch); (18a) Axillary girth – immediately behind flipper, around body (Girth flippers); (18b) Axillary girth – at the navel, around body (Girth navel); (18c) Axillary girth – at the anus, around body (Girth anus).

2.4 Results

2.4.1 Body length and age

Total body length (TBL) for the data set ranged from 82 to 244 cm (*n* = 335), with a modal size class of 191 to 200 cm (median ± SE, 195 ± 0.39 cm, Figure 2.3a). Females ranged from 82 to 233 cm (*n* = 173, mean ± SE, 176.7 ± 2.5 cm), with a modal size class of 191 to 200 cm (median ± SE, 195 ± 0.5 cm). Males ranged from 89 to 244 cm (*n* = 148, mean ± SE, 179.1 ± 3.3 cm), with a modal size class of 211 to 220 cm (median ± SE, 216 ± 0.5 cm). Aged females and males ranged from 0 to 29 years (*n* = 108) and from 0 to 26 years (*n* = 82), respectively (Figure 2.3b). Minimum ages were determined for an additional 11 individuals due to difficulty in counting GLGs in the dentine. The highest proportion of the aged sample comprised of individuals < 1 year of age (*n* = 34, female: *n* = 18 (16.2%), male: *n* = 16 (19.3%)).

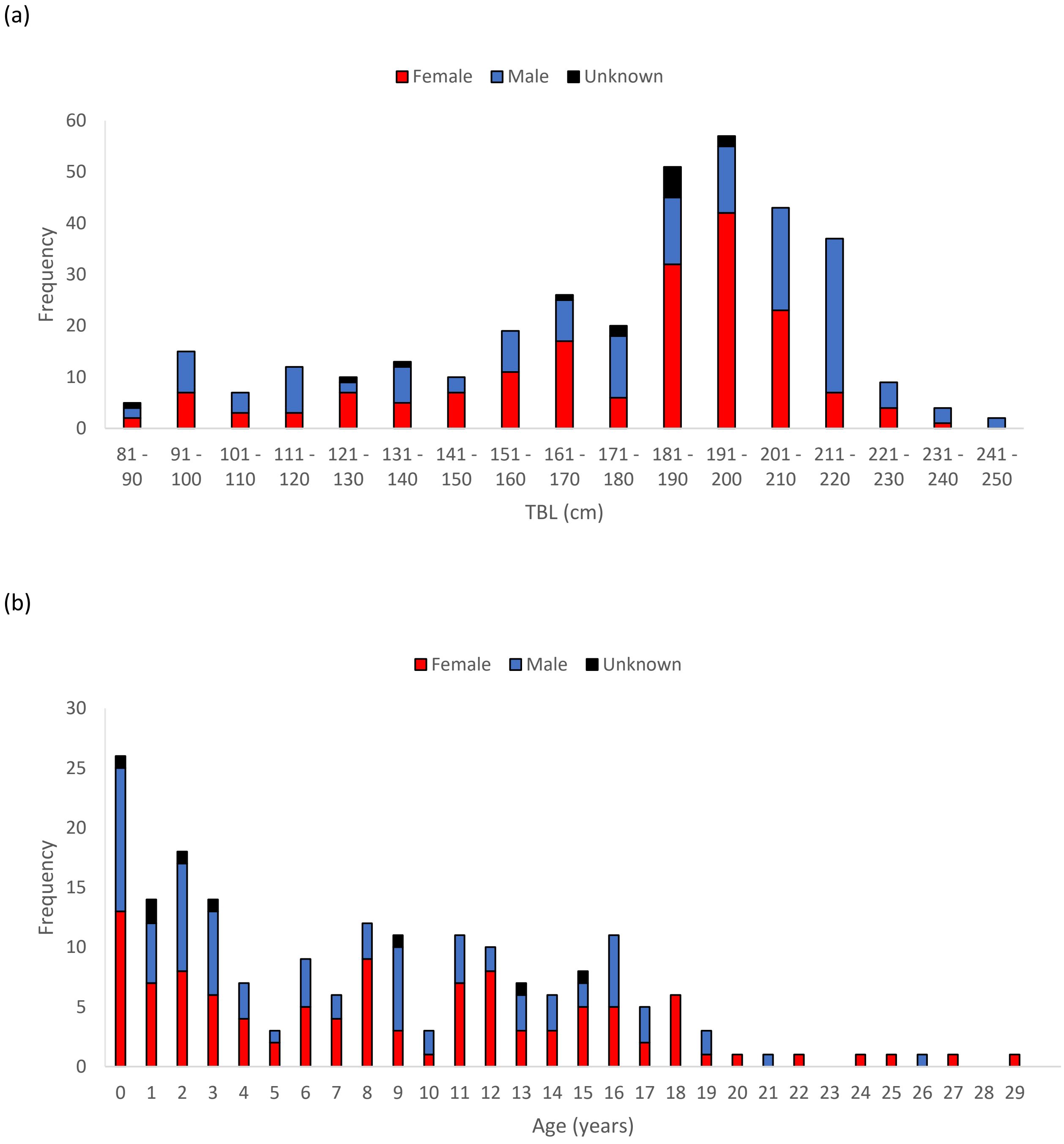

Figure 2.3. (a) Length (*n* = 340) and (b) age (*n* = 198) frequency distribution for female, male and unknown sex common dolphins (*Delphinus delphis*) stranded and bycaught along the Aotearoa New Zealand coast between 1997 and 2020.

2.4.2 Length at birth

A total of 13 foetuses were recorded in the dataset, ranging from 3.9 to 101 cm TBL. The largest female foetus was 92 cm, and the largest male foetus was 101 cm. The smallest born female and male calves measured at 82 and 89 cm, respectively. There were 2 foetuses and 20 neonates measuring between 82 cm (the smallest neonate/calf) and 101 cm (the largest foetus). Results for each of the three methods used to estimate length-at-birth are presented in Table 2.1.

Table 2.1. Estimated length-at-birth (cm) of common dolphins examined from Aotearoa New Zealand between 1997 and 2019 (*n* = 103), using three different methods. The logistic regression is considered the best method of estimating length-at-birth. The estimate and 95% interval from the logistic regression model is the mean and highest posterior density interval from the posterior distribution of the median length-at-birth (i.e., the length at which the probability of birth is 50%). For the mean overlap and mean neonatal length, the standard mean and 95% confidence intervals are reported.

Method	***n***	**Estimate**	**95% interval**
Logistic regression	103	85.41	78.0–91.5
Mean overlap	10	93.9	93.5–94.3
Mean neonatal length	22	98.1	96.7–99.5

The median length at birth was estimated as 85.4 cm (Figure 2.4, 95% CrI: 78.0–91.5 cm, *n* = 103), based on the weighted HOF logistic regression model. Two additional methods (mean overlap and mean neonatal length) were calculated for comparison with previous studies of other common dolphin populations. The mean overlap statistic calculated length-at-birth as 93.9 cm (95% CI = 93.5–94.3, *n* = 22). This method is sensitive to having an unbalanced sample as it only takes the pre- and postnatal individuals that fall within the overlap criteria. The overall dataset used in this study has 6.9 times more postnatal than prenatal individuals, which emphasises this sensitivity. The mean neonatal length statistic calculated length at birth as 98.1 cm (95% CI = 96.7–99.5, *n* = 10). This method has a small sample size and only includes postnatal animals and so tends to overestimate length-at-birth. As there are several caveats known for the mean neonatal length and mean overlap methods, the weighted HOF logistic regression model was selected as the preferred method for estimating length-at-birth. This method uses both pre- and postnatal data and can define and summarise values of quantities of interest.

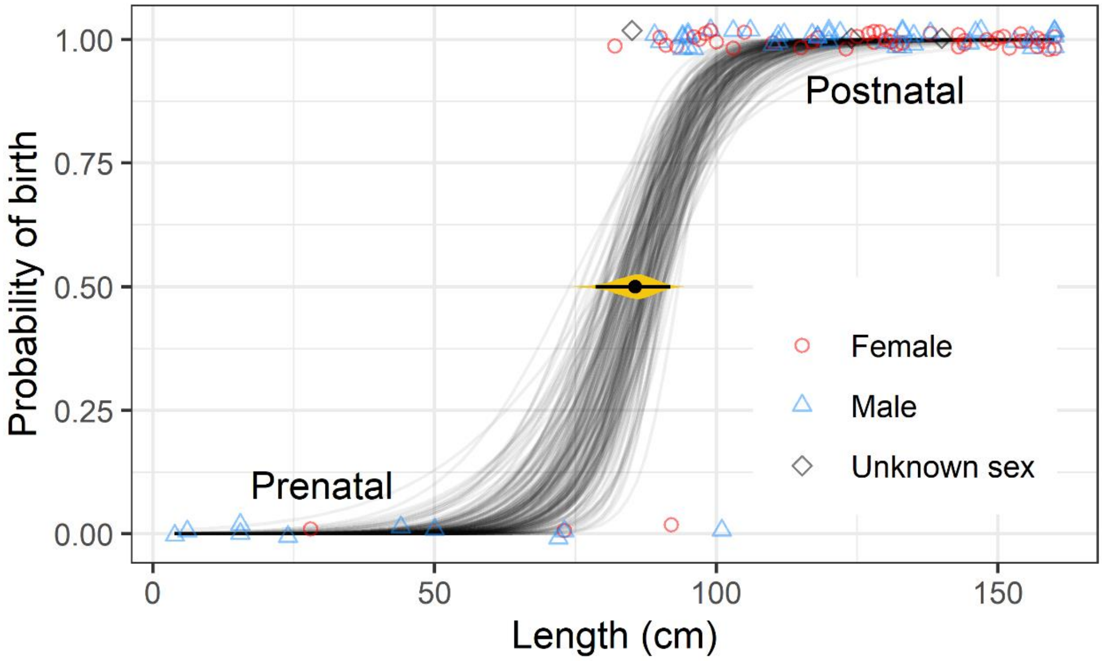

Figure 2.4. The total body lengths of prenatal and postnatal common dolphins examined in Aotearoa New Zealand from 1997 to 2019 (*n* = 103). Logistic curves show the mean probability of birth as a function of length (thin grey lines) using the partially weighted model that disregards sex and is fitted to *n* = 103 cases. 'Jitter' and a small amount of transparency was used to aid in the visualisation of the overlapping points. The small centre point and thin horizontal line show the mean and 95% highest posterior density interval for the length at which the probability of birth is 50% i.e., the estimated median length-at-birth. The gradient plot is highlighted in yellow (Kay 2021).

2.4.3 Growth models

Gompertz, Richards, and Double-Richards growth models were used to describe growth in male and female common dolphins from Aotearoa New Zealand waters. The Gompertz growth model was selected as the preferred model to describe growth in both female and male common dolphins from Aotearoa New Zealand waters for the following reasons. Firstly, the Double-Richards model provided an unrealistically large estimate of asymptotic length (256.8 cm; Figure 2C in Appendices) for male common dolphins, i.e., greater than the largest male recorded in this study. It appears that the lack of biological data for males in certain age classes (5–8 years and > 20 years) heavily influenced the growth curve in the Double-Richards model. Secondly, there was little difference between the AIC scores of the Gompertz (AIC = 781) and the Richards (AIC = 776) growth models for females, nor between the Gompertz (AIC = 630) and Double-Richards (AIC = 618) growth models for males (Table 2.2). Both precision and complexity need to be accounted for when fitting models (Burnham and Anderson 2004) as well as balance between underfitting and overfitting (Gavrilov et al. 2018). Aside from the AIC scores, the number of parameters used in a model also indicates how well a model fits, where the fewest number of parameters is favoured (Bozdogan 1987). The less complex a model i.e., the least number of parameters, the more data can be used to estimate the value of each parameter and the less variance (the loss of predictive accuracy) there will be (Forster and Sober 2011). This is especially important in smaller datasets. The Gompertz growth models have fewer model parameters than the Richards and Double-Richards models and they have been used extensively in other populations of common dolphins (Chivers et al. 2016; Danil and Chivers 2007; Ferrero and Walker 1995; Grandi et al. 2022; Murphy and Rogan 2006; Murphy et al. 2009; Westgate 2005).

Table 2.2. Estimated growth parameters, standard errors (SE) and Akaike Information Criterion (AIC) scores for Gompertz, Richards and Double-Richards growth curves derived from female and male common dolphins (*Delphinus delphis*) examined from New Zealand from 1997 to 2020 (*n* = 182).

Parameters	**Gompertz**		**Richards**	**Double-Richards**
	Female	Male	Female	Male
***A* (SE)**	198.31 (1.47)	212.14 (2.89)	201.65 (2.48)	256.83 (0.41)*
***b* (SE)**	0.65 (0.27)	0.64 (0.04)	-	-
***k* (SE)**	0.66 (0.22)	0.73 (0.28)	0.22 (0.06)	1.36 (0.36)
***i* (SE)**	-	-	-5.40 (2.25)	-0.43 (0.07)
***m* (SE)**	-	-	-2.92 (0.91)	0.10**
Rk				0.32 (0.07)
Ri				5.16 (0.86)
AIC score	781	630	776	618
K^{+}	3	3	4	6

The Gompertz growth model for both females and males are considered to provide the best estimates of asymptotic length for common dolphins in New Zealand waters.

*This value is the asymptote of the second curve (A') in the model. ** This value is set by the package in R

$^{+}$K refers to the number of model parameters

Using the Gompertz growth model, the predicted TBL for females at one year of age was 129.4 cm. Female growth was rapid within the first six years (up to TBL 188.0 cm), gaining 58.6 cm from length at birth (85.4 cm). Past this age, growth slowed around the average age and length at attainment of sexual maturity (7.5 years and 183.5 cm; Chapter 4) until the age of 12 years (TBL 197.4 cm). After 12 years of age, growth was less than 1 cm/year and continued to slow until an asymptote of 198.3 cm (red lines Figure 2.5). Age at asymptotic length was at 18 years of age.

The Gompertz growth model was also used in males where the predicted length from the output of the model at one year was 133.4 cm. Growth was rapid for the first six years in males with TBL increasing by 59.1 cm to 192.5 cm. Past this age, growth is slower, reaching 206.4 cm at 10 years of age. After 10 years of age, growth is steadily slowing, gaining ca. 1 cm till 15 years of age. Past this age, the growth rate is less than 0.5 cm/year and continues to slow until an asymptote of 212.1 cm, as shown by the predicted length-at-age data (blue line, Figure 2.5). Age at asymptotic length was at 20 years.

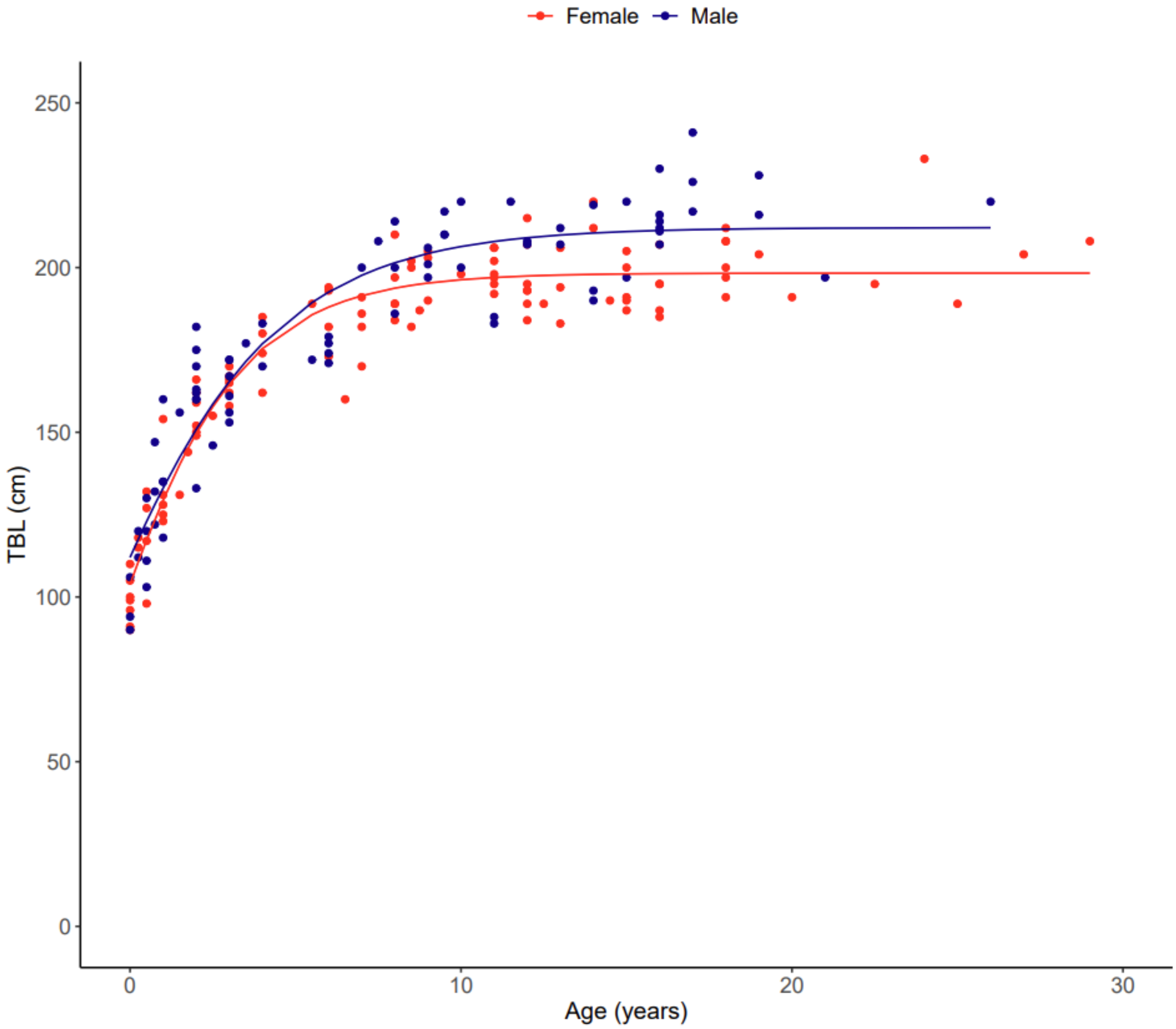

Figure 2.5. Gompertz growth curves superimposed on length-at-age data for female and male common dolphins (Delphinus delphis) stranded and bycaught in New Zealand from 1997 to 2020 (n = 182). The coloured dots represent the length-at-age data and the solid lines represent the sex-specific growth curves.

2.4.4 Allometry

Positive, isometric and negative allometry was observed in the linear measurements of females, but only isometric and negative allometry were observed in males (Table 2.3). For both sexes, isometric allometry was observed for eight out of 12 linear body measurements (Snout-anus, Snout-genital slit, Snout-navel, Snout-origin flipper, Snout-origin dorsal fin, Snout-tip dorsal fin, Snout-blowhole, Eye-blowhole). Negative allometry was observed for both sexes in Genital slit and Rostrum measurements. For the remaining two linear body measurements, females and males exhibited different allometry. Females exhibited positive allometry for the Snout-cnr mouth measurement and males exhibited isometric allometry (t = 0.60, df =303.47, $P > 0.5$). For the Cnr mouth-eye measurement, females exhibited negative allometry whereas males exhibited isometric allometry. However, there was no significant variation in the growth rate for these measurements between males and females (t = -0.81, df = 154.61, $P > 0.1$).

For the eight appendage measurements, males and females demonstrated negative allometry for five measurements (Dorsal fin height, Fluke width, Fluke notch, Flipper internal, Flipper width) and isometric allometry for two measurements (Fluke length, Flipper exterior). For the one remaining appendage measurement (Dorsal fin lat base), females demonstrated negative allometry whereas males exhibited isometric allometry. However, there was no significant variation in the growth rate for this measurement between males and females (t = 0.87, df = 148.06, $P > 0.1$). For the three girth measurements, males and females exhibited isometric allometry for all measurements (Girth flippers, Girth navel, Girth anus).

When comparing growth rates between the sexes, there were four measurements (Snout-genital slit, Rostrum, Genital slit, Fluke width) where there were significant differences in the growth coefficients between males and females (Table 3). Males had higher growth rates in the Rostrum (t = -2.72, df = 320.8, $P < 0.01$) and Fluke width (t = -2.25, df = 396.12, $P < 0.05$) measurements, and females had higher growth rates in Snout-genital slit (t = 1.98, df = 377.43, $P < 0.05$) and Genital slit (t = 4.29, df = 190.03, $P < 0.01$) measurements.

Table 2.3. Allometric growth relationships for 23 external body measurements regressed against total body length (TBL) for physically female (F) and male (M) common dolphins (*Delphinus delphis*) stranded on the Aotearoa New Zealand coast between 1979 and 2020.

Measurement	Female equation	SE (*b*)	*n*	r^2	*b*	Male equation	SE (*b*)	*n*	r^2	*b*	F vs M
Snout-anus	$y = 0.388x^{0.986}$	0.051	213	0.977	b=1	$y = 0.569x^{0.946}$	0.068	222	0.953	b=1	F = M
Snout-genital slit	$y = 0.477x^{0.980}$	0.067	193	0.962	b=1	$y = 0.956x^{0.893}$	0.100	197	0.905	b=1	F > M
Snout-navel	$y = 0.423x^{1.06}$	0.233	33	0.928	b=1	$y = 0.387x^{1.078}$	0.171	26	0.969	b=1	F = M
Snout-origin flipper	$y = 0.871x^{1.136}$	0.094	221	0.906	b=1	$y = 0.888x^{1.136}$	0.129	222	0.858	b=1	F = M
Snout-origin dorsal fin	$y = 0.410x^{1.088}$	0.097	106	0.958	b=1	$y = 0.491x^{1.073}$	0.119	78	0.952	b=1	F = M
Snout-tip dorsal fin	$y = 0.944x^{0.908}$	0.164	201	0.768	b=1	$y = 0.665x^{0.972}$	0.121	205	0.875	b=1	F = M
Snout-blowhole	$y = 2.095x^{0.866}$	0.131	161	0.773	b=1	$y = 1.726x^{1.006}$	0.114	156	0.859	b=1	F = M
Snout-cnr mouth	$y = 1.702x^{1.502}$	0.114	129	0.878	b>1	$y = 1.628x^{1.083}$	0.114	114	0.895	b=1	F = M
Genital slit	$y = 4.405x^{0.329}$	0.095	103	0.376	b<1	$y = 4.274x^{0.450}$	0.084	92	0.564	b<1	F > M
Rostrum	$y = 3.462x^{0.667}$	0.067	195	0.772	b<1	$y = 3.680x^{0.578}$	0.090	197	0.590	b<1	F < M
Cnr mouth-eye	$y = 4.166x^{0.558}$	0.138	95	0.337	b<1	$y = 3.813x^{0.740}$	0.161	75	0.464	b=1	F = M
Eye-blowhole	$y = 1.777x^{1.216}$	0.244	96	0.668	b=1	$y = 1.538x^{1.295}$	0.188	73	0.840	b=1	F = M
Dorsal fin height	$y = 3.010x^{0.757}$	0.089	185	0.760	b<1	$y = 3.180x^{0.700}$	0.077	183	0.788	b<1	F = M
Dorsal fin lat base	$y = 2.281x^{0.881}$	0.129	105	0.823	b<1	$y = 1.951x^{0.990}$	0.103	76	0.926	b=1	F = M
Fluke width	$y = 3.149x^{0.560}$	0.120	219	0.566	b<1	$y = 2.860x^{0.640}$	0.074	211	0.830	b<1	F < M
Fluke length	$y = 3.331x^{0.695}$	0.232	95	0.387	b=1	$y = 3.483x^{0.620}$	0.233	70	0.409	b=1	F = M
Fluke notch	$y = 4.864x^{0.408}$	0.042	90	0.360	b<1	$y = 4.757x^{0.472}$	0.066	67	0.329	b<1	F = M
Flipper internal	$y = 3.058x^{0.713}$	0.152	129	0.600	b<1	$y = 3.514x^{0.570}$	0.181	105	0.442	b<1	F = M
Flipper exterior	$y = 1.424x^{1.116}$	0.138	142	0.837	b=1	$y = 1.287x^{1.159}$	0.129	120	0.884	b=1	F = M
Flipper width	$y = 3.659x^{0.663}$	0.108	190	0.504	b<1	$y = 3.278x^{0.835}$	0.080	184	0.758	b<1	F = M
Girth flippers	$y = 1.747x^{0.761}$	0.176	173	0.687	b=1	$y = 2.054x^{0.693}$	0.195	148	0.633	b=1	F = M
Girth navel	$y = 1.208x^{0.877}$	0.175	91	0.849	b=1	$y = 1.320\,x^{0.853}$	0.160	64	0.898	b=1	F = M
Girth anus	$y = 1.916x^{0.827}$	0.125	95	0.877	b=1	$y = 1.960x^{0.806}$	0.123	69	0.907	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 2.2.

Table 2.4. Mean (x̄), standard error (SE), range and sample size (*n*) of 23 external body measurements, with results of Welch's ANOVAs, ANCOVAs, and multivariate linear discriminant function analysis (LDFA) comparing data collected from physically mature female (F) and male (M) common dolphins (*Delphinus delphis*) stranded on the Aotearoa New Zealand coast between 1979 and 2020.

	Female				**Male**						
	x̄ (cm)	***SE***	**Range (cm)**	***n***	**x̄ (cm)**	***SE***	**Range (cm)**	***n***	**ANOVA**	**ANCOVA**	**LDFA**
TBL	207.9	1.1	200–240	55	222.3	1.1	213–250	55	***	na	1.32
Snout-anus	148.1	0.9	125–163	50	157.8	1.1	136–177	51	***	***	0.63
Snout-genital slit	140.0	1.0	125–160	45	138.5	1.1	122–160	43		na	-0.90
Snout-navel	101.7	8.3	91–118	3	97.3	1.8	94–100	3		na	na
Snout-origin flipper	48.6	0.6	26–56	52	49.5	0.4	44–60	50			-0.07
Snout-origin dorsal fin	92.1	1.3	83–107	19	92.0	1.6	84–106	15			na
Snout-tip dorsal fin	118.4	2.0	87–139	43	127.1	1.5	91–145	49	***	***	-0.52
Snout-blowhole	34.9	0.7	17–39	35	35.8	0.5	30–47	38			0.40
Snout-cnr mouth	30.4	0.3	27–35	30	30.3	0.4	26–34	24			-0.29
Genital slit	12.5	0.7	5–20	20	10.2	0.7	5–18	24	*	*	na
Rostrum	16.4	0.8	12–36	40	16.4	0.6	12–35	49			-0.03
Cnr mouth-eye	6.2	0.3	5–10	17	6.9	0.3	6–9	15			na
Eye-blowhole	17.6	0.3	16–20	18	18.2	0.5	13–21	15			na
Dorsal fin height	19.9	0.4	16–24	41	23.1	0.5	17–35	44	***	***	0.49
Dorsal fin lat base	30.2	0.8	26–38	20	33.3	0.7	30–40	15	**	**	na
Fluke width	42.8	1.5	13–66	50	49.0	1.0	25–62	51	**	**	0.20
Fluke length	16.5	2.1	11–51	18	16.1	0.4	12–18	15	**	*	na
Fluke notch	2.4	0.1	2–3	17	2.8	0.1	2–3	14	*	*	na
Flipper internal	22	0.4	19–27	30	22.4	0.6	18–27	26			-0.08
Flipper exterior	32.2	0.5	26–40	33	33.9	0.4	28–37	26	*	*	0.32
Flipper width	11.1	0.3	9–19	44	11.9	0.2	7–15	44	*	*	-0.20
Girth flippers	104.6	2.8	55–152	37	109.2	3.3	56–148	35			-0.09
Girth navel	108.3	4.9	89–184	18	111.7	1.8	100–125	13			na
Girth anus	60.2	1.0	52–69	19	73.6	3.7	60–118	14	***	***	na

LDFA = Linear Discrimination Function Analysis coefficients, na = not analysed, *P < 0.05, **P < 0.01, ***P < 0.001. M > F for all sexually dimorphic measurements apart from Genital slit where F > M. For an explanation of the measurement codes, see Figure 2.2.

2.4.5 Sexual dimorphism

Table 2.4 summarises the mean (x̄), standard error (SE), range and sample size (*n*) for physically mature individuals (defined as TBL ≥ asymptotic length). A sexual size dimorphism ratio of 1.07 was calculated from a mean body length of 222.3 and 207.9 cm in physically mature males and females, respectively. Significant sexual size dimorphism was found in mature common dolphins for 12 out of 24 measurements. Males were larger than females in 11 of these measurements (TBL, Snout-anus, Snout-tip dorsal fin, Dorsal fin height, Dorsal fin lat base, Fluke width, Fluke length, Fluke notch, Flipper exterior, Flipper width and Girth anus). Females were found to be significantly larger than males for one measurement, the Genital slit. In addition, 12 of the 24 measurements (TBL, Snout-anus, Snout-tip dorsal fin, Genital slit, Dorsal fin height, Dorsal fin lat base, Fluke width, Fluke length, Fluke notch, Flipper exterior, Flipper width and Girth anus) exhibited sexual shape dimorphism. Irrespective of TBL, males were significantly larger in all measurements apart from Genital slit where females were significantly larger. As observed in Figure 2.6, 2.7 and 2.8, there is overlap in many measurements however in the measurements that exhibited sexual dimorphism there is some delineation between males and females, especially in TBL, Snout-anus, Dorsal fin lat base and Girth anus.

A single linear discriminant function accounted for 79% of the sexual dimorphism observed (SD = 0.4). The coefficients of the allometric equations are listed in Table 2.4. The Linear Discriminant Function Analysis (LFDA) determines the measures that best discriminate between males and females where the larger the absolute value of the output, the greater the difference between males and females. Using the LFDA, TBL (1.32) displayed the greatest difference between males and females, followed by Snout-genital slit (-0.90) and Snout-anus (0.63). The measurements with the least difference between males and females were Snout-origin flipper (-0.07) and Rostrum (-0.03).

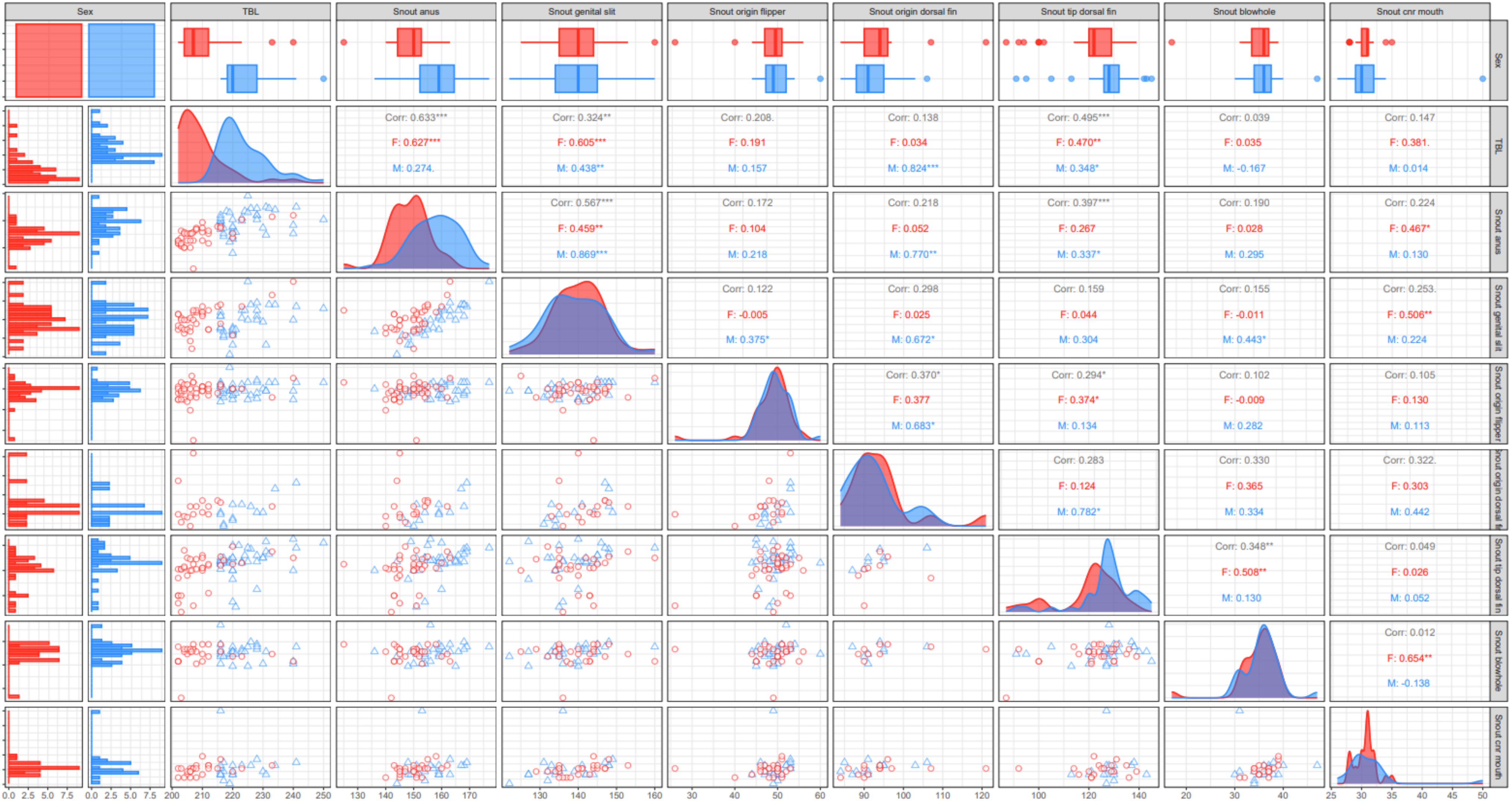

Figure 2.6. Sex (male and female) versus Total body length [male: n = 46, female: n = 46] and 7 linear measurements (Snout-anus [male: n = 42, female: n = 42], Snout-genital slit [male: n = 35, female: n = 37], Snout-origin flipper [male: n = 42, female: n = 44], Snout-origin dorsal fin [male: n = 13, female: n = 17], Snout-tip dorsal fin [male: n = 41, female: n = 37], Snout-blowhole [male: n = 31, female: n = 28], Snout-cnr mouth [male: n = 22, female: n = 25]) of mature common dolphins (Delphinus delphis) from Aotearoa New Zealand waters between 1979 and 2020.

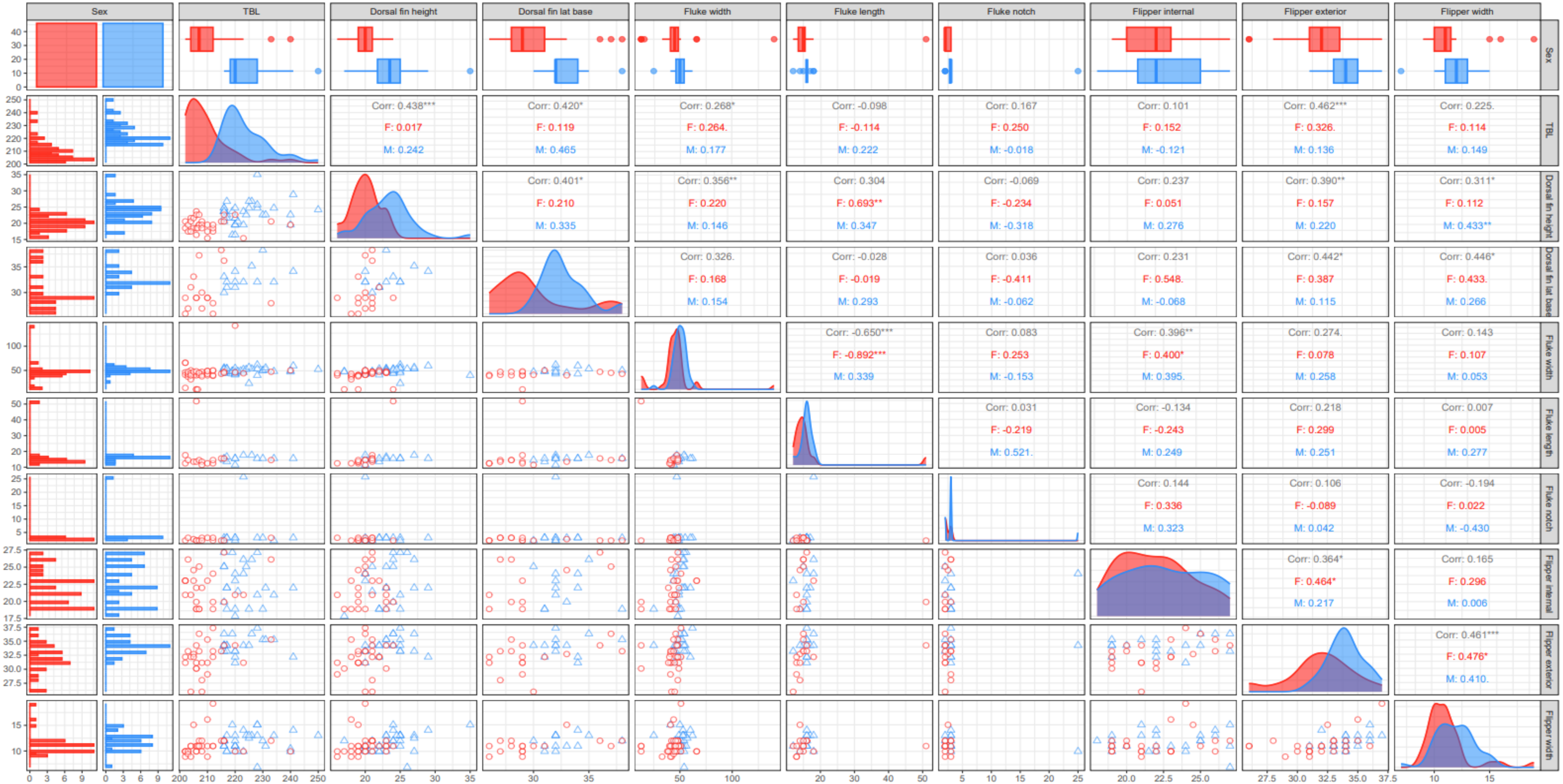

Figure 2.7. Sex (male and female) versus Total body length [male: n = 46, female: n = 46] and 8 appendage measurements (Dorsal fin height [male: n = 36, female: n = 33], Dorsal fin lat base [male: n = 13, female: n = 17], Fluke width [male: n = 42, female: n = 43], Fluke length [male: n = 13, female: n = 15], Fluke notch [male: n = 12, female: n = 14], Flipper internal [male: n =24, female: n = 25], Flipper exterior [male: n = 23, female: n = 27], Flipper width [male: n = 36, female: n = 35]) of mature common dolphins (Delphinus delphis) from Aotearoa New Zealand waters between 1979 and 2020.

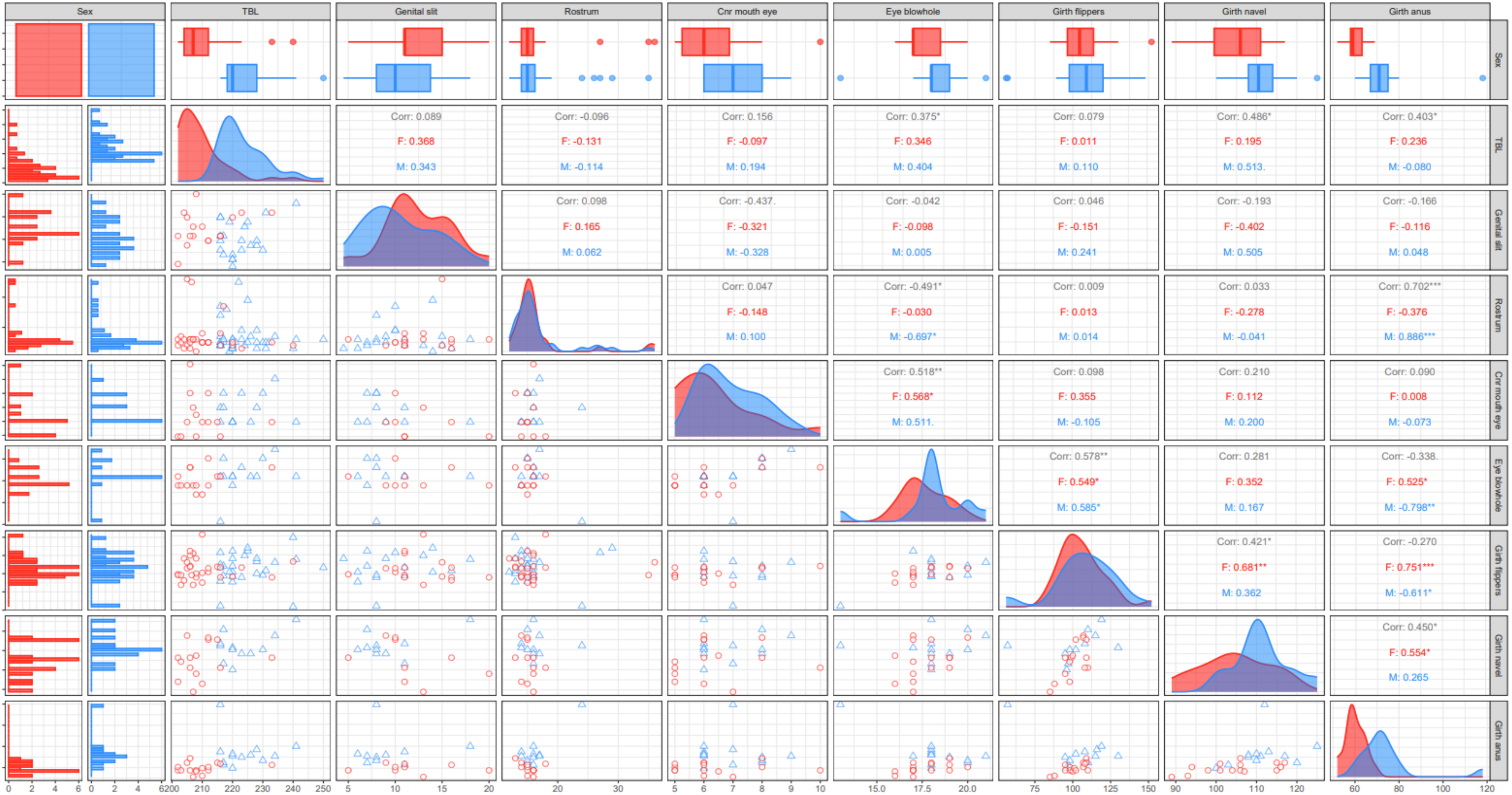

Figure 2.8. Sex (male and female) versus Total body length [male: n = 46, female: n = 46] and 7 linear and girth measurements (Genital slit [male: n = 22, female: n = 17], Rostrum [male: n = 40, female: n = 33], Cnr mouth eye [male: n = 13, female: n = 14], Eye blowhole [male: n = 13, female: n = 15], Girth flippers [male: n = 28, female: n = 30], Girth navel [male: n = 12, female: n = 15], Girth anus [male: n = 13, female: n = 16]) of mature common dolphins (Delphinus delphis) from Aotearoa New Zealand waters between 1979 and 2020.

2.5 Discussion

2.5.1 Body length and age

Previous maximum records for body length of common dolphins in Aotearoa New Zealand waters are 206 cm for females and 235 cm for males (*n* = 15; Amaha 1994). This study presents the maximum TBL as 233 cm and 244 cm for females and males, respectively. Current maximum body lengths are comparable to international populations, with the largest female measuring at 252 cm (Read et al. 2019) and the largest male measuring at 250 cm in the eastern North Atlantic (Table 2D in Appendices; Murphy et al. 2013). In the eastern tropical Pacific, the largest female was 213 cm (Danil and Chivers 2007), which is considerably smaller than both the maximum for the species and in Aotearoa New Zealand waters. Smaller maximum lengths are also observed off the coast of California (North Pacific Ocean), with the largest male measuring at 201 cm from aerial surveys (Leander et al. 2021). Differences in water temperature can drive geographical variation in body size. Habitat temperature influences body size as the rate at which heat dissipates decreases as size increases (Barbieri 2005). In warmer waters, being small does not decrease survival as it does in cooler habitats (Ahlborn and Blake 1999; Goldbogen 2018). Variation in body size can also be driven by several other factors including availability of resources such as quality and quantity of prey, population density and bycatch rates (Amano and Miyazaki 1992; McClain et al. 2015; Ross and Cockcroft 1990). Evidence of body size changing with anthropogenic impacts has been observed in sperm whales (*Physeter macrocephalus*) with a significant decline in average body size, possibly due to heavy whaling on larger individuals (McClain et al. 2015). In exploited populations, average declines of almost 20% in size-related traits have been recorded (Darimont et al. 2009; Wade et al. 2012), as energy is shifted from growth to reproduction to increase population numbers.

Maximum ages for common dolphins in Aotearoa New Zealand waters were 29 years and 26 years for females and males, respectively. This is similar to Northern Hemisphere populations where the maximum age for common dolphins is ≥30 for females (Danil and Chivers 2007; Murphy et al. 2010; Westgate and Read 2007). For males, maximum ages of between 25 and 29 years old have been reported for Northern Hemisphere populations (Murphy and Rogan 2006; Read et al. 2019; Westgate 2005). Similarities of maximum ages across numerous studies would suggest that 30 years of age is the approximate maximum age for the species in the wild (Murphy et al. 2014).

Despite the maximum ages of this study being close to 30, the largest group (18%) of aged individuals in the study is the yearling age class (< 1 year old). This is consistent with the eastern North Atlantic population where 26% of the aged sample consisted of < 1-year olds, with 77% of all calves obtained from bycatch (Murphy and Rogan 2006). In this study, all yearling individuals are from stranding events. A likely explanation for the high proportion of yearling calves could be due to maternal separation, as when calves are separated from their mothers before weaning they are most likely to strand and die (Roe 2007). Contaminant offloading is also of concern due to maternal offloading being observed in common dolphins in Aotearoa New Zealand waters (Stockin et al. 2007). This is seen in other common dolphin populations with the transfer of organochlorine compounds from mother to calf (Borrell and Aguilar 2005). In Aotearoa New Zealand, infant mortality has been observed in other species such as the bottlenose dolphin (*Tursiops truncatus*) but reasons for this are currently unknown (Tezanos-Pinto et al. 2015).

There are several ways to estimate age in cetaceans and each method comes with its advantages and disadvantages (Hohn 1989; Rosas et al. 2003). With strict quality controls and best practice applied when aging teeth (Murphy et al. 2014), it is unlikely that methodological error had a significant impact on the results of this study. Blind readings were made across three experienced readers with no prior knowledge of the individual's biological data. Barratclough et al. (2023) recently published new research on the accuracy of tooth GLG aging and a new methodology, bone aging using pectoral fins. Pectoral fin aging can be performed on live, captive animals. This is unlike tooth GLG aging, which requires teeth to be collected from a deceased individual. The aging of teeth, especially in older individuals, comes with potential challenges such as the curving of the tooth, accessory layers, compression of the GLGs and the wearing down of the tooth. All of these challenges can inhibit the ability to determine age accurately (Barratclough et al. 2023). Radiographic bone aging of pectoral fins was found to be more accurate than tooth GLG aging in bottlenose dolphins (Barratclough et al. 2023). Despite this, there are difficulties with this new methodology including gaining access to the necessary equipment, having subjective assessment and obtaining true dorsoventral radiographs. Currently, tooth GLG aging is the 'gold standard' way to age odontocetes, especially in the case of this study as only deceased individuals were examined from strandings and bycatch.

2.5.2 Length at birth

Three methods were applied to calculate length-at-birth in this study to allow for comparisons with international common dolphin populations (Table 2D in Appendices; Danil and Chivers 2007; Grandi et al. 2022; Murphy et al. 2009; Westgate and Read 2007). Length-at-birth was calculated as 85.4 cm using the logistic regression method. Applying the same method, Danil and Chivers (2007) reported length-at-birth at between 87 and 88 cm for the eastern tropical Pacific. In the eastern North Atlantic, 93 cm was reported as the length-at-birth using the mean overlap statistic (Murphy et al. 2009). The western North Atlantic used the mean neonatal statistic and estimated length-at-birth as 92.7 cm

(Westgate and Read 2007). Grandi et al. (2022) also estimated the length at birth by the mean neonatal statistic and estimated 91.4 cm as length-at-birth in the western South Atlantic. Aotearoa New Zealand estimates when using these respective methods are 93.9 cm (mean overlap) and 98.1 cm (mean neonatal length). The preferred method for this study was the logistic regression method (85.4 cm) due to the mean neonatal and mean overlap statistical tendency to overestimate length-at-birth with an unbalanced sample.

Estimated length-at-birth (85.4 cm) of Aotearoa New Zealand common dolphins is one of the smallest estimated for the species alongside the eastern tropical Pacific population (Table 2D in Appendices; Danil and Chivers 2007). This is likely explained by the use of different methods of estimating length-at-birth across these studies. The mean-overlap statistic calculated for this study (93.9 cm) aligns with the eastern North Atlantic estimate which also used this method (93 cm; Murphy et al. 2009). The mean-overlap statistic estimated for Aotearoa New Zealand would have been influenced by the smallest calf (82 cm) and the largest foetus (101 cm) in the dataset. The calf was just less than a month earlier than the estimated birth date, using the estimated foetal growth rate of 6.95 cm/month. Conversely, the foetus was estimated to be over two months past the estimated birth date. This is likely from the mother live stranding due to birthing issues where the foetus was in reverse breech position (head instead of tail first). There was also evidence of dystocia, which could explain why the foetus was so large (Massey University, unpubl. data). The other large foetus (92 cm) was full term but appeared ‘normal’ at post-mortem as it was enclosed within the uterus with fluid and had no obvious evidence of deformation (Massey University, unpubl. data).

The mean neonatal length statistic estimated in this study (98.1 cm) is larger than the length-at-birth estimate for the western North Atlantic (92.7 cm; Westgate and Read 2008) and the western South Atlantic (91.4 cm; Grandi et al. 2022), who also used this method. The mean neonatal statistic usually overestimates the result as it only considers postnatal calves. As this estimate is the largest length-at-birth estimate recorded for common dolphins, it may indicate that the neonatal line is not formed exactly at birth, but instead weeks or even months later (Kemper et al. 2019). This has been previously suggested for other species including northern (*Globicephala melas melas*) and southern (*G. m edwardii*) long-finned pilot whales (Betty et al. 2022; Bloch et al. 1993) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*; Kemper et al. 2019).

2.5.3 Growth models

Growth models are an important tool for obtaining age-specific growth, fecundity and mortality rates of a species (Gormley et al. 2012; van Schaik and Isler 2012). The Gompertz growth model used in this study has also been used in previous common dolphin studies (Table 2D in Appendices; Chivers et al. 2016; Danil and Chivers 2007; Ferrero and Walker 1995; Grandi et al. 2022; Murphy and Rogan 2006; Murphy et al. 2009; Westgate 2005). Male common dolphins in Aotearoa New Zealand waters obtain physical maturity (i.e., asymptotic length) at 212.1 cm, which align with males in the eastern North Atlantic who reach asymptotic length at 211.6 cm (Murphy and Rogan 2006). In the western North Atlantic, males are slightly larger when they reach asymptotic length at 221.5 cm (Westgate 2005). An asymptotic length of 215.9 cm was estimated for common dolphins off southeastern Brazil (Siciliano et al. 2007), which aligns here with other studies though this study did not split males and females due to small sample size (*n* = 20) and therefore cannot be used in comparisons. Aotearoa New Zealand female common dolphins reach asymptotic length at 198.3 cm, which is similar to females in the western North Atlantic (202.2 cm; Westgate 2005), the North Atlantic (194.7 cm; Murphy and Rogan 2006) and the eastern tropical Pacific (197.2 cm; Danil and Chivers 2007). In the North Pacific, females reach asymptotic length at 179.4 cm (Ferrero and Walker 1995). Interestingly, the North Pacific female estimate is the smallest of all global estimates however, the western North Atlantic estimate of male asymptotic length is the largest (Table 2D in Appendices).

Body lengths for < 1 year old females and males ranged from 82 to 154 cm and 90 to 160 cm, respectively. This is similar to other populations, with females measuring between 93 to 145 cm and males between 105 to 155 cm in the eastern North Atlantic (Murphy and Rogan 2006). In the eastern tropical Pacific, the estimated length at 1 year old was approximated at 135 cm (Chivers et al. 2016; Danil and Chivers 2007), which aligns to this study; the predicted length at 1 year old is 129.4 cm for females and 133.4 for males. Similarities across geographical ranges and populations could be due to the need to increase size rapidly after birth for survival in the marine environment. As water conducts heat 25 times faster than air (Pendergast and Lundgren 2009), thermoregulation is extremely important (Dejours 1987) and size plays a large role in this (Ridgway 1972). Being small makes individuals extremely vulnerable to thermal stress (Liwanag 2010; Rutishauser et al. 2004) so rapid growth rates in the first year of life are seen across common dolphin populations, regardless of habitat.

The dataset of this study has a larger number of individuals from stranding events (83%) compared to bycatch events (17%). Murphy and Rogan (2006) have a comparable number of individuals from stranding and bycatch events. Most of the dataset for the western North Atlantic (Westgate 2005) and the full dataset from the North Pacific (Ferrero and Walker 1995) comes from fisheries bycatch. This is likely to influence the age structure of the sample as immature individuals tend to be bycaught more often due to inexperience (Erbe et al. 2016; Negri et al. 2016; Plön et al. 2020). The growth models in this study can be improved, along with the accuracy of estimated age at asymptotic length, with the addition of older individuals. Currently, this study has few individuals above 20 years of age which may be influencing the estimated age and length at physical maturity.

2.5.4 Allometry

Allometry describes how body measurements grow in comparison to the overall growth rate of the body. Similarities and differences in overall growth and of certain measurements were observed in males and females. This can be an indication of sexual dimorphism but more so demonstrates the relative investment of energy into development of body parts (Mclellan et al. 2002). Male and female common dolphins in Aotearoa New Zealand shared allometric similarities in most linear (10 out of 12) and appendage (7 out of 8) measurements and in all girth measurements. Negative or isometric allometry was observed for 22 out of 23 measurements, meaning that these parts of the body are growing slower than or at the same rate as the overall growth of the body. This aligns to common dolphins in the eastern North Atlantic and off South Africa, where appendage and girth measurements displayed either isometric or negative growth in these populations for both males and females (Table 2E in Appendices; Murphy and Rogan 2006; Ngqulana et al. 2017). This likely reflects the need for early development of flukes and associated muscles to be able to swim and breathe immediately after birth (Amano and Miyazaki 1993).

Other appendage measurements such as dorsal fin height demonstrated negative allometry for both sexes in Aotearoa New Zealand and South Africa, as well as females from the eastern North Atlantic (Murphy and Rogan 2006; Ngqulana et al. 2017). However, this measurement displayed positive allometry for males in the eastern North Atlantic, which may be linked to sexual dimorphism where males would use a larger dorsal fin in display competition. The negative allometry observed for Aotearoa New Zealand and South Africa could be due to thermoregulatory constraints where a larger surface area, so a larger dorsal fin, would mean that heat loss occurs more easily (Ngqulana et al. 2017). When assessing the Flipper exterior measurement, there were apparent differences between the Northern Hemisphere compared to the Southern Hemisphere. Common dolphins from the eastern North Atlantic display negative allometry for Flipper exterior growth whereas individuals from Aotearoa New Zealand and South Africa display isometric growth. This was also seen with the Fluke width measurement where common dolphins from Aotearoa New Zealand and South Africa displayed negative allometry yet eastern North Atlantic individuals displayed positive (Female) and isometric (Male) allometry. The variation in allometry across different measurements may be due to taxonomic or morphological variation between sub-species of common dolphins. There is ongoing debate regarding the different species of Delphinus and at the time of publishing, Ngqulana et al. (2017) are referring to the long-beaked common dolphins (*D. capensis*) whereas Murphy and Rogan (2006) are referring to the short-beaked common dolphin (*D. delphis*). Geographical and environmental differences may also play a role in the variation observed. As data continues to be collected in the future, drivers of potential differences in the allometry between regions can be further explored.

External head measurements for the Aotearoa New Zealand population showed variation (positive, isometric and negative) in type of growth relative to body size. This differs to common dolphins off South Africa where all external head measurements (including characters not addressed in this study) exhibited negative allometry. This aligns with common dolphins in the eastern North Atlantic where many measurements associated with the anterior portion of the body (e.g. Snout to eye) exhibited negative allometry (Murphy and Rogan 2006). Read and Tolley (1997) suggest that this may reflect the significance and/or importance of early development of the cranium as needed for efficient respiration from birth (Ngqulana et al. 2017). The variation observed across the different populations may be due to differing environmental factors such as resources and water temperature.

Girth measurements assessed in this study demonstrate isometric growth for all three measurements (Flippers, Navel, Anus) and this aligns with the eastern North Atlantic where girth measurements (Flippers, Navel, Anus, genital slit, behind dorsal fin) demonstrated isometric growth (Murphy and Rogan 2006). This is likely explained by the need for posterior muscle development as the dolphin reaches maturity (Murphy and Rogan 2006; Tolley et al. 1995). In contrast, most girth measurements from common dolphins off South Africa exhibit negative allometry and this is thought to reflect the potential early development of muscle mass for swimming (Ngqulana et al. 2017).

Aotearoa New Zealand common dolphins share similarities with global populations of common dolphins. For girth measurements, the species tends to align more with the Northern Hemisphere population (eastern North Atlantic), whereas the appendage measurements tend to align more with other Southern Hemisphere populations (South Africa). This may reflect the similarities in habitat and resources of both regions and the similarities and differences that Aotearoa New Zealand waters share with these regions.

2.5.5 Sexual dimorphism

Sexual dimorphism is where the two sexes of a species differ in external appearance or other features (Mesnick and Ralls 2018). Within odontocetes this is usually observed in the shape of the skull, differences in girth and general body size, and the size of appendages such as tail flukes and dorsal fins. Sexual dimorphism in TBL was observed in this study with a sexual size dimorphism ratio (SSD) of 1.07, with males being larger than females. A similar SSD ratio (of 1.06) was observed in the eastern North Atlantic with male common dolphins being larger than female common dolphins (Murphy and

Rogan 2006). Males have also been reported to attain a larger TBL than females in populations off the coast of California (Leander et al. 2021), and in the western North Atlantic where males are 9% longer in TBL than females (Westgate 2005; Westgate and Read 2007). Sexual dimorphism has also been observed in other regions and via different methods. For example, skull and external head characteristics across several populations, including Aotearoa New Zealand, have demonstrated significant differences between the sexes (Jordan 2012; Murphy 2006; Nicolosi and Loy 2019). Contrastingly, Bell et al. (2002) found that male and female common dolphins around Australia (Western Australia to New South Wales) had considerable overlap across all cranial characteristics.

Within the Aotearoa New Zealand population (this study), 12 out of 23 measurements assessed showed sexual size dimorphism with males being significantly larger than females in all but one measurement. Overall, common dolphins in Aotearoa New Zealand waters display less sexually dimorphic traits compared to other populations (Murphy and Rogan 2006; Ngqulana et al. 2017). For common dolphins off South Africa, 22 of 26 measurements showed sexual size dimorphism with males being significantly longer and more robust than females (Ngqulana et al. 2017). These included all measurements assessed in this study apart from Snout-navel which was not assessed by Ngqulana et al. (2017). In the eastern North Atlantic, sexual size dimorphism was found in 20 out of 23 measurements where males were significantly larger than females, and again included the same measurements in this study, with the exception of Snout-navel (Murphy and Rogan 2006; Neumann et al. 2002).

Mating tactics, and therefore sexually dimorphic traits, are influenced by social and ecological factors (Orbach 2019). For common dolphins, sperm competition has long been the suggested mating system due to the relative size of testes and the presence of moderate sexual dimorphism observed (Murphy et al. 2005; Westgate and Read 2007). Connor et al. (2000) predicted that odontocete species with large testes size relative to body size were more likely to compete via sperm competition and be more promiscuous (Orbach 2019). Development of gonadal tissue and sperm development is energetically costly (Kenagy and Trombulak 1986) and therefore sperm competition is an important way for males to increase reproductive success in a polygynous mating system (delBarco-Trillo and Ferkin 2004). Populations off South Africa and in the eastern North Atlantic appear to have more sexually dimorphic traits than the Aotearoa New Zealand population. This may be due to ecological differences or behaviour of social groups between the populations and the underlying mechanism of sexual selection (Breed et al. 2006; Mesnick and Ralls 2018; Murphy and Rogan 2006). Additionally, the fact that females appear to reproduce year-round (Palmer et al. 2022) may be influencing sexually dimorphic features of males and females in Aotearoa New Zealand and causing them to be more similar.

No external head measurements were found to be sexually dimorphic in this study which differs slightly to previous knowledge for the Aotearoa New Zealand population. Jordan (2012) found ca. 23% of cranial measures taken to be sexually dimorphic with larger skulls found in males; however, none of these measurements were taken in the current study so a direct comparison is not possible. Sexually dimorphic cranial measurements (with males having larger skulls) have also been observed in common dolphins from South Africa (Ngqulana et al. 2017), the eastern North Atlantic (Murphy 2006; Murphy and Rogan 2006) and the eastern North Pacific (Heyning and Perrin 1994). Ngqulana et al. (2017) included five of the same measurements used in this study (Snout-blowhole, Snout-cnrmouth, Rostrum, Cnrmouth-eye and Eye-blowhole) as well as three additional measurements when assessing skull/cranial sexual dimorphism. Murphy and Rogan (2006) assessed two of the same measurements (Snout-blowhole, Snout-cnrmouth) and one other whereas Heyning and Perrin (1994) assessed 27 skeletal cranial measurements, of which none were included in this study. In other species such as bottlenose whales (genus *Hyperroodon*), sexual dimorphism of skulls is thought to be due to defensive encounters between males, which require densely ossified skulls (Ralls and Mesnick 2009). Common dolphin external head measurements from Aotearoa New Zealand show no sexual dimorphism unlike other populations (e.g. eastern North Atlantic and South Africa), which could reflect potential differences in mating behaviours but further research is required to extrapolate on this idea. The small sample size of individuals in this study with external head measurements, as well as there being five total measurements to compare, would limit any inferences made here.

For appendage measurements, sexual dimorphism aligned across the three populations (Aotearoa New Zealand, South Africa, eastern North Atlantic) with males having larger dorsal, flipper, and fluke measurements. This is likely due to swimming, propulsion, manoeuvrability and agility to better pursue females for mating (Ngqulana et al. 2017; Tolley et al. 1995). Longer and broader tail flukes and pectoral fins may function to maintain hydrodynamic stability (Clark and Odell 1999). Larger appendages have also been associated with use in aggressive combat between males (Connor et al. 2000; MacLeod 1998) in species such as humpback dolphins (*Sousa sahulensis*; Brown et al. 2016) and bottlenose dolphins (Scott et al. 2005). For other odontocete species, larger appendages are thought to act as ‘ornaments’ such as in killer whales (*Orcinus orca*; Dines et al. 2015) and long-finned pilot whales (Betty et al. 2022). For common dolphins there is no concrete evidence of male combat however, rake marks have been observed on both male and female common dolphins from the Aotearoa New Zealand population (pers. obs.) and so could potentially be a result of mating interactions. Rake marks, as a result of sexual interactions and male-male competition, have been observed for bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Australia (Scott et al. 2005) and on the west coast of Scotland (Marley et al. 2013).

2.6 Conclusions

Parameters such as average age and length at physical maturity, length at birth, and allometric growth rates play a critical role in understanding the life history of a species. This study presents first insights of age, growth and sexual dimorphism for common dolphins in Aotearoa New Zealand waters. Being able to place Australasia in the context of global understanding fills an important knowledge gap that allows comparisons to international populations. With new biological information obtained including growth models and allometry, age-at-length data and age and length at physical maturity, monitoring of these parameters can allow for identification of any changes to the populations. Significant insights are provided here for future conservation management of the species in Aotearoa New Zealand.

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Chapter 3

Reproductive biology of male common dolphins (*Delphinus delphis*) in Aotearoa New Zealand waters

Common dolphin in the Hauraki Gulf, Auckland

This chapter is a reformatted version of the following manuscript:

Palmer EI, Betty EL, Murphy S, Perrott MR, Smith ANH, Stockin KA (2023). Reproductive biology of male common dolphins (*Delphinus delphis*) in Aotearoa New Zealand waters. Marine Biology 170. https://doi.org/10.1007/s00227-023-04266-5.

3.1 Abstract

Reproductive parameters were assessed in 64 male common dolphins (*Delphinus delphis*) examined post-mortem from stranding and bycatch events in Aotearoa New Zealand between 1999 and 2020. The stages of male sexual maturation were assessed using morphological measurements and histological examination of testicular tissue. Age was determined via growth layer groups (GLGs) in teeth. The average age (ASM) and length (LSM) at attainment of sexual maturity were estimated to be 8.8 years and 198.3 cm, respectively. Individual variation in ASM (7.5–10 years) and LSM (190–220 cm) was observed in Aotearoa New Zealand common dolphins. However, on average, sexual maturity was attained at a similar length but at a marginally younger age (< 1 year) in Aotearoa New Zealand compared to populations in the Northern Hemisphere. All testicular variables proved better predictors of sexual maturity compared to demographic variables (age and total body length), with combined testes weight the best outright predictor of sexual maturity. Reproductive seasonality was observed in male common dolphins, with a significant increase in combined testes weight in austral summer. This aligns with other studied populations where seasonality in reproduction is typically observed. Given the known anthropogenic impacts on Aotearoa New Zealand common dolphins, it is recommend that these findings be used as a baseline from which to monitor population level changes as part of conservation management efforts.

3.2 Introduction

An understanding of male reproductive parameters can provide insights into population structure, intraspecific competition, mating behaviours and systems, group structure, and sexual dimorphism within a population or species (Bronson 2009; De Bruyn et al. 2011; delBarco-Trillo and Ferkin 2004; Dixson and Anderson 2004). Within Cetacea (whales, dolphins and porpoises) a wide range of reproductive parameters are displayed, including large variation in average age and length at attainment of sexual maturity and gonadal size (Clapham 1996; Danilewicz et al. 2004; MacLeod and MacLeod 2009; Nicolosi and Loy 2019; Ramos et al. 2000).

Spermatogenesis, the production of haploid spermatozoa, is the primary indicator of sexual development in male cetaceans (Katsumata 2010; Kemper et al. 2014; Plön and Bernard 2007). Reproduction is predominantly seasonal in cetaceans, with most males producing sperm only at certain times of the year (Neimanis et al. 2000; Robeck and O'Brien 2018; Sørensen and Kinze 1994; Vu et al. 2015). Sexual features of male cetaceans vary widely, but may include a prominent postanal hump, large testes size, long penises, and retained bodily scarring caused by intraspecific interactions (Betty et al. 2019; Dines et al. 2014; Dines et al. 2015; Dixson and Anderson 2004; Neumann et al. 2002). In life history studies, sexual maturity is typically assessed via the gross and histological examination of testes post-mortem (Murphy et al. 2005; Reddy 1996), although hormone analysis of blubber, plasma and blow exhalant samples are increasingly used for live, free-ranging individuals (Galligan et al. 2018; Hogg et al. 2009; Kellar et al. 2009; Robeck et al. 2019).

Reproductive parameters of male cetaceans have been assessed across many species (Betty et al. 2019; Matkin et al. 2014; Olesiuk et al. 2005; Plön et al. 2020; Wells 2014), with variation often linked to body size and longevity. For example, male harbour porpoises (*Phocoena phocoena*) in Scottish waters attain sexual maturity at 5 years of age and 132 cm in length (Learmouth et al. 2014); whereas male bottlenose dolphins (*Tursiops aduncus*) in the Indo-Pacific attain sexual maturity at ca. 12 years of age and between 208 and 220 cm in length (Kemper et al. 2014). Furthermore, there is considerable variation between populations and ecotypes of the same species (Chen et al. 2011; Olesiuk et al. 1990; Robeck and Monfort 2006). For example, male harbour porpoises in the Celtic and Irish seas obtained sexual maturity at a significantly larger body length than those in the North Sea (Murphy et al. 2020). Individuals in this region experience mixing with the larger, recently proposed sub-species of Iberian harbour porpoises, which would increase the length at sexual maturity shown by males (Murphy et al. 2020).

The reproductive biology of male common dolphins (*Delphinus delphis*) has been examined in several Northern Hemisphere populations including the western (Westgate and Read 2007) and eastern (Murphy et al. 2005) North Atlantic, the eastern tropical Pacific (Oliver 1973) and the North Pacific (Ferrero and Walker 1995). Less is known for common dolphins in the Southern Hemisphere, with only a single study in the western South Atlantic (Grandi et al. 2022) having detailed male common dolphin reproduction. Such paucity of data has been of concern for Australasia, where common dolphins are subject to several anthropogenic impacts including pollutants (Lavery et al. 2008; Stockin et al. 2021a; Stockin et al. 2021b), tourism (Meissner et al. 2015; Neumann and Orams 2005, 2006; Stockin et al. 2008a) and fisheries bycatch (Allen et al. 2014; Barceló et al. 2021; Hamer et al. 2008; Mackay and Goldsworthy 2017; Parra et al. 2021; Stockin et al. 2009; Thompson et al. 2013).

As part of the wider Australasian population, Aotearoa New Zealand common dolphins demonstrate significant genetic connectivity with their Australian counterparts (Barceló et al. 2021), which raises concerns about the sustainability of levels of fisheries bycatch on both sides of the Tasman Sea (Allen et al. 2014; Du Fresne et al. 2007; Mackay and Goldsworthy 2017; Stockin et al. 2009; Thompson et al. 2013). However, management units are currently based on Australia and Aotearoa New Zealand having separate populations (Barceló et al. 2021). Given recent declines of common dolphins observed internationally (e.g., in the Mediterranean Sea; Bearzi et al. 2003; Piroddi et al. 2011; Vella et al. 2021), careful management based on a fuller understanding of the reproductive biology of male common dolphins on both sides of the Tasman Sea is required to ensure long-term viability of the species in this region. As male life history is comparatively less described (Chivers 2009), this study will complement recently published data on female common dolphin reproductive parameters (Palmer et al. 2022), offering population level insights to common dolphins in Aotearoa New Zealand waters.

3.2.1 Study aims and objectives

In this chapter, the reproductive biology of male common dolphins in Aotearoa New Zealand waters was assessed using histological examination of testicular tissue and a set of testicular measures (combined testes length, combined testes weight, an index of testicular development and mean seminiferous tubule diameter). Specifically, these testicular parameters were used to examine (1) how testis characteristics change with age, body length and sexual maturity, (2) the average age and length at attainment of sexual maturity, (3) potential indicators of sexual maturity, and (4) evidence of reproductive seasonality in mature males.

3.3 Materials and Methods

3.3.1 Sample collection

Reproductive data were collected and assessed post-mortem in 64 male common dolphins following Geraci and Lounsbury (2005). The sample size included 56 individuals (54 independent events) that either live-stranded or were found beachcast on the Aotearoa New Zealand coastline between 1999 and 2020. Additionally, six individuals incidentally captured within the commercial fishery for jack mackerel (*Trachurus novaezelandiae*) off the west coast of the North Island between 2001 and 2003 were included (Figure 3.1). The origin of a further two males remain unknown.

Testes and associated epididymides were removed and the testes weighed without the associated epididymis to the nearest 0.1 g. Measurements of the length of each testis were taken to the nearest 0.1 cm. Small samples (approx. 1 cm^3) were subsequently dissected from each testis and epididymis and fixed in 10% neutral buffered formalin. Total body length (TBL) was measured to the nearest 0.5 cm. Teeth were carefully extracted for age determination following methods outlined in Murphy et al. (2014). Decomposition state was further noted for each individual (*fresh*, *mild*, or *moderate*) as per Stockin et al. (2007).

3.3.2 Age estimation

Age was estimated by examining decalcified, stained thin sections of tooth from an individual (Murphy et al. 2014). Annual growth layer groups (GLGs) in the dentine were counted as described by Lockyer (1995) and Myrick Jr et al. (1983). This process is explained in depth in Chapter 2.

3.3.3 Histological assessment of reproductive organs

Stages of sexual maturity were determined by histological examination of testicular tissue (Betty et al. 2019; Murphy et al. 2005). Testicular tissue was processed using standard histological techniques, i.e., by dehydration, clearing and embedding in paraffin wax. Tissues were sectioned at 5 µm, stained with H&E (haematoxylin and eosin), and mounted on glass slides. Histological slides were examined microscopically (100x – 400x), and the stage of sexual maturity was determined via assessment of all seminiferous tubules in approximately 1 cm^2 section of the testicular tissue. Parameters used to assess sexual maturity included the mean diameter of seminiferous tubules (mean DT), the relative proportion of Sertoli cells, interstitial tissue, germinal cells (spermatogonia, spermatocytes, spermatids, and spermatozoa), the activity in the epididymis, and the presence and proportion of spermatozoa in the epididymis (Murphy 2004; Murphy et al. 2005).

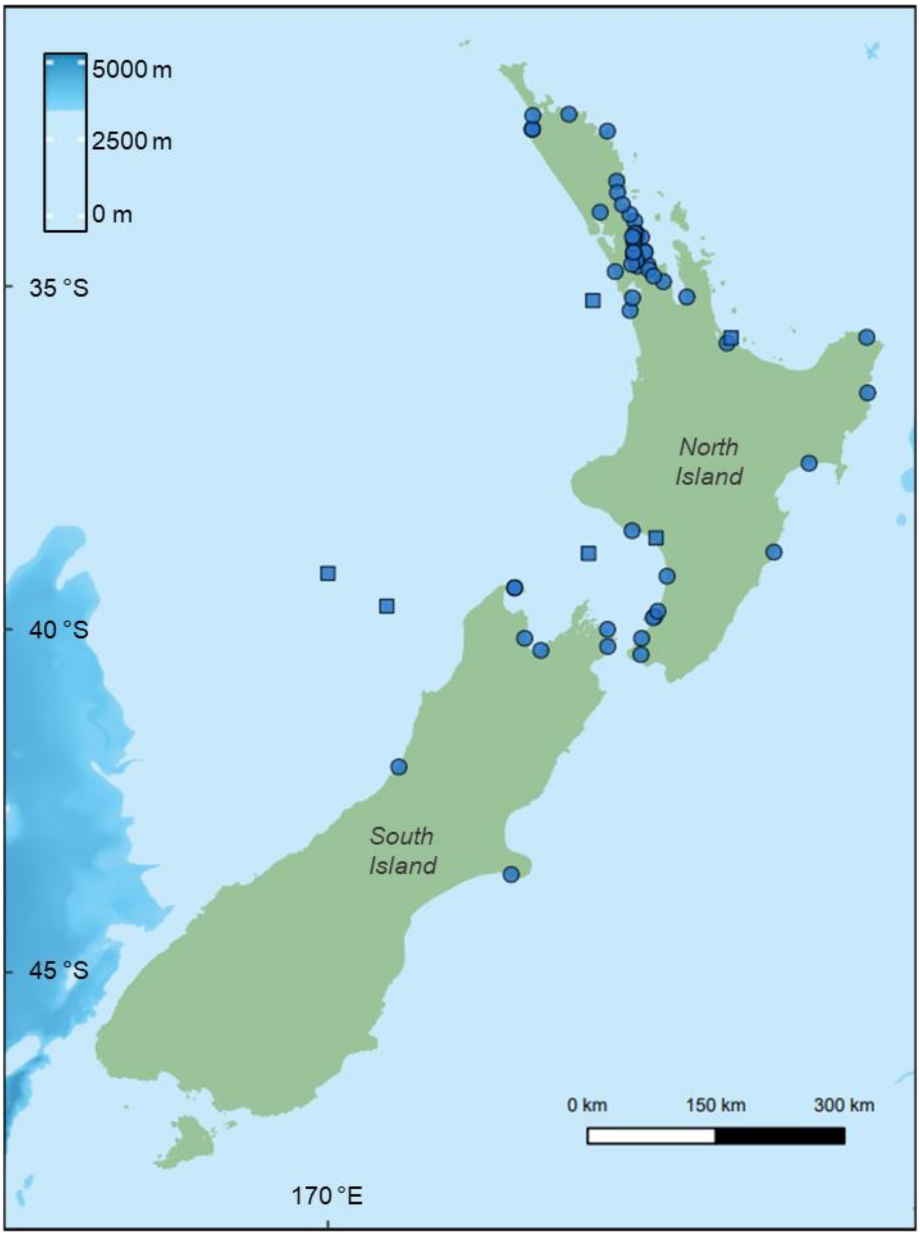


Figure 3.1. Location of male common dolphin (*Delphinus delphis*) stranding (blue circles) and bycatch (blue squares) events around Aotearoa New Zealand (1995-2020), from which male reproductive samples were collected for this study (*n* = 62).

Neimanis (1996) suggested that in slightly autolysed tissue, the basement membrane may detach from the seminiferous epithelium in some areas, but this would not significantly change the diameter measurements of the tubules in comparison to fresh tissue. Therefore, a mean diameter of the seminiferous tubules was taken by measuring the basement membranes of 10 tubule cross-sections. These measurements were collected from images taken using Axiocam 105 with associated Zeiss software (Zeiss 2013) and ImageJ, an image analysis system (Schneider et al. 2012). Only clear circular tubules were measured to ensure an accurate cross-section of the longitudinal axis were taken, in accordance with other cetacean reproductive studies (Betty et al. 2019; O'Hara et al. 2002; Neimanis et al. 2000). If the tissue was observed to be in a state of moderate or advanced autolysis, measurements were not taken as the basement membrane could not be clearly distinguished.

Males were classified into three maturity stages: immature, pubescent, and mature (Kemper et al. 2014; Murphy et al. 2005). Maturity stages were based on the presence and proportion of cell types in the seminiferous tubules, as follows: immature individuals had only Sertoli cells and spermatogonia present; pubescent individuals had both spermatogonia and spermatocytes present; mature individuals had all stages of spermatogenesis present in the tubules (including spermatids and spermatozoa).

3.3.4 Statistical analysis

3.3.4.1 Models of maturity status given length, age and testicular measurements

A dataset of six individual-level variables was compiled for 35 males, including two demographic variables (age and TBL) and four testicular variables (combined testes length, combined testes weight, index of testicular development, and mean seminiferous tubule diameter). The index of testicular development was calculated as the combined testes weight in grams (excluding epididymis) divided by the combined testes length in millimetres (Hohn et al. 1985). Relationships among these six variables were explored using charts and Spearman's rank correlation coefficients. The index variable was log-transformed as it was found to be a better predictor of sexual maturity than its raw form.

The average age (ASM) and length (LSM) at attainment of sexual maturity were estimated for male common dolphins using two methods: (1) Bayesian modelling as detailed hereafter, and (2) the sum-of-fraction of immature (SOFI) method (Hohn 1989, Equation 3A in Appendices).

Progression through the maturity stages (immature, pubescent, mature) was modelled with Bayesian cumulative logit models fitted with the 'brms' package for R (Bürkner 2017). To compare the utility of each of the individual-level variables to predict maturity stage, each variable was used as the single predictor variable (x) in turn. Maturity stage (Y) was treated as an ordinal variable with three categories (immature, pubescent and mature) represented as k = {1, 2, 3}, respectively. The probability of a male being in stage k or below ($\pi_k = P(Y \leq k)$) was modelled as:

$$\log\left(\frac{\pi_k}{1-\pi_k}\right) = \alpha_k - \beta x_i$$

for k = 1, 2; $\pi_3 = 1 - \pi_2$. For all three parameters (α_1, α_2, and β), weakly informative prior distributions (Student's $t(3, 0, 10)$) were assumed. To estimate x_{50}, the value of x at which 50% of males were classified as mature, the posterior distribution of α_2/β was used. The posterior distribution was then summarised using the mean and 95% credible intervals ('CrI'; based on 2.5% and 97.5% percentiles).

3.3.4.2 Comparison of models

The relative utility of the demographic and testicular variables as indicators of maturity in the cumulative logic models was compared using the Bayesian LOO (Leave-One-Out) estimate of the expected log pointwise predictive density (using the 'elpd_loo' package for R; Vehtari et al. (2017)). ELPD-LOO is a criterion used to estimate out-of-sample predictive accuracy – that is, how accurately a model will predict new data that were not used in the fitting of the model (Vehtari et al. 2017). ELPD-LOO scores are used to compare models fit to the same dataset (Vehtari et al. 2017). In our case, not all individuals had data for all six variables available (due to tissue quality) and so only 35 complete cases were available for comparing all the fitted models with ELPD-LOO. There was only one case of a 'pubescent' male in the 'complete' dataset, so this case was excluded from the comparison of the models. Thus a dataset of 34 complete cases was used for comparisons and the pubescent category was omitted. For the more specific comparison of the models with age and TBL as predictor variables, a larger data set was used (*n* = 52), with all the complete cases for these two predictor variables. Two models were fitted to each of the four testicular variables (combined testes weight, combined testes length, index of testicular development, mean diameter of the seminiferous tubules) as these variables had skewed distributions. One of the models used the raw values (x) and the other used the log-transformed values (log x). These models were compared based on the ELPD-LOO criterion, which indicated that the log-transformed variables were a better fit. Therefore, the models that use the log-transformed testicular variables are presented.

3.3.4.3 Quantifying reproductive seasonality

To assess potential reproductive seasonality in mature males, the variation in mean diameter of seminiferous tubules and combined testes weight between seasons, and across the year (using Julian dates), was tested using Kruskal-Wallis and randomisation tests. Due to the small sample size, males were grouped into austral seasons instead of months following Murphy et al. (2005) and Westgate and Read (2007). Austral seasons were defined as summer (December to February), autumn (March to May), winter (June to August) and spring (September to November). Differences between combined testes weight and mean seminiferous tubule diameter among seasons were assessed with t-tests. The testicular and seasonality data were first tested for normality using Shapiro-Wilk tests.

All statistical analyses were conducted using R version 2021.4.1.1 (R Development Core Team 2021).

3.4 Results

3.4.1 Stages of sexual maturation

Of the 64 males assessed, 37 (58%) and 24 (38%) were classified as immature and mature, respectively. A further 3 (5%) were classified as pubescent (Table 3.1). From the sample set, 18 individuals had missing data and/or testicular tissue too autolysed to assess testicular features such as seminiferous tubule measurements. Histological appearances of immature, pubescent and mature testis and epididymis are shown in Figure 3.2 and described herein.

Table 3.1. Mean (±SE), range and number of samples obtained for each variable (TBL, age, combined testes weight, combined testes length, an index of testicular development [index], and seminiferous tubule diameter) at each stage of male sexual maturation (immature, pubescent, mature) for common dolphins (*Delphinus delphis*) examined in the study (1999–2020).

Stages	*n*	TBL (cm)	Age (years)	Combined testes weight (g)	Combined testes length (mm)	Log_index (g/mm)	Seminiferous tubule diameter (µm)
Immature	37	145 (±6) 89–200 (*n* = 36)	2.9 (±0.4) 0–9 (*n* = 30)	15.3 (±2.6) 2–57.8 (*n* = 35)	143.5 (±8.0) 27–274 (*n* = 35)	0.1 (±0.0) 0.02–0.74 (*n* = 34)	17.3 (±0.9) 10.46–27.93 (*n* = 24)
Pubescent	3	207 (±6) 201–220 (*n* = 3)	9.5 (±0.5) 9–10 (*n* = 2)	209 (±74) 135–283 (*n* = 2)	373.5 (±55.5) 318–429 (*n* = 2)	0.5 (±0.1) 0.42–0.66 (*n* = 2)	57.6 (±4.9) 52.68–62.45 (*n* = 2)
Mature	24	215 (±3) 190–241 (*n* = 23)	14.4 (±1.0) 7.5–26 (*n* = 21)	1921.2 (±294.4) 492–5796.5 (*n* = 24)	666.8 (±34.2) 275–965 (*n* = 23)	2.7 (±0.4) 0.88–7.05 (*n* = 23)	92.0 (±8.2) 51.13–165.53 (*n* = 19)
Total	64	173.4 (±5) 89–241 (*n* = 63)	7.7 (±0.9) 0–26 (*n* = 53)	771.5 (±165.5) 2–5796.5 (*n* = 61)	351.8 (±35.6) 27–965 (*n* = 60)	1.1 (±0.2) 0.02–7.05 (*n* = 59)	50.6 (±6.5) 10.46–165.53 (*n* = 45)

Immature testes (Figure 3.2a, b, *n* = 37) had seminiferous tubules that were narrow ($\bar{x}$ = 17.3 ± 0.9 µm; range 10.5–27.9), tightly arranged, and embedded in abundant interstitial tissue. Enclosed by the basement membrane were one or two layers of two types of cells: the supportive Sertoli cells and spermatogonia (germinal cells). These cells were undergoing mitosis and neatly aligned the edges of the tubules. The epididymis was empty and exhibited a resting epithelium, indicating that it was undeveloped. In immature testes (and epididymides), no spermatocytes, spermatids or spermatozoa were observed.

Pubescent testes (Figure 3.2c, d, *n* = 3) contained medium-sized seminiferous tubules (x̄ = 57.8 ± 4.9 µm; range 52.7–62.5), with spermatogonia and spermatocytes present. A reduction in interstitial tissue and Sertoli cells was noted. Zonation of the spermatogonia and spermatocytes was evident as spermatogonia were undergoing meiosis to produce spermatocytes. No spermatozoa were present in the epididymis.

Mature testes (Figure 3.2e, f, *n* = 24) contained large seminiferous tubules with a mean diameter of 92.0 ± 8.2 µm (range 51.1–165.5). 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 noted. Spermatozoa were present in the lumen of the tubules and the epididymis, and the epididymis was enlarged.

3.4.2 Models of maturity status given with demographic variables

Males ranged from 89 to 241 cm in TBL (*n* = 62; two individuals were excluded due to missing TBL data), with a modal size class of 211 to 220 cm (median = 178 cm; Figure 3.3a). The estimated age of male common dolphins ranged from 0 to 26 years (*n* = 55), with two males (KS08-11Dd and KS18-01Dd) only having minimum ages estimated. Of the males that had sexual maturity stage determined, 82% (*n* = 40) of individuals were aged less than 15 years. Immature males ranged from 89 to 200 cm in length and 0 to 9 years in age. Pubescent males ranged from 201 to 220 cm in length and 9 to 10 years in age. Mature males ranged from 190 to 241 cm in length and 7.5 to 26 years in age. Age and TBL increased with maturity stage (Table 3.1 and Figure 3.3), though some overlap between age 8 and 9 years, and 195 cm and 199 cm were evident.

Bayesian modelling estimated the ASM and LSM to be 8.8 years (95% CrI = 7.8–9.8, *n* = 51) and 198.3 cm (95% CrI = 191.4–204.9, *n* = 61; Table 3.2 and Figure 3.5), respectively. Model comparison based on ELPD_LOO scores for the dataset with both age and length (*n* = 34) provided little statistical support for a difference between the utility of age and TBL as indicators of maturity stage, given the difference in ELPD_LOO scores (1.31) was less than the respective standard errors (SE = 3.68 and 3.19). Using the larger 'age vs TBL' dataset (*n* = 52), the ELPD_LOO score for the model with age was 2.2 units greater than that of the model using TBL, but the large standard error (SE = 4.1) once again indicated no evidence of one being a better predictor than the other. Applying the SOFI method for comparison across previously studied populations (Ferrero and Walker 1995; Murphy et al. 2005; Westgate and Read 2007), the ASM and LSM were estimated as 8.8 years (SE = 0.16, *n* = 11) and 200 cm (SE = 0.15, *n* = 13) respectively, where *n* is the number of individuals in the indeterminate age or length classes (i.e., age or length classes in which both immature and mature individuals occur in the sample).

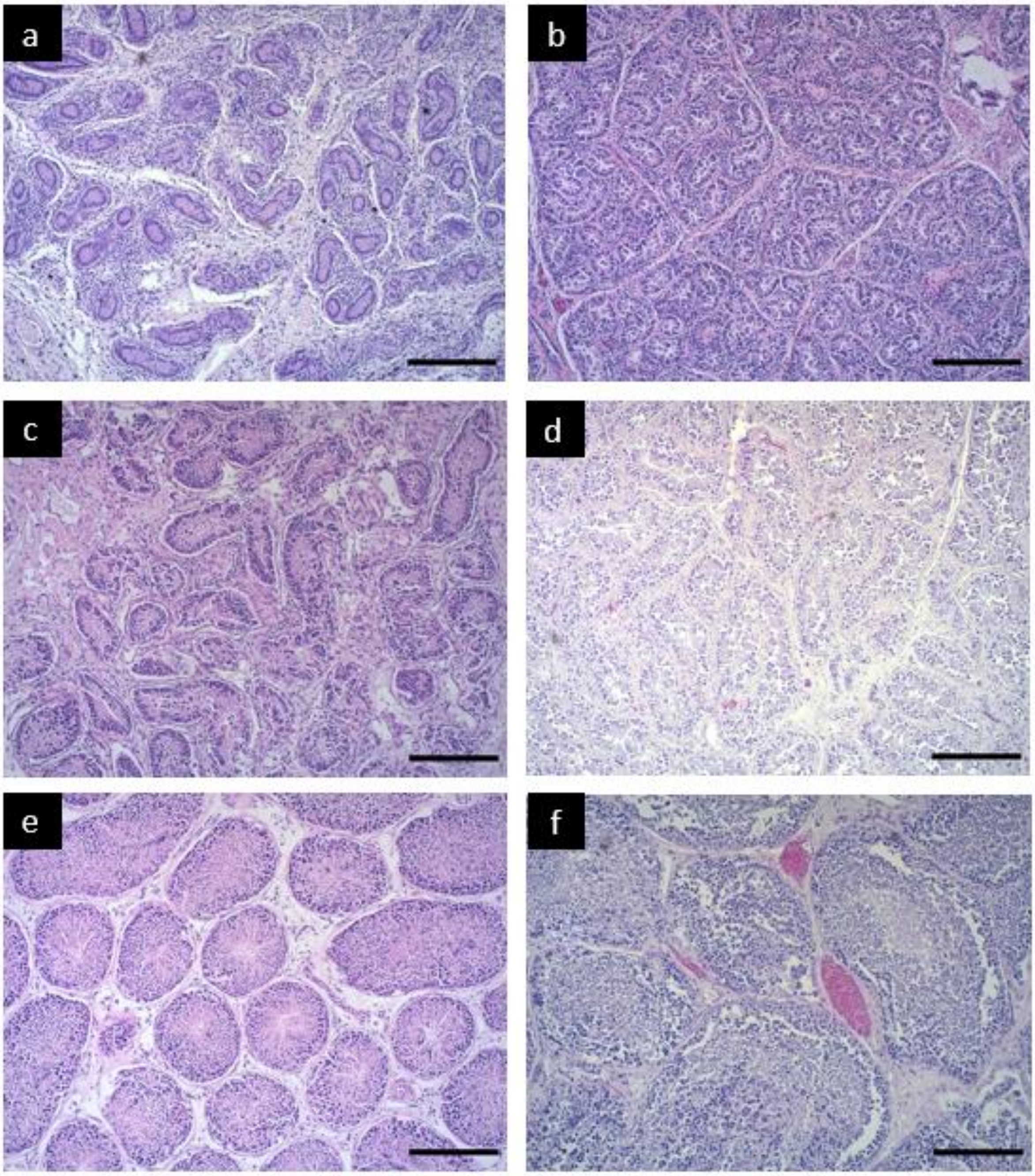
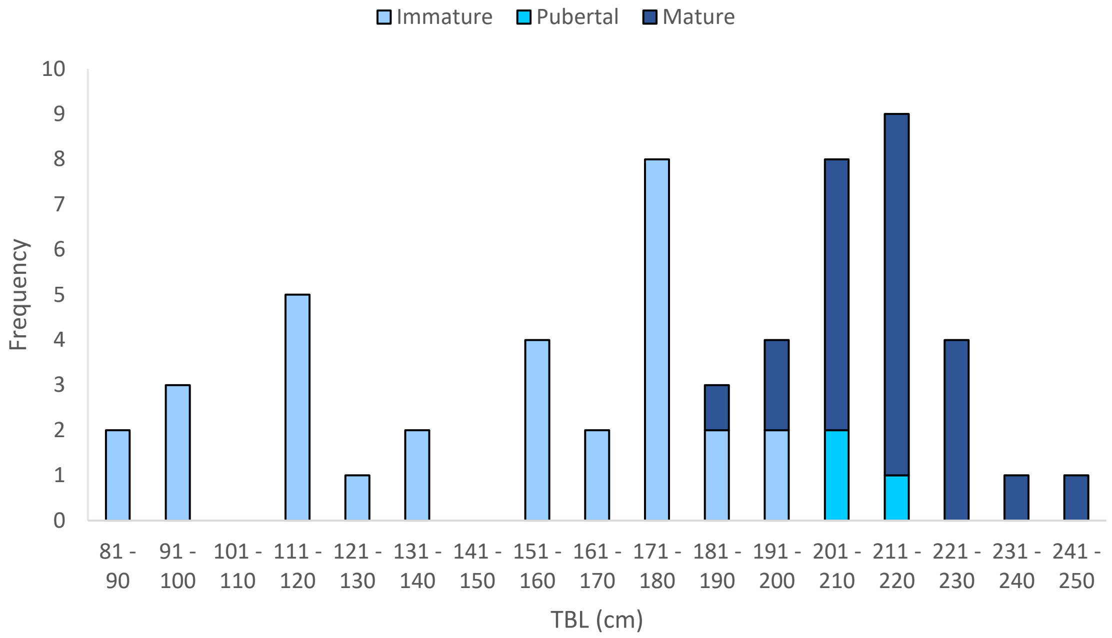
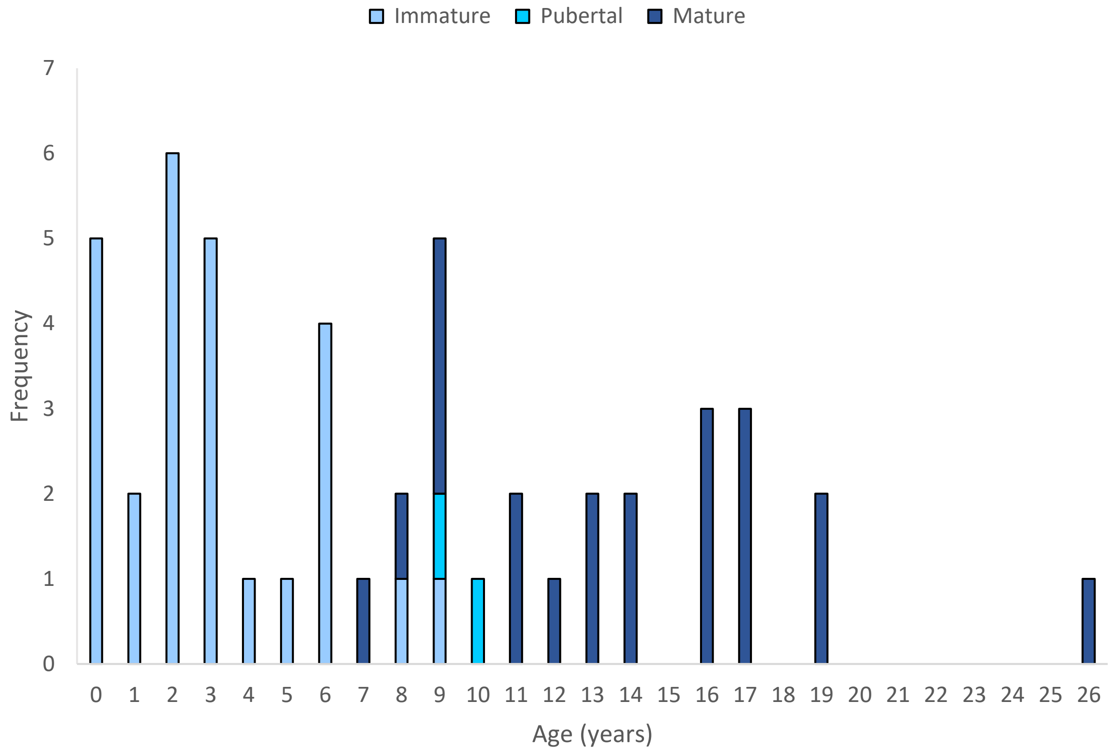


Figure 3.2. Histological appearance of immature, pubescent, and mature common dolphin (*Delphinus delphis*) testes examined from Aotearoa New Zealand waters (1999–2020). Shown are two individuals for each maturity stage and the scale bar is 100 µm. (a) KS14-63Dd; immature, TBL 95 cm, combined testes weight 3.1 g, mean seminiferous tubule diameter 18.95 µm, and (b) KS20-30Dd; immature, TBL 163 cm, combined testes weight 10 g, mean seminiferous tubule diameter 27.93 µm. (c) KS19-12Dd; pubescent, TBL 201 cm, combined testes weight 429 g, mean seminiferous tubule diameter 52.68 µm, and (d) KS10-78Dd; pubescent, TBL 201 cm, mean seminiferous tubule diameter 62.45 µm. (e) KS20-05Dd; adult, mature, TBL 210 cm, combined testes weight 1505 g, mean seminiferous tubule diameter 109.18 µm, and (f) KS17-01Dd; adult, mature, TBL 208 cm, combined testes weight 2430 g, mean seminiferous tubule diameter 165.53 µm



(a)



(b)

Figure 3.3. Frequency of distribution of each maturity stage at (a) TBL (*n* = 62) and (b) age (*n* = 55) for male common dolphins stranded and bycaught on the Aotearoa New Zealand coast between 1995 and 2020.

Table 3.2. Estimates of the age, total body length (TBL), combined testes weight, combined testes length, index of testicular development (index) and mean ($\bar{x}$) diameter of seminiferous tubules (mean DT) at the transition values for each case/estimate cutoffs for each model i.e., from immature to pubescent and pubescent to mature, for male common dolphins (*Delphinus delphis*) examined in Aotearoa New Zealand waters (1995–2020).

Indicator	*n*	Immature to Pubescent $\bar{x}$ (95%CrI)	Pubescent to Mature $\bar{x}$ (95%CrI)	ELPD_LOO (SE)
Age (years)	53	7.86 (6.74–8.91)	8.77 (7.81–9.84)	-6.28 (3.19)
TBL (cm)	63	190.80 (183.38–197.81)	198.33 (191.39–204.89)	-4.97 (3.68)
Combined testes weight (g)	61	88.44 (58.45–146.00)	301.62 (156.51–471.20)	-0.31 (0.10)
Combined testes length (mm)	60	279.77 (236.36–334.30)	351.38 (290.50–426.77)	-4.69 (3.15)
Index (g/mm)	59	0.83 (0.76–0.90)	0.92 (0.85–0.98)	-3.72 (3.08)
Mean DT (µm)	45	35.57 (27.54–45.52)	49.97 (40.62–58.26)	-1.08 (0.65)

Posterior distributions of model parameters were obtained using Bayesian cumulative logit regression based on all the data available for each measure in turn. Estimates presented here are summarised with means and 95-percentile credible intervals (CrI) of the posterior distributions of model parameters credible intervals. CrI = credible interval; ELPD_LOO = Expected Log Predictive Density_Leave-One-Out (all variables together; n = 34); SE = standard error.

3.4.3 Models of maturity status given with testicular variables

Testicular variables (combined testes weight, combined testes length, index of testicular development, and mean seminiferous tubule diameter) for immature, pubescent and mature male common dolphins are summarised in Table 3.1. The testicular and demographic variables were all highly correlated with each other (Figure 3.5). A general pattern of increasing size with maturity stages was observed with testicular variables, though some overlap between the stages was evident (Table 3.1, Figure 3.4). A significant difference ($p < 0.001$) between the combined testes weight of immature (x̄ ± SE: 15.3 ± 2.6 g) versus mature (x̄ ± SE: 1921.2 ± 294.4 g) individuals was detected. A similar difference ($p < 0.001$) was further observed in the mean seminiferous tubule diameter between immature (x̄ ± SE: 17.3 ± 0.9 µm) and mature (x̄ ± SE: 92.0 ± 8.2 µm) males.

Combined testes weight and length were both larger in sexually mature animals (8.8 years of age, 198.3 cm TBL). However, significant variation in combined testes weight (492–5796 g) and combined testes length (275–965 mm) remained evident in mature males (Figure 3.4). A steep increase in the mean seminiferous tubule diameter was further observed at approximately 190–200 cm TBL and 8–

10 years of age (Figure 3.4). An estimated 50% of males had reached sexual maturity at 351.38 mm combined testes length, 301.62 g combined testes weight, 0.92 index of testicular development, and 49.97 µm seminiferous tubule diameter (Table 3.2, Figure 3.5). Comparison of the modelled variables with ELPD_LOO indicated that combined testes weight (g) was the best indicator of sexual maturity (Table 3.2). All testicular variables were better predictors of sexual maturity than age or TBL.

3.4.4 Reproductive seasonality

Mean combined testes weight (g) differed among seasons, indicating reproductive seasonality (Kruskal-Wallis test, $p \leq 0.01$). The greatest and smallest combined testes weights were recorded in austral summer (December to February, $\bar{x}$ ± SE: 8923 ± 378 g), and winter (June to August, $\bar{x}$ ± SE: 710 ± 505 g; Figure 3.6b), respectively. This aligns with the higher combined testes weights recorded at the start (Julian date 0–50) and end (Julian date 300–365) of the year (Figure 3.6a). Significant differences in combined testes weight between seasons ($p = 0.025$) were observed. However, no difference in mean tubule diameter was noted between seasons (Kruskal-Wallis test, $p = 0.106$, Figure 3.6c and 3.6d).

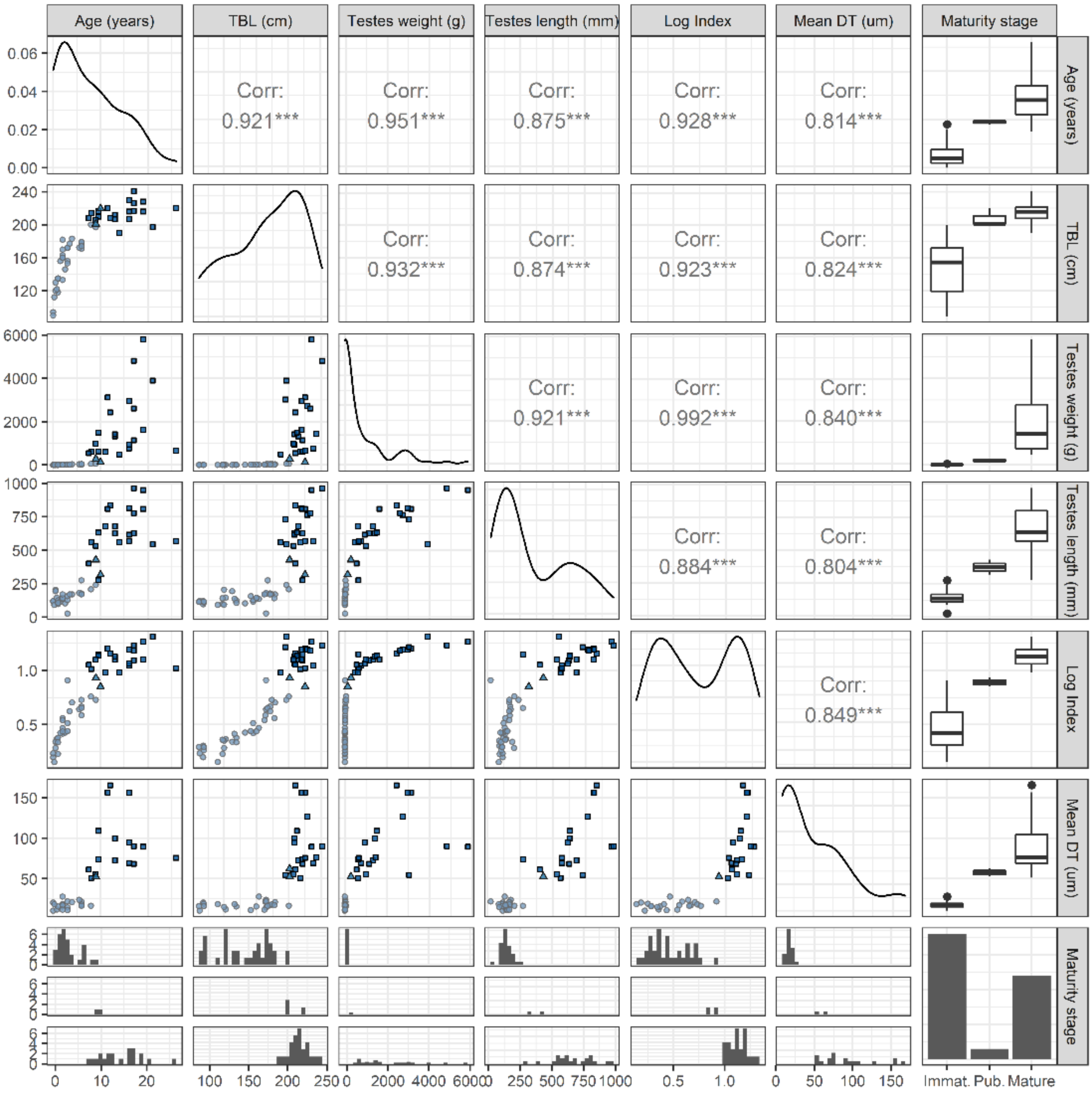


Figure 3.4. Demographic variables (age and TBL) versus testicular variables (combined testes length [age: n = 52, TBL: n = 59], combined testes weight [age: n = 52, TBL; n = 60], log of index of testicular development [age: n = 51, TBL: n = 58] and mean diameter of seminiferous tubules [mean DT; age: n = 37, TBL: n = 45]) for male common dolphins (*Delphinus delphis*) examined in Aotearoa New Zealand waters (1995–2020).

Note: All variables, demographic and testicular, were highly positively correlated (Spearman’s rank correlation coefficients). The type and colour of the data points represent the individuals’ sexual maturity stage: immature = light blue circle, pubescent = medium blue triangle, mature = dark blue square. The index of testicular development was log-transformed as it was a better predictor in that form.

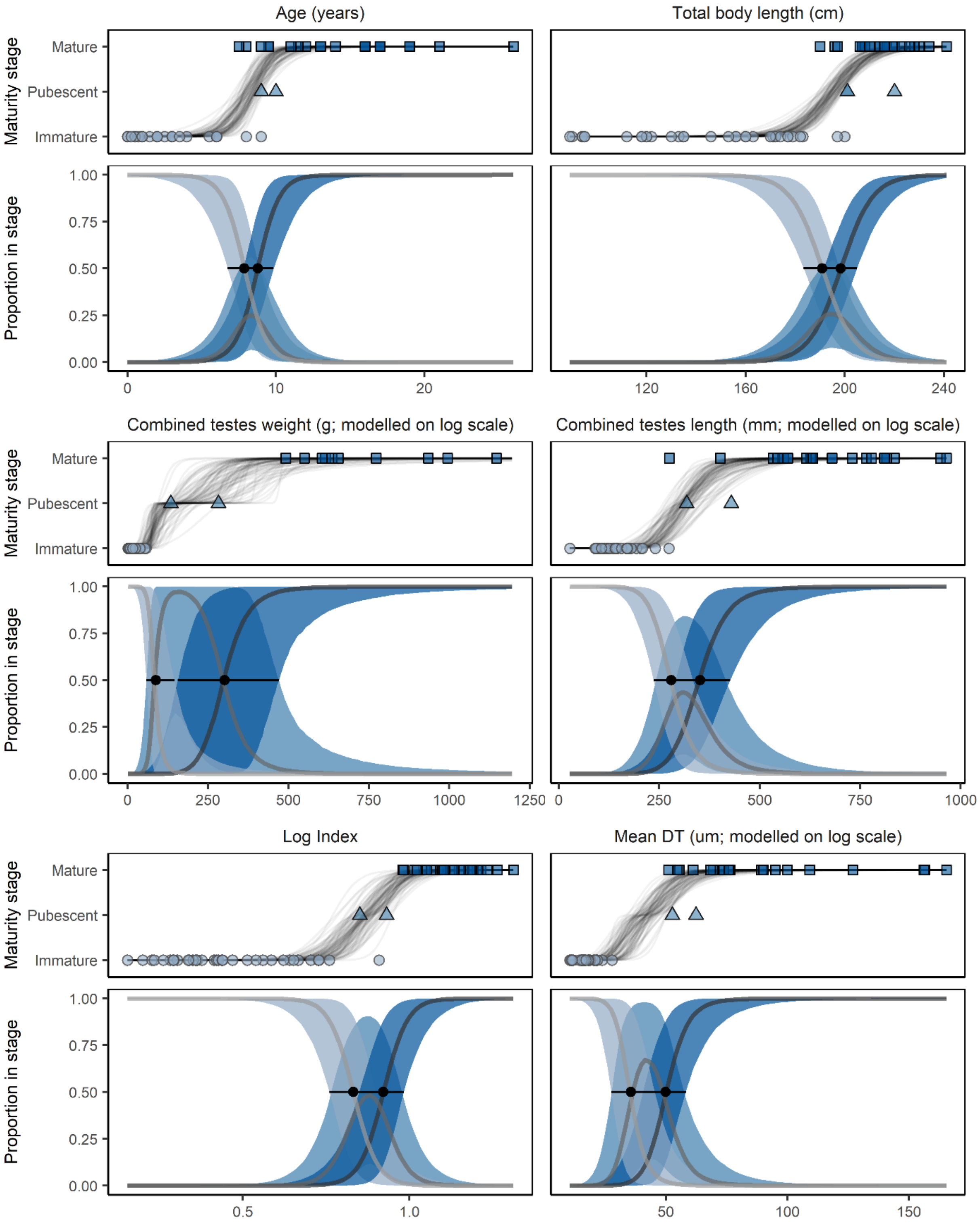


Figure 3.5. Bayesian cumulative logit regression of the sexual maturation of male common dolphins (*Delphinus delphis*) examined in Aotearoa New Zealand waters (1995–2020) through three stages (immature, pubescent and mature) modelled as a function of one of six individual measures: age, total body length, combined testes weight, combined testes length, index of testicular development (combined testes weight/combined testes length), and mean seminiferous tubule diameter (mean DT).

Each measure has two plots shown. The upper plot shows each maturity stage and the data values for the measure within each stage. The lines on the plot represent the posterior predictions of the transitions through stages. The lower plot shows the probability of being in each of the three stages where an increase in maturity stage is shown by lighter to darker lines and intervals, which track left to right. The thick lines show the estimated mean and the 95% credible intervals. The black points show the mean, and the thin horizontal lines show the 95% credible intervals of the estimated value of x. This is the point at which 50% of males were classified as pubescent (left point and line) and mature (right point and line). The measures for age and TBL on the x-axis are shown on the raw scale but the models were fitted to log-transformed testicular variables, as indicated.

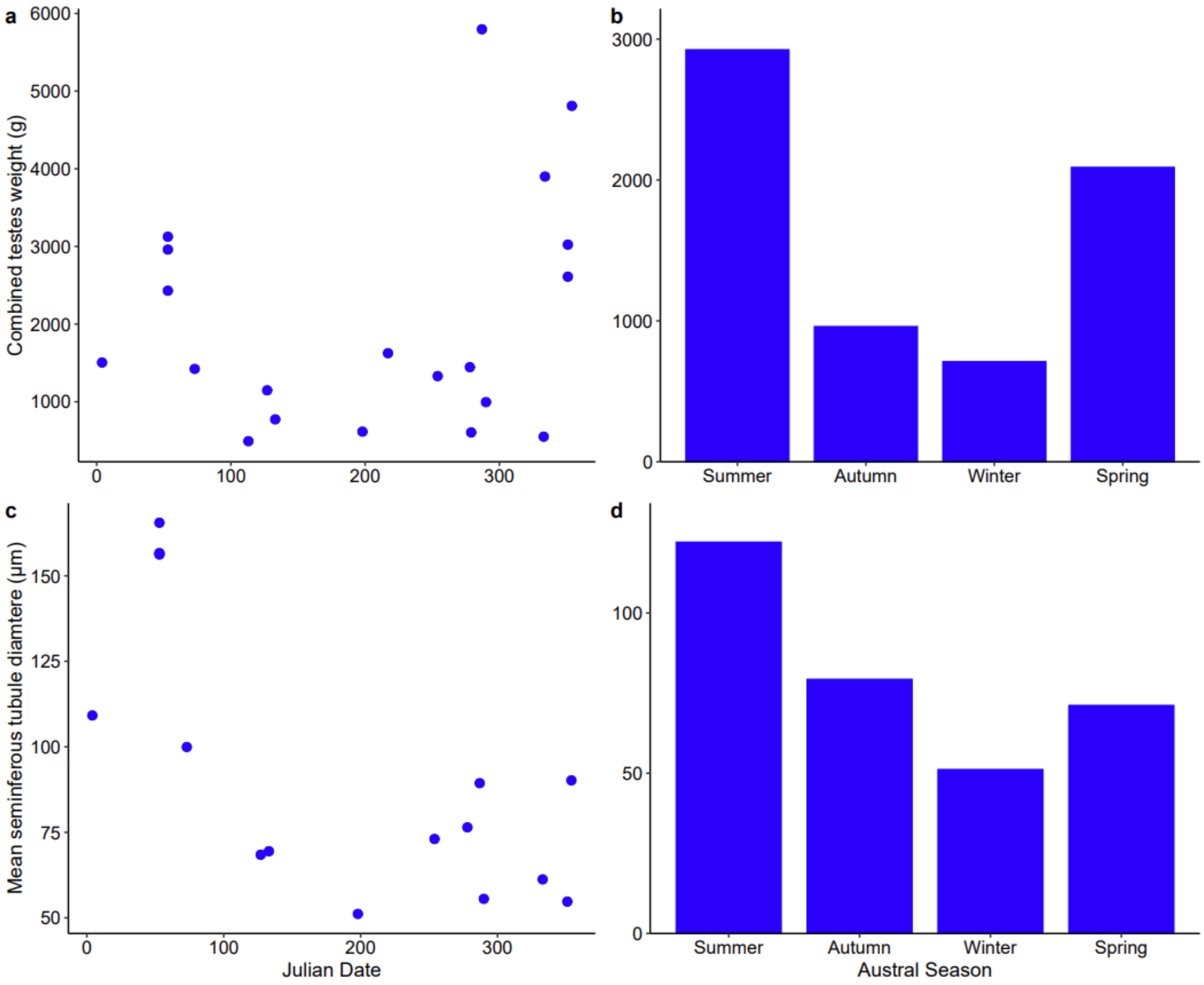


Figure 3.6. Annual variation in (a) combined testes weight (g) vs. Julian date (n = 20) and (c) mean seminiferous tubule diameter (µm) vs. Julian date (n = 15) and seasonal variation in (b) combined testes weight (g, n = 20) and (d) mean seminiferous tubule diameter (µm, n = 15) of mature male common dolphins (*Delphinus delphis*) examined in Aotearoa New Zealand waters between 1995 and 2020.

3.5 Discussion

3.5.1 Stages of sexual maturation

This study examined the reproductive biology of 64 male common dolphins, including both stranded and bycaught individuals. This allowed comparison with prior international studies of male reproduction in common dolphin populations (Table 3B in Appendices) in both the eastern (*n* = 212, Murphy et al. 2005) and western (*n* = 161, Westgate and Read 2007) North Atlantic, and the western South Atlantic (*n* = 54, Grandi et al. 2022). Only three male common dolphins examined in our study were classified as pubescent, with just one having all demographic and testicular variables required for inclusion in Bayesian modelling.

3.5.2 Comparison of predictors of sexual maturity

For common dolphins, the sexual maturity status, assessed via histological examination, was strongly related to both the demographic variables (age and TBL) and testicular measurements. In particular, sexual maturity is characterised by a rapid increase in the size of the testis and seminiferous tubules (Murphy et al. 2005; Westgate and Read 2007; this study). This has been observed in other delphinid species such as bottlenose dolphins (*Tursiops aduncus* and *Tursiops truncatus*; Kasuya et al. 1997; Kemper et al. 2014) and pilot whales (*Globicephala melas edwardii*; Betty et al. 2019). The best predictor of sexual maturity in Aotearoa New Zealand common dolphins was combined testes weight, which aligns with international studies (Murphy et al. 2005; Westgate and Read 2007). However, there was substantial overlap in the testicular and demographic variables among the maturity stages, likely due to variation in the maturation process among individuals (Betty et al. 2019; Kemper et al. 2014; Murphy et al. 2005).

The demographic variables, age and TBL, were useful predictors of sexual maturity although they were not as accurate as the testicular variables (Figure 3.5). This has important management implications, as TBL is the easiest and most accessible parameter to collect in the field. Therefore, when post-mortem examinations cannot be undertaken, precise linear measurements of TBL are useful. Additionally, the usefulness of both demographic and testicular variables may change with a larger dataset.

Several challenges come with assessing sexual maturity via histological examination of testicular tissue. For example, testicular tissue of odontocetes is susceptible to rapid post-mortem autolysis (Betty et al. 2019; Kemper et al. 2014; Laws 1961) and can be further impacted by freeze-thaw artefacts, which are known to affect histological quality (Schäfer and Kaufmann 1999). In the present study, the testes of some dolphins (*n* = 22) were frozen prior to fixation while others were fixed fresh (*n* = 23). Such challenges can be mitigated by the exploration of alternative methods to assess sexual maturity in males. For example, blubber testosterone methods, from biopsy samples, can be assessed in live, free-ranging animals and takes away the need to rely on testicular tissue (Kellar et al. 2009). Like any method of data collection, there are still advantages and disadvantages to these alternative methods. Other distinguishing features, such as the prominent postanal hump, have been used in real time (in the field) or retrospectively (via photo-ID) to identify mature male common dolphins (Heyning and Perrin 1994; Murphy 2004; Neumann et al. 2002; Ngqulana et al. 2017).

3.5.3 Attainment of sexual maturity

Male common dolphins in Aotearoa New Zealand waters attain sexual maturity at an average body length (TBL) of 198.3 cm (*n* = 61) as estimated by the logistic regression method (or 200 cm, *n* = 11, as estimated using the SOFI method). These estimates are comparable to previous studies of male common dolphins (Table 3B in Appendices). In the eastern North Atlantic, sexual maturity is attained between approximately 200 (Collet and Saint-Girons 1984; Murphy et al. 2005) and 204 cm (Read et al. 2019). This also aligns with the eastern tropical Pacific where males are estimated to attain sexual maturity at approximately 202 cm (Gurevich and Stewart 1978; Oliver 1973). In the western North Atlantic, males are reported to attain sexual maturity at ca. 215 cm (Westgate 2005). In contrast, males from the North Pacific attain sexual maturity at ca. 182 cm (Ferrero and Walker 1995). This likely reflects males in the two populations having different asymptotic lengths (i.e., length at physical maturity). Males in the North Pacific attain physical maturity at 188 cm, whereas males in the western North Atlantic attain physical maturity at 221.5 cm. Asymptotic length is positively correlated with length at sexual maturity, meaning the larger the asymptotic length, the greater the total body length at sexual maturity (Stamps et al. 1998). In the western North Atlantic, immature and mature males overlap between 184 and 209 cm (Grandi et al. 2022).

The average age at attainment of sexual maturity in Aotearoa New Zealand common dolphins is 8.77 years (*n* = 51) as estimated by the logistic regression method (or 8.75 years, *n* = 13, as estimated using the SOFI method). This is the youngest reported ASM estimate for male common dolphins in any international population (Table 3B in Appendices). In the eastern North Atlantic (Irish and French dataset), males attain sexual maturity at 11.86 years (Murphy et al. 2005), and at approximately 10.5 years in North-West Spain (Read et al. 2019) and the North Pacific (Ferrero and Walker 1995). In the western North Atlantic, sexual maturity is attained at 9.45 years (Westgate and Read 2007). In Argentine waters, immature and mature males overlap in age between 6 and 9 years (Grandi et al. 2022). Due to a small sample size (*n* = 52), LSM and ASM estimates were not obtained for the western South Atlantic.

Geographic variation in attainment of sexual maturity can arise from differences in biological and/or environmental factors including habitat, diet composition, anthropogenic impacts, and population size and density (Alberts 2019; Barceló et al. 2022; Clutton-Brock and Sheldon 2010; Kemper et al. 2014; Murphy 2004). Interestingly, male common dolphins in Aotearoa New Zealand attain sexual maturity at a similar TBL to other populations, despite being at the younger end of reported ASM in international populations. Asymptotic length of males from Aotearoa New Zealand waters (212.1 cm; Chapter 2) aligns with asymptotic lengths for males in the eastern North Atlantic (211.6–214 cm; Murphy et al. 2005) and western South Atlantic (211 cm; Grandi et al. 2022). Additionally, Aotearoa New Zealand waters are relatively productive (Murphy et al. 2001), potentially providing abundant prey to support faster growth rates, assuming no disruption to the food web (Stockin et al. 2022; Stockin et al. 2023). There is no evidence, however, that male common dolphins in Aotearoa New Zealand have an expedited growth rate (Chapter 2) compared to other populations (Murphy et al. 2005; Westgate 2005).

Intra-specific competition for access to females may reflect the slightly older age at sexual maturity for males in comparison to females in Aotearoa New Zealand (Palmer et al. 2022; 2023). This longer stage of growth before sexual maturity could indicate sexual dimorphism within the population, as a larger size is more favourable for competition (Murphy et al. 2005; Read et al. 1993). Additionally, male common dolphins in Aotearoa New Zealand waters obtain sexual maturity at a marginally younger age compared to their international counterparts (Ferrero and Walker 1995; Murphy et al. 2005; Read et al. 2019; Westgate and Read 2007). This may indicate earlier allocation of resources to testicular mass and the postanal hump (Ngqulana et al. 2017). Such a strategy may reflect the mating system of common dolphins in Aotearoa New Zealand, where females mate with many males, inducing sperm competition (Murphy et al. 2005).

Alternative explanations for the younger ASM are methodological error and a small sample size. While aging cetaceans is not without error (Hohn 1989; Rosas et al. 2003), an underestimated ASM is unlikely in the current study due to strict quality controls and best practice applied (Murphy et al. 2014). Specifically, blind readings were made across multiple experienced readers, with no *a priori* biological knowledge of the individual. The sample size for this study is smaller compared to most other studies on male reproduction in common dolphins (e.g. Murphy et al. 2005) which may impact the parameters estimated here. The small sample size of this study is acknowledged yet it spans more than a quarter of a century, offering a baseline for which mortality effects on the populations' reproductive biology can be monitored. With increasing sample size, the aim is to establish whether the reproductive parameters reported here represent a natural baseline for the population and identify any temporal variation should it exist.

3.5.4 Reproductive seasonality

Reproductive seasonality was evident in Aotearoa New Zealand male common dolphins, with the largest combined testes weight observed in austral summer (2898.5 ± 464.2 g). Combined testes weight was, on average, three times heavier than in austral winter (710 ± 505 g). Fluctuations in combined testes weight across seasons aligned with testicular activity, which was also greatest in austral summer and lowest in austral winter. Similar patterns have been observed in Northern Hemisphere populations. For example, in the western North Atlantic the mean mass of regressed testes was 802.9 ± 455.5 g, compared to 4049.6 ± 1317.4 g for testes in full production (Westgate and Read 2007). The full production peak in the western North Atlantic was observed in July (boreal summer) and aligned with the female reproductive cycle for that region. Reproductive seasonality is also observed in the eastern North Atlantic common dolphin population. Spermatogenesis occurs throughout the year, with a marked increase in testicular activity and mass from late May to September. A more active period is reported in July and August, which aligns with the female reproductive cycle (Murphy et al. 2005; Murphy et al. 2009).

For males to maximise reproductive output, they align their reproductive cycle with females (Pomeroy 2011). Reproduction tends to also be associated with the availability of resources (Bronson 2009; Clapham 1996). Interestingly, seasonality is not so distinctly observed in females in Aotearoa New Zealand waters, which is more similar to common dolphins examined from the eastern tropical Pacific (Danil and Chivers 2007). For female common dolphins in Aotearoa New Zealand waters, breeding occurs year-round with slight peaks between August and November, which corresponds to late austral winter to late austral spring (Palmer et al. 2022). This does not align with testicular mass (which is associated with sperm production) of male common dolphins in Aotearoa New Zealand waters, which is greatest in austral summer. Common dolphins in Aotearoa New Zealand waters have been previously reported to copulate outside the ‘mating period’ (Neumann 2001b), which has been presumed to be recreational (Murphy et al. 2005). These previous observations could have been successful copulations as female common dolphins do not appear to have a defined mating period. Additionally, testicular activity occurs year-round, so there is the possibility that mating is still occurring successfully even though the male and female ‘peaks’ do not align in the Aotearoa New Zealand population.

3.5.5 Male mating strategy

Although male investment in reproductive tissues varies among delphinid species, there is a strong relationship between body mass and testes mass in cetaceans (MacLeod 2010). Delphinids exhibit one of the greatest investments in male reproductive tissues as well as having the largest testes relative to body size of all amniotes (MacLeod and MacLeod 2009). For example, the most investment is noted in dusky dolphins (*Lagenorhynchus obscurus*) where testicular tissue accounts for up to 8% of total body mass (Van Waerebeek and Read 1994). Common dolphins were ranked comparatively high among cetacean species for the relative investment in testicular tissue as they account for 3.2% of the total body mass in the species (Macleod 2010). Such high reproductive investment is also observed in male common dolphins in both the Northern Hemisphere (Murphy et al. 2005; Westgate and Read 2007) and Southern Hemisphere (this study; Plön et al. 2012). For common dolphins in the western North Atlantic the testes mass of sexually mature individuals is reported to vary between 2.3 and 4.4% of body weight (Westgate and Read 2007), and for males off South Africa on average testes account for 2% of total body weight (Plön et al. 2012). Sperm competition has been suggested as the primary driver of the large reproductive investment in male common dolphins (Dixson and Anderson 2004), but not the only factor (Kenagy and Trombulak 1986; MacLeod 2010). Common dolphins are considered to have a promiscuous mating system, which would support this large investment (Kelley et al. 2014; Ngqulana et al. 2017; Vella et al. 2021). Additionally, as postanal humps are positively correlated with testis size, it is thought they may act as a visual signal via mate choice by females and establishing dominance hierarchies among males (Lewis 1991; Murphy 2004; Murphy et al. 2005; Murphy and Rogan 2006; Neumann et al. 2002). Future research into how postanal humps are related to mating systems, maturity and growth is recommended for the Aotearoa New Zealand population.

3.6 Conclusions

This study provides first insights into the reproductive biology of male common dolphins in Aotearoa New Zealand waters. Knowledge of parameters such as ASM, LSM, reproductive seasonality and predictors of sexual maturity will aid better understanding of the long-term viability of this population and inform future management decisions. Specific information on the Australasian population is timely, since density-dependent changes may already be in play and, without prior baseline data, remain undetected. Reproductive parameters allow for early detection of population level changes, which is integral for effective species management and conservation. While support exists for a single Australasian population management plan due to the genetic structure of Aotearoa New Zealand and

Australian common dolphins, ongoing trans-Tasman collaboration is crucial to allow management of Australasian common dolphins to be effective.

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Chapter 4

Reproductive biology of female common dolphins (*Delphinus delphis*) in Aotearoa New Zealand waters

Mother and calf common dolphin in the Hauraki Gulf, Auckland.

This chapter is a reformatted version of the following manuscript:

Palmer EI, Betty EL, Murphy S, Perrott MR, Smith ANH, Stockin KA (2022) Reproductive biology of female common dolphins (*Delphinus delphis*) in New Zealand waters. Marine Biology 169. https://doi.org/10.1007/s00227-022-04139-3

4.1 Abstract

Reproductive biology was assessed in 106 female common dolphins (*Delphinus delphis*) examined post-mortem from stranding and bycatch events along the Aotearoa New Zealand coastline between 1997 and 2019. The average age (ASM) and length (LSM) at sexual maturity was estimated at 7.5 years and 183.5 cm, respectively. The total number of *corpora* in mature individuals increased with age and appeared to persist throughout life. Ovarian asymmetry was apparent, with the left ovary displaying higher rates of ovulation, with a maximum number of *corpora* of 19 recorded for a 24-year-old female. The estimated ovulation and annual pregnancy rates for mature females were 0.39 year^{-1} and 30%, respectively. Conception and calving occurred year-round, with a weak seasonal increase observed in late austral spring and early austral summer. As these data did not clearly show whether seasonality was present, the gestation, lactation and resting periods were calculated as either 12.6 or 12.8 months based on the presence/absence of seasonality, respectively. Similarly, calving interval ranged from 3.15 to 3.2 years, depending whether the seasonality was considered. The estimated LSM of the Aotearoa New Zealand population aligns with other populations globally, although the estimated ASM is younger by approximately 6 months. Other reproductive parameters align with Northern Hemisphere populations although demonstrate variation, which may reflect adaptations to local conditions such as water temperature and prey availability. As the species is subject to anthropogenic impacts including pollution and bycatch, it is suggested these findings be used as a baseline with which to monitor trends in population parameters.

4.2 Introduction

Robust estimates of reproductive parameters such as attainment of sexual maturity, gestation and lactation periods, annual pregnancy rates, and calving intervals are essential for effective conservation and management (Lanyon and Burgess 2014; Rossi et al. 2017), especially for declining populations (Botta et al. 2010). Differences in reproductive parameters, mating strategies and behaviour exist among cetacean species, and body size is reported to play a role in this variation (Fedak et al. 2002; González-Suárez and Revilla 2013). Females of small odontocete species, such as harbour porpoises (*Phocoena phocoena*), attain sexual maturity around 2–4 years (Kesselring et al. 2017; Learmonth et al. 2014; Murphy et al. 2020), whereas females of larger species, such as long-finned pilot whales (*Globicephala melas edwardii*), obtain sexual maturity at around 6–7 years of age (Betty 2019). In comparison, females of the largest odontocete species, sperm whales (*Physeter macrocephalus*), reach sexual maturity at approximately 9 years of age (Best et al. 1984).

Average age at attainment of sexual maturity (ASM) can vary across populations of the same species and within a population over time. Variation in ASM can reflect differences in reproductive potential and success and can therefore be used to identify populations at risk (Wade 2018). Annual pregnancy rate (APR) is another critical parameter when assessing the viability of populations, since it indicates the proportion of sexually mature females in the population likely to be pregnant at any given time. Like ASM, APR can vary markedly among species. Striped dolphins (*Stenella coeruleoalba*) off the southeast coast of southern Africa have an estimated APR of 26% (Bishop, 2014). In comparison, harbour porpoises across the Northern Hemisphere have APRs that range from 47–50% (Murphy et al. 2015) to 98% (Ólafsdóttir et al. 2003) depending on location and population. Variation in reproductive parameters within species may be driven by several factors including anthropogenic pressures and differences in habitat and availability of resources. For example, survival rates are influenced by the types and amounts of prey available. This in turn may influence the number of reproducing females, and the viability of their offspring, in a population (Wade 2018). In the case of the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), mortality rates of calves are higher in Adelaide, South Australia compared to other areas due to the intensity of anthropogenic impacts such as entanglement, pollution and boat strike (Steiner and Bossley 2008).

The reproductive biology of female common dolphins (*Delphinus delphis*) has been studied in a small number of populations in the Northern Hemisphere, especially in the North Atlantic (Murphy et al. 2009; Westgate and Read 2007) and eastern tropical Pacific (Danil and Chivers 2007). In contrast, there has been little examination of reproductive parameters in Southern Hemisphere populations, except for the western South Atlantic, off Argentina (Grandi et al. 2022). Notably, reproductive parameters remain unknown for female common dolphins in Oceania despite documented anthropogenic impacts including bycatch in commercial fisheries in this region (Abraham and Berkenbusch 2017; Barceló et al. 2021; Du Fresne et al. 2007; Goldsworth et al. 2019; Ministry for Primary Industries 2016). Recent genomic insights detailed by Barceló et al. (2021) suggest Aotearoa New Zealand and Australian common dolphin populations are substantially connected and should be considered a single fisheries management unit (Barceló et al. 2021). Monitoring trends in life history parameters of the management unit also allows for the monitoring of anthropogenic impacts. As there are no abundance estimates available for the whole management unit (Stockin and Orams 2009) and (annual) data on the total number of individuals bycaught within the unit is lacking, this is particularly important.

A common method of quantifying population viability is to calculate the maximum rate of increase (r_{max}, Dans et al. 2003; Mannocci et al. 2012). If the incidental mortality rate exceeds the rate of increase (r_{max}), then the population will decline (Dans et al. 2003). If abundance data are unavailable, then knowledge of key reproductive parameters is required to reliably estimate r_{max}. Our understanding of the viability of both the Aotearoa New Zealand and Australian populations of common dolphins is currently hindered by a lack of knowledge, which is concerning given the number of observed fisheries bycatch events in the region (Barceló et al. 2021; Parra et al. 2021; Fisheries New Zealand 2020; Thompson et al. 2013; Tulloch et al. 2020).

4.2.1 Study aims and objectives

Here, reproductive parameters for female common dolphins are estimated based on post-mortem data taken from stranded and bycaught female common dolphins in Aotearoa New Zealand waters. Specifically, the following parameters were addressed: (1) average age (ASM) and body length (LSM) at attainment of sexual maturity, (2) classification of reproductive status, (3) ovarian characteristics and persistence of scars, (4) gestation and lactation periods, (5) annual pregnancy rate, and (6) reproductive seasonality.

4.3 Materials and Methods

4.3.1 Sample collection

Reproductive data were collected post-mortem from a total of 106 female common dolphins following Geraci and Lounsbury (2005). The sample included 97 dolphins that had either live-stranded or were found beachcast during 75 independent events along the Aotearoa New Zealand coastline between 1997 and 2019. A further 9 bycaught dolphins from 7 incidental captures in the commercial jack mackerel (*Trachurus novaezelandiae*) fishery off the west coast of North Island of

Aotearoa New Zealand between 1999 and 2003 (Figure 4.1) were obtained. As this is an opportunistic dataset with a limited sample size, there is a possibility that the sample may not be fully representative of the population.

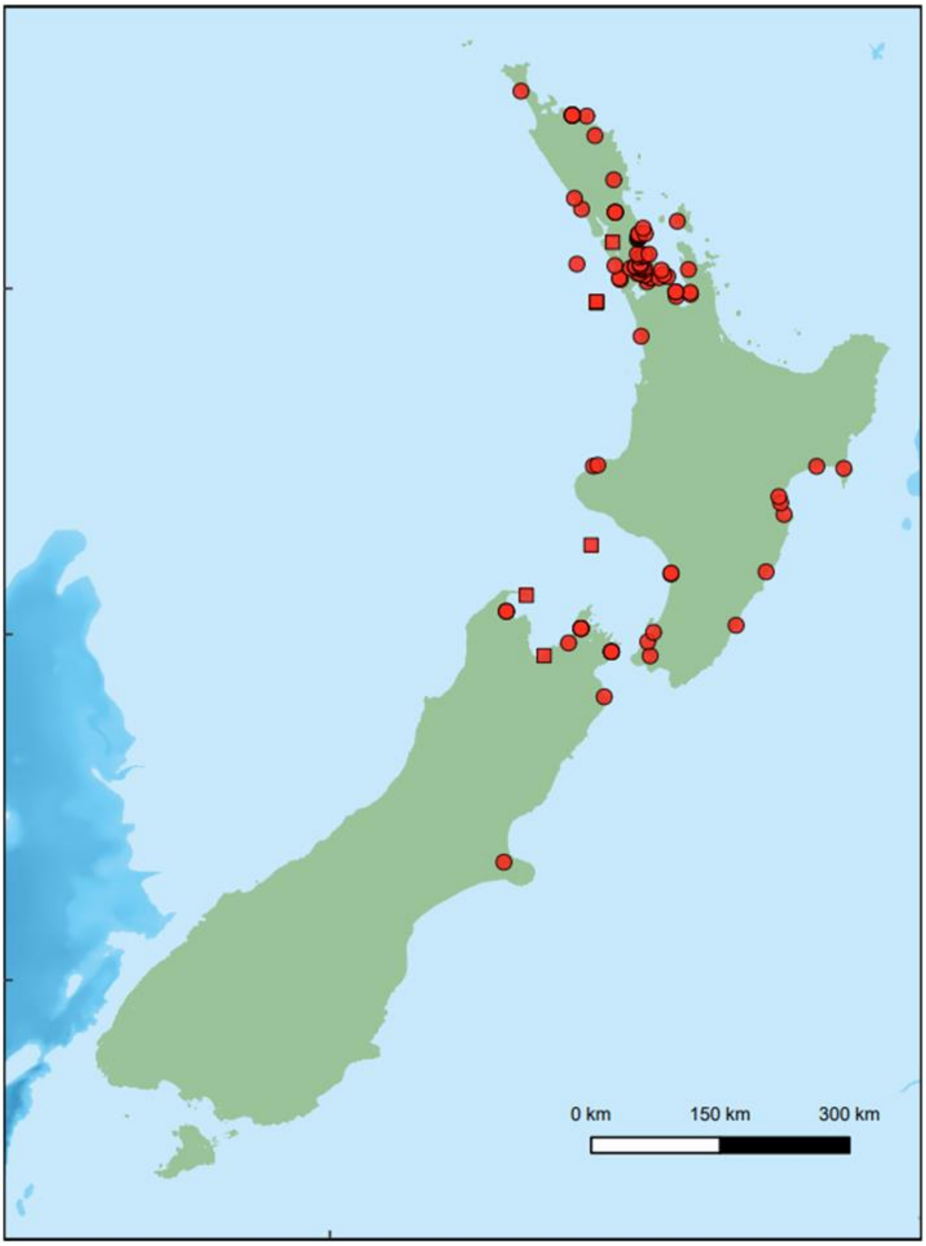


Figure 4.1. Location of common dolphin (*Delphinus delphis*) stranding (red circles) and bycatch (red squares) events around Aotearoa New Zealand (1997-2020), from which female reproductive samples were collected for this study (*n* = 101).

Ovaries and the associated reproductive tract were removed and examined grossly. Ovaries were initially examined for the presence of *corpora albicantia* (CAs) and *corpora lutea* (CLs), with photographs taken *in situ*. The ovaries were subsequently extracted from the reproductive tract and additional photographs were taken, with emphasis on scars or prominent ovarian features. Ovaries were weighed (g) and measured (mm) before being fixed in 10% neutral buffered formalin. A foetus in the uterus indicated a pregnancy. The foetus was then measured (crown to rump) to the nearest mm, weighed to the nearest g, photographed, and where possible sexed anatomically. The mammary glands were examined for evidence of lactation by pressing externally around the mammary slit and noting any fluid emission, and internally by cross-sectioning the gland and noting the presence of milk. Not all variables were measured from each carcass and so sample sizes vary.

Teeth were extracted and collected for age determination following methods summarised in Murphy et al. (2014). The straightest, least worn teeth were selected from the middle of the bottom jaw. Total body length (TBL) and associated morphometrics were measured to the nearest 0.5 cm. Decomposition state was noted for each individual (*fresh*, *mild*, or *moderate*) as per Stockin et al. (2007).

4.3.2 Age estimation

Age was estimated by examining decalcified, stained thin sections of teeth from each individual (Murphy et al. 2014) where annual growth layer groups (GLGs) in the dentine were counted as described by Lockyer (1995) and Myrick Jr et al. (1983). This process is outlined in depth in Chapter 2.

4.3.3 Reproductive status

Female reproductive status was determined through the assessment of ovaries, uteri and mammary glands, as outlined in Murphy et al. (2009). Females were considered sexually mature if there was at least one CA or CL present on the ovaries and/or they were pregnant and/or lactating, otherwise they were considered sexually immature. For mature females, reproductive status was classified according to Perrin and Donovan (1984) as follows: (1) pregnant, when a foetus is present in the uterus and a CL is present on one ovary, (2) pregnant and lactating, where a foetus is observed, a CL is present on one ovary, and milk is being produced (detected in the mammary glands), (3) lactating, milk is being produced, and (4) resting mature, a sexually mature female that is neither pregnant nor lactating.

4.3.4 Average age and body length at attainment of sexual maturity

The ASM and LSM were estimated for female common dolphins using two methods: (1) Bayesian modelling (Huisman et al. 1993) and (2) the sum-of-fraction of immature (SOFI) method (Hohn 1989, Equation 4A in Appendices).

Female ASM and LSM were modelled using Bayesian logistic regression with ‘HOF’ parameterisation (Huisman et al. 1993), fitted with Stan (Stan Development Team 2021) in R (R Development Core Team 2021). The HOF equation is as follows:

$$P(y = 1|x, m, \omega) = \frac{1}{1 + \exp(-\omega(x - m))}$$

where y is maturity status (0 = immature; 1 = mature), and x is either age or TBL. The two model parameters were a slope ω and a midpoint m, representing the age or length at which the probability of sexual maturity is 0.5 (i.e., the median age or length at attainment of sexual maturity). Prior distributions for the model parameters were m ~ Normal (190,20), ω ~ Normal$^+$ (0,1) for TBL, and m ~ Normal (8,2), ω ~ Normal$^+$ (0,2) for age. Prior predictive modelling was done to ensure these priors were reasonable.

The model was fitted to age and length data separately to obtain the ASM and LSM. The utility of age and TBL (*n* = 83 complete cases) for predicting maturity status were compared using the Leave-One-Out Expected Log Predictive Density (ELPD) and estimated using Pareto-smoothed importance sampling (Vehtari et al. 2017). ELPD scores give a measure of predictive accuracy for out-of-sample data.

4.3.5 Ovarian assessment

Prior to examination, formalin-fixed ovaries were rinsed in water for 24 hours and transferred back to containers with 70% ethanol. For each ovary, maximum length, width and depth were measured and recorded to the nearest 0.1 mm using vernier callipers. The weight of each ovary was recorded to the nearest 0.1 g. Combined ovarian weight was calculated for females where both ovaries were collected (*n* = 92). If a CL was present (>9 mm in diameter and yellow pigmentation), the position of the CL was recorded. Each ovary was then hand sectioned into 2 mm slices and examined under a 5x magnifying lamp to count the total number of *corpora* present. Ovaries were sectioned with the hilar region, where the ovaries attach to a broad ligament of the uterus (Saksouk and Johnson 2004), left intact to hold the sections together. The diameters of any CLs and CAs, and the largest follicle, were measured to the nearest 0.1 mm on three planes all perpendicular to each other using vernier callipers.

The activity of both ovaries via *corpora* was recorded to assess symmetry. *Corpora* data were tested for normality with a Shapiro-Wilk test. As these data were not normally distributed, a Kruskal-Wallis test was applied to compare the total *corpora* count between left and right ovaries, testing the null hypothesis of ovarian symmetry. A linear regression was additionally applied to assess if CL size increased with foetus TBL.

4.3.6 Ovulation rate

The total count of *corpora* (CL + CAs) scars was used to provide an indication of ovulation rate, as *corpora* count typically increases with size and/or age for mature females (Boyd et al. 1999; Takahashi et al. 2006; Ellis et al. 2018). Age and TBL were regressed against *corpora* count to determine the persistence of ovulation scars. The ovulation rate was subsequently estimated by regressing mean *corpora* count on age. This is under the assumption that CAs persist indefinitely (Betty 2019; Danil and Chivers 2007; Murphy et al. 2010; Westgate and Read 2007), and the slope of the regression corresponds to the rate at which the *corpora* are formed (Perrin and Reilly 1984).

4.3.7 Length at birth

Median length at birth was modelled using the Bayesian logistic regression with 'HOF' parameterisation (Huisman et al. 1993) described above. After prior predictive simulations, the following weakly informative priors were chosen for the two parameters, m ~ N(90,20), ω ~ N^+ (0,1). The dataset of this model included all foetuses and postnatal dolphins ≤ 160cm (*n* = 103) for which TBL was available. This dataset comprised of 13 unborn (n_0) and 90 born dolphins (n_1). To mitigate any potential effects of the unbalanced sample on estimates (Salas-Eljatib et al. 2018), weights were assigned to each case. These cases were from group k according to the sample size of the group n_k, relative to the overall sample size, n, using w_k = $\sqrt{0.5/(\frac{nk}{n})}$. For the weights w_i to have an average of 1, the vector of weights w_i were normalised.

Two models were fitted, the fully-weighted model and the square-root weighted model. These models were compared using model weights and Leave-One-Out diagnostics (via Pareto-smoothed importance sampling and refitting models for 103 observations with Pareto k > 0.7; 'loo' package in R; Vehtari et al. 2017). The partially weighted model, taking the square root of the sample size difference, was a better fit and so was used. The posterior distribution of the parameter m (i.e., the length at which the probability of birth is 50%) was summarised by the mean and 95% highest-posterior-density credible interval.

4.3.8 Gestation period and foetal growth

A plot of total body length (TBL) of foetuses and neonatal calves against day of year of collection (Julian date) was created for the Aotearoa New Zealand dataset (Perrin and Reilly 1984, Figure 4B in Appendices). The plot indicated that births were not clearly synchronised and/or gestation length was longer than 12 months as both very small and very large foetuses were recorded between April and July (Julian dates 103–202). Following Martin and Rothery (1993), these data were copied three times to mimic three consecutive 'years' to assess the temporal spread of conceptions. Three orientated concentrations of points from smallest to largest foetuses were clearly identified, which provided a basis for allocating a 'cohort' to foetal specimens and suggested there may be a seasonal component to conceptions and births (Figure 4.7, Figure 4B in Appendices).

Gestation period was estimated two ways: (1) Huggett and Widdas (1951) nonlinear growth phase method, adapted by Laws (1959), and (2) Perrin et al. (1977) gestation regression equation. The dataset fits the assumptions required for the two different equations (presence vs. absence of seasonality), hence why both were used to calculate the gestation period for Aotearoa New Zealand common dolphins.

The Huggett and Widdas (1951) equation assumes that seasonality is present in the dataset and is calculated as follows:

$$\text{Total gestation period } (t_g) = t_0 + (\ t_g - t_0)$$

where t_0 is the nonlinear phase of growth, and ($t_g - t_0$) is the linear phase of growth.

Using the Hugget and Widdas (1951) equation, the linear phase of growth ($t_g - t_0$) was calculated, using 85.4 cm (95% CrI: 78.0–91.5 cm) as the best estimate of length at birth. An estimate of non-linear growth for this study is reliant on previously published estimates of the relationship of t_0 to t_g, or (t_g– t_0). This is because it cannot be ruled out that some exceptionally small embryos were missed from the data collection. Furthermore, previous calculations of non-linear growth in common dolphins also applied mass as a parameter (Murphy et al. 2009; Westgate and Read 2007). While mass was not systematically collected in our study, the proportion of nonlinear to linear growth phase (0.126) reported in previous studies was used to calculate the non-linear growth phase for Aotearoa New Zealand common dolphins.

The Perrin et al. (1977) regression equation was also used as there was evidence from our dataset that conceptions and births may not have a seasonal component. This method is used when there is no reproductive seasonality observed and is as follows:

$$\text{Log}(y) = 0.1659 + 0.4856 \log(x)$$

where (y) is the length of gestation in months and (x) is the length at birth in cm.

4.3.9 Lactation period, length at weaning, and resting period

The lactation period was calculated as the proportion of lactating females divided by the proportion of pregnant females in the sample, multiplied by the gestation period expressed in years:

$$\text{Lactation period } (t_l) = t_g \times l/p$$

where t_g is the length of gestation, l is the proportion of the sample lactating, and p is the proportion of the sample pregnant (including females simultaneously pregnant and lactating; Perrin and Reilly 1984).

The length at weaning was calculated using the Huang et al. (2009) equation:

$$\text{Length at weaning } (L_w) = 1.2399 L_x^{0.877}$$

where L_x is the female asymptotic length (cm).

The resting period was calculated as the proportion of resting females divided by the proportion of pregnant females in the sample, multiplied by the gestation period expressed in years:

$$\text{Resting period } (t_r) = t_g \times r/p$$

where t_r is the length of the resting period, t_g is the length of gestation, r is the proportion of the sample resting, and p is the proportion of the sample pregnant (including females simultaneously pregnant and lactating; Perrin and Reilly 1984).

4.3.10 Annual pregnancy rate and calving interval

The annual pregnancy rate (APR) was estimated by dividing the proportion of pregnant females in the sample by the length of gestation, expressed in years (Murphy et al. 2009; Perrin and Reilly 1984):

$$\text{Annual pregnancy rate (APR)} = p/t_g$$

where t_g is the length of gestation, and p is the proportion of sample pregnant (including females that were simultaneously pregnant and lactating).

Several assumptions are implicit in this model: (1) there is no sampling bias i.e., the reproductive condition in the sample is the same as the population that is being sampled, (2) there is no seasonal bias that exists within the sample collection, (3) all pregnancies are detected (Perrin and Reilly 1984), and (4) that the length of gestation is calculated accurately. To avoid missing the presence of early embryos, it is recommended to exclude samples collected during the mating period (Murphy et al. 2009). However, as no clear mating season was established for the population and given the sample size, all data were included. To follow previous recommendations, an additional calculation of gestation period was performed with the exclusion of individuals sampled between August and November (slight calving peak).

The calving interval (CI) was calculated in two ways: (1) the reciprocal of the APR, and (2) the summation method (gestation + lactation + resting phases) after Perrin et al. (1977). For summation, the length of lactation needs to be adjusted downward by a factor equal to the percentage of females that are simultaneously pregnant and lactating. This considers any overlap between pregnancy and lactation (Perrin et al. 1977).

4.3.11 Reproductive seasonality

Conception and birth dates were estimated for each foetus and yearling calf (i.e., < 1-year old), based on their estimated age (Börjesson and Read 2003).

$$\text{Foetal } (t) = (L_t/u) \times 30.5 + t_0$$

$$\text{Yearling calf } (t) = (L_t - L_b/(u/\ 30.5))$$

where t is the foetal/calf age in days, L_t is the actual length of the foetus/calf (cm), u is the appropriate foetal, male calf, or female calf growth rate (cm mo^{-1}), 30.5 is the average number of days in a month, t_0 is the nonlinear foetal growth rate, and L_b is the estimated length-at-birth.

Calf age was estimated using 85.4 cm as the average length-at-birth, and the length at one year of age was 129.4 cm for females and 133.4 cm for males (determined from sex-specific growth curves; Chapter 2). From this, the first-year growth rate for female and male common dolphins was estimated at 46 cm/year and 52.2 cm/year, respectively. The nonlinear foetal growth rate was calculated based on the proportion of nonlinear/linear growth phases as in Murphy et al. (2009). Using the Huggett and Widdas method for calculating gestation, the nonlinear growth phase was 43 days and u was 6.95 cm/month. Using the regression method, the nonlinear growth phase was 44 days and u was 6.84 cm/month. Yearling calves (n = 32) were chosen if they were aged < 1 year or below, by counting GLGs in the dentine of the teeth (Chapter 2).

Individual conception dates for foetuses were calculated by subtracting the estimated foetal age (t in days) from the date stranded (Julian date). Birth dates for foetuses were estimated by adding the estimated conception date to the estimated gestation length (Huggett and Widdas method = 384 days or 12.6 months; regression method = 391 days or 12.8 months). Birth dates for calves were calculated by subtracting the estimated calf age (t in days) from the date stranded (Julian date), and conception dates were estimated by subtracting the estimated gestation period from the estimated birth date.

Data such as stranding dates of neonatal calves and near-term foetuses, the presence of large follicles, and the number of ovulating females in the sample were also used in the assessment of reproductive seasonality.

4.4 Results

4.4.1 The sample

Females ranged from 82 to 233 cm in TBL ($\bar{x}$ = 177; SD = 33; *n* = 106), with a modal size class of 191 to 200 cm (Figure 4.2a, Table 4.1). Age was determined for 100 female common dolphins, which ranged from 0 to 29 years (Figure 4.2b, Table 4.1). The age distribution had a modal class of yearling calves (i.e., < 1-year old) and 83% of females (*n* = 88) were aged at 15 years or below.

4.4.2 Reproductive status

Reproductive status was determined for 106 females of which 47% (*n* = 50) were sexually immature and 53% (*n* = 56) were sexually mature (Table 4.1). Sexually immature individuals ranged from 82 to 193 cm in length and from 0 to 8.75 years. An additional immature female had a minimum age determined (>= 9 years) and was not included is the ASM calculations/modelling. Sexually mature females ranged from 183 to 233 cm in length and from 7 to 29 years. Of the mature sample (*n* = 56), 13 were pregnant, 18 were lactating, four were simultaneously pregnant and lactating, 18 were resting mature, and reproductive status was not determined for three mature females (Table 4.1). Of the four females that were simultaneously lactating and pregnant, three foetus ‘crown to rump’ measurements were recorded: 101 cm, 6.1 cm and 3.9 cm. This would suggest that one female was lactating for impending birth and two were assumed to be lactating from a previous pregnancy.

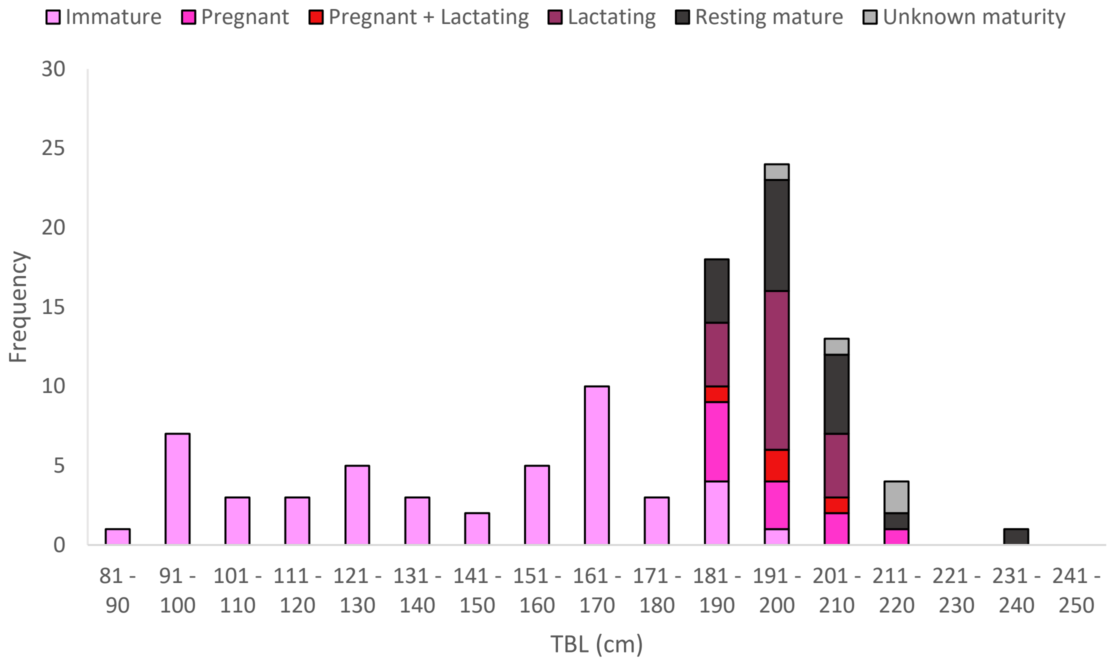
4.4.3 Average age and length at attainment of sexual maturity

Overlap was noted between immature and mature females of 183 to 193 cm TBL and 7 to 9 years of age (Table 4.1). Using the Bayesian logistic regression method, the LSM was estimated to be 183.5 cm (95% Credible Interval [CrI] = 179.5–186.5 cm, *n* = 100, Figure 4.3a) and the ASM was estimated as 7.5 years (95% CrI = 6.7–8.3 yrs, n = 84, Figure 4.3b). Using the SOFI method, the LSM and ASM were 188.9 cm (95% CI = 187.9–189.9 cm, n = 27) and 8.39 years (95% CI = 7.25–9.53 yrs, n = 17, Table 4H in Appendices), respectively. The smallest sexually mature female (WS03-43Dd) measured 183 cm in TBL and had a maturity status of resting mature with a total of 12 *corpora* scars. The youngest sexually mature female (KS19-23Dd) was estimated to be 7 years old, was lactating, and the uterus exhibited signs of a recent pregnancy. A total of 12 *corpora* scars were recorded for this female. The

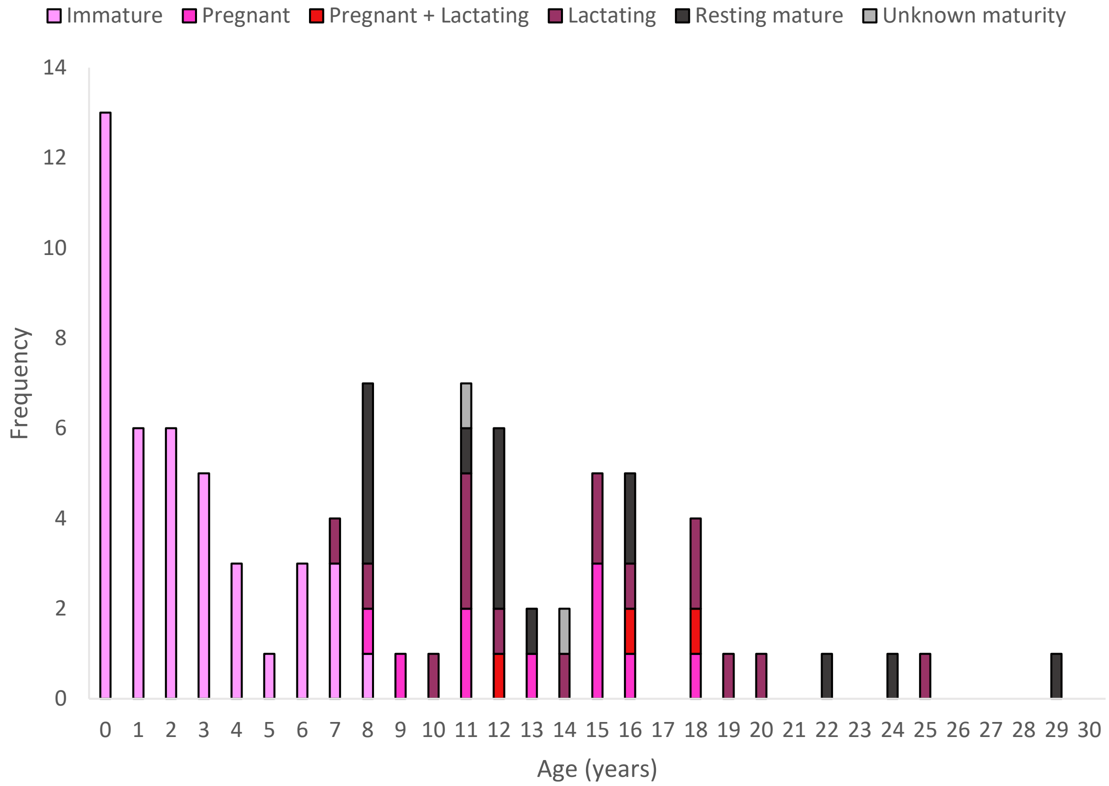
ELPD score for the model with age (0, SE = 0) was significantly greater than the model with TBL (-47.8, SE = 4), indicating that age was a better predictor of sexual maturity than TBL.

Table 4.1. Mean (±SE), range and number of samples obtained for total body length (TBL), age and ovarian characteristics of all reproductive groups of female common dolphins (*Delphinus delphis*) examined from Aotearoa New Zealand waters (1997–2019).

Stage	***n***	**TBL (cm)**	**Age (yrs)**	**Total ovarian weight (g)**	**Total ovarian volume (mm^3)**	**Corpora count (CAs + CL)**		**CL present**	
						L	**R**	**L**	**R**
Immature	50	141 (±5) 82–193 (*n* = 50)	1.8 (±0.3) 0–>=9 (*n* = 44)	2.5 (±0.5) 0.3–11.1 (*n* = 40)	2.4 (±0.8) 0.1–32.0 (*n* = 41)	0	0	0	0
Pregnant	13	198 (±3) 185–216 (*n* = 13)	12.9 (±1.0) 8–18 (*n* = 11)	13.3 (±1.0) 7.8–17.1 (*n* = 10)	11.2 (±2.1) 4.6–20.9 (*n* = 9)	3.8 (±1.2) 0–12 (*n* = 10)	2.6 (±1.0) 0–9 (*n* = 11)	5	5
Lactating	18	196 (±2) 189–208 (*n* = 18)	14.4 (±1.2) 7–25 (*n* = 17)	6.2 (±0.6) 2.5–12.5 (*n* = 16)	5.5 (±0.7) 0.8–12.2 (*n* = 17)	4.6 (±1.1) 0–16 (*n* = 17)	0.7 (±0.4) 0–6 (*n* = 17)	5	2
Pregnant + lactating	4	197 (±4) 189–207 (*n* = 4)	15 (±3.0) 12–18 (*n* = 3)	13.9 (±2.5) 9.4–19 (*n* = 4)	8.2 (±1.4) 6.1–10.6 (*n* = 4)	5.5 (±1.4) 2–9 (*n* = 4)	1.5 (±1.0) 0–4 (*n* = 4)	2	2
Resting mature	18	199 (±3) 184–233 (*n* = 18)	14.2 (±1.6) 8–29 (*n* = 16)	6.5 (±0.7) 2.9–10.6 (*n* = 16)	9.7 (±4.1) 0.8–70.2 (*n* = 16)	5.9 (±1.2) 0–14 (*n* = 16)	2 (±1.0) 0–14 (*n* = 16)	3	2
Indeterminate mature	3	206 (±6) 200–212 (*n* = 3)	14 (±0.0) 14– >20 (*n* = 3)	12.7 (±9.4) 3.3–22 (*n* = 2)	7.3 (±1.9) 5.4–9.2 (*n* = 2)	2.5 (±2.5) 0–5 (*n* = 2)	2.5 (±2.5) 0–5 (*n* = 2)	1	1
All mature individuals	56	198 (±1) 183–233 (*n* = 56)	14.4 (±0.7) 7–29 (*n* = 51)	8.7 (±0.7) 2.5–22 (*n* = 48)	8.3 (±1.5) 0.8–70.2 (*n* = 48)	4.8 (± 0.6) 0–6 (*n* = 49)	1.7 (±0.4) 0–14 (*n* = 50)	16	12
Total	106	171 (±4) 82–233 (*n* = 106)	8.5 (±0.7) 0–29 (*n* = 94)	6.2 (±0.6) 0.3–22 (*n* = 88)	5.6 (±0.9) 0.1–70.2 (*n* = 89)	2.4 (±0.4) 0–16 (*n* = 96)	0.9 (±0.2) 0–14 (*n* = 97)	16	12



(a)



(b)

Figure 4.2. Frequency distribution of each maturity stage at (a) TBL (*n* = 104) and (b) age (*n* = 86) for female common dolphins (*Delphinus delphis*) stranded and bycaught on the Aotearoa New Zealand coast between 1997 and 2019.

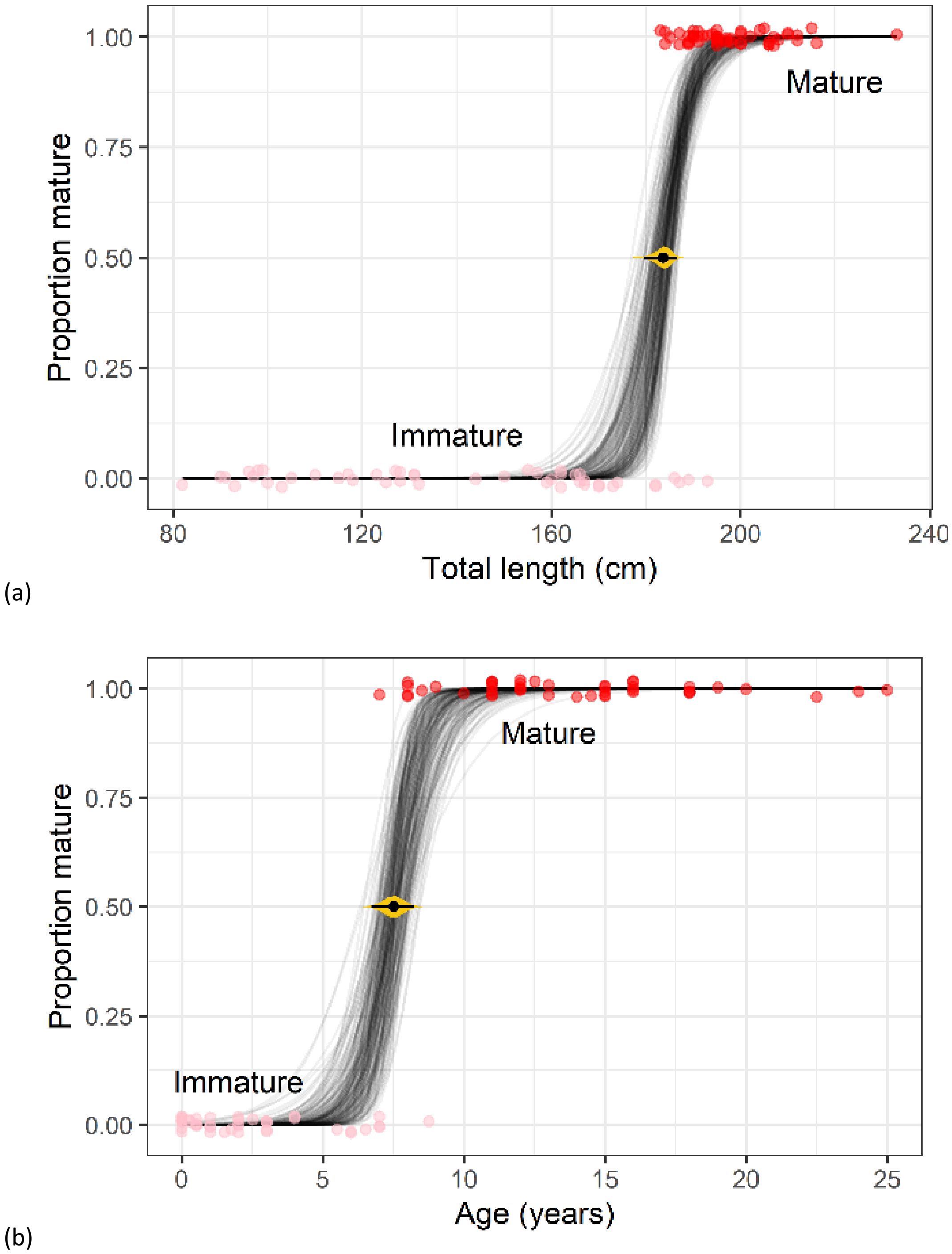


Figure 4.3. Bayesian cumulative logit regression of the sexual maturation of female common dolphins (*Delphinus delphis*) from Aotearoa New Zealand waters (1997–2019), modelled as a function of (a) total body length (TBL) and (b) age. These plots show the age and TBL values for immature (light pink) and mature (red) individuals. The lines represent posterior predictions of the mean. To aid the visualisation of overlapping points, a small amount of transparency and vertical 'jitter' was added. The central black point with the thin horizontal line shows the mean and 95% confidence intervals, with gradient plot in yellow (Kay 2021) of the estimated values of x at which 50% of females were classified as mature.

4.4.4 Ovarian characteristics

Ovarian characteristics were assessed in 56 mature female common dolphins. Combined ovarian weight increased from birth until the approximate time of sexual maturity (7.5 yrs, 183.5 cm; Figure 4.4). The combined weight of immature ovaries ranged between 0.3 and 11 g and the ovaries were pale and smooth in colour and texture, respectively. Ovaries of mature females ranged from 2.5 to 22 g in weight, were ochre in colour, had visible blood vessels, and were less smooth in texture. The combined weight of mature ovaries ($\bar{x} = 8.7 \pm 0.7$ g) were significantly heavier (t-test, $p < 0.001$) than immature ovaries ($\bar{x} = 2.5 \pm 0.5$ g), despite overlap between the heaviest immature ovaries (11 g) and the smallest mature ovaries (2.5 g).

The combined *corpora* count recorded for sexually mature females ranged from 1 to 19 ($\bar{x} = 8.7 \pm 0.7$; $n = 48$). *Corpora* scars were observed on both ovaries in mature individuals (Table 4.1), though the left ovary ($\bar{x} = 5 \pm 0.6$) had significantly more *corpora* than the right ovary ($\bar{x} = 1.7 \pm 0.4$, $p < 0.001$). Of a total of 123 *corpora*, 97 were observed on the left ovary and 26 on the right ovary. The smallest *corpora* measured at 2.5 mm and the largest at 25 mm in mean diameter. The individual with the highest number of *corpora* scars ($n = 19$) also had a CL present (mean diameter of 12 mm) and was an older, resting mature female (WS05-37Dd, 24 years). The youngest pregnant female (KS12-13Dd, 8 years) was in her first pregnancy as evidenced by a foetus present in the uterus and only one *corpora* present on the ovaries. In comparison two other young females, KS19-23Dd (7 years) and WS06-13Dd (8.5 years), had 12 and 14 recorded CAs, respectively.

CLs were observed on the ovaries of sexually mature females in all reproductive classes. The largest were present on both pregnant, and pregnant and lactating, females ($\bar{x} = 27.4 \pm 1.9$ mm, $n = 11$, range = 16–36 mm). Lactating ($\bar{x} = 16.3 \pm 2.0$ mm, $n = 3$, range = 13–20 mm) and resting ($\bar{x} = 8.3 \pm 1.9$ mm, $n = 3$, range = 6–7 mm) females also had CLs recorded but these were smaller in size, indicating a recent pregnancy or ovulation. As no histology was carried out on the ovaries, active CLs could not be distinguished from regressing CLs/young CAs. This may have resulted in misclassification of young CAs vs CLs. No relationship between CL size and foetal TBL was evident ($p = 0.771$, $r^2 = 0.01524$, $n = 8$; Figure 4C in Appendices).

4.4.5 Persistence of corpora scars and ovulation rate

Positive linear relationships between the number of *corpora* scars (CAs + CL) and both TBL ($r^2 = 0.008$, $p = 0.5412$, $n = 48$, Figure 4.5a) and age ($r^2 = 0.2245$, $p = 0.002$, $n = 39$, Figure 4.5b) were found, though only the relationship with age was significant. The size-frequency distribution of all CAs ($n = 123$) was plotted to further examine the persistence of *corpora* scars over time.

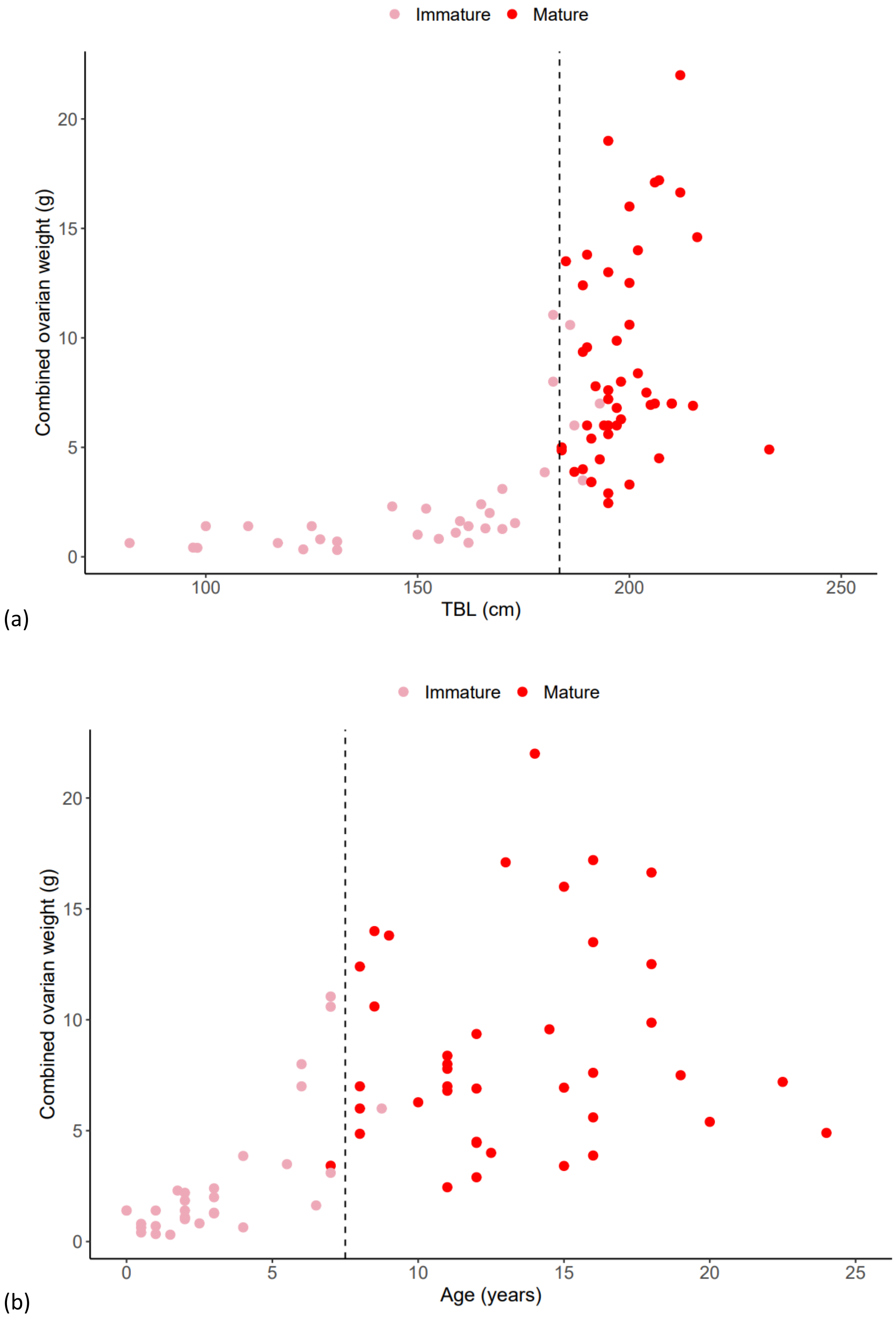


Figure 4.4. Combined ovarian weight vs (a) total body length (TBL; *n* = 104) and (b) age (*n* = 68) in female common dolphins (*Delphinus delphis*) stranded and bycaught on the Aotearoa New Zealand coast between 1997 and 2019. The dashed line indicates the best estimate of average length (i.e., 183.5 cm) and age (i.e., 7.5 years) at attainment of sexual maturity.

This distribution formed a typical bell-shaped curve, which is indicative of a normal and complete sample (Figure 4D in Appendices). A peak in the mean diameter of *corpora* at 6mm was noted. Few, very large CAs suggest an initial period of rapid decline in *corpora* size. The ovulation rate for Aotearoa New Zealand common dolphins was considered to be 0.3924 *corpora* per year i.e., the slope of the linear regression of the mean number of *corpora* scars on age ($r^2 = 0.1692$, $p = 0.08$, $n = 19$, Figure 4.6).

4.4.6 Length at birth

A total of 19 foetuses were recorded in the dataset, ranging from 15.2 to 101 cm TBL ($n = 9$). The largest female foetus was 92 cm and the largest male foetus was 101 cm. The smallest born female and male calves measured at 82 cm and 89 cm, respectively. There were 2 foetuses and 17 neonates measuring between 90 cm (the smallest neonate/calf) and 101 cm (the largest foetus). The median length at birth was calculated as 85.4 cm (Figure 4E in Appendices, Chapter 2, 95% CrI: 78.0–91.5 cm), based on the HOF logistic regression model.

4.4.7 Gestation period, foetal growth and dates of conception and birth

The outputs from both methods of calculating gestation period were closely aligned. The Huggett and Widdas method for estimating linear foetal growth phase of the gestation period, by regressing foetus/neonate TBL on sampling data for a nominal 'cohort' ($t_g - t_0$), was estimated to be 341 days or 11.2 months ($y = 0.3083x - 176531$, $r^2 = 0.8553$, $p < 0.001$, $n = 22$, Figure 4.7). The length of nonlinear growth phase was calculated as 43 days ($t_0 = 0.126 \times 341$ days), which gave a total gestation period of 384 days or, 12.6 months ($t_g = 341 + 75$ days). A foetal growth rate of 6.95 cm/month was estimated.

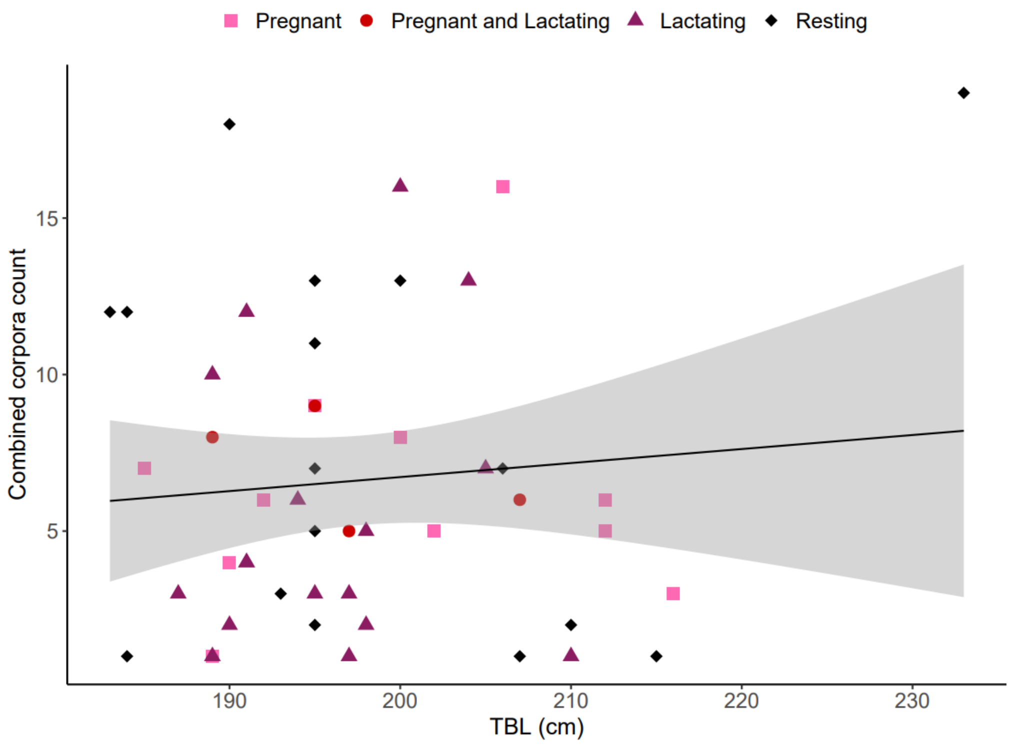
The regression method for calculating gestation period, which allows for low breeding synchrony/no reproductive seasonality, estimated a gestation period of 391 days or 12.8 months, based on the length-at-birth estimate of 85.4 cm. A foetal growth rate of 6.84 cm/month was calculated for this method. For this study, both the Huggett and Widdas and the regression methods for calculating gestation period were used, as although these data demonstrated some degree of seasonality, the evidence for seasonality was not conclusive.

4.4.8 Lactation, length at weaning, and resting period

Length at weaning was calculated as 128.3 cm (95% CI = 125.4–131.2) based on Huang et al. (2009), and an estimated female asymptotic length of 198.3 cm (95% CI = 195.4–201.2, Chapter 2). Using fitted growth curves from examined carcasses (Chapter 2), the length at weaning corresponds to 10 and 11 months of age for male and female calves, respectively. This is not consistent with the lactation period which is estimated to exceed a year. Applying the Perrin and Reilly (1984) equation, the resting period was also calculated to be either 12.6 or 12.8 months, where the Huggett and Widdas and the regression methods for calculating the gestation period were applied, respectively. There were equal proportions of pregnant/pregnant and lactating females (*n* = 18), lactating females (*n* = 18), and resting mature females (*n* = 18) in our sample.

4.4.9 Annual pregnancy rate and calving interval

The sample for estimating pregnancy rate was collected between 1997 and 2019 and included 56 sexually mature females, of which 18 (32%) were pregnant. The annual pregnancy rate (APR) was calculated as 30% when including all mature females. When excluding females during the peak calving period (August to November), the APR was calculated as 33% (16/48). By taking the gestation, lactation and resting periods, 12.6 or 12.8 months each, a calving interval of either 37.8 months (3.15 years) or 38.4 months (3.2 years) was calculated. The calving interval was also calculated by taking the inverse of the APR, which gives 3.33 or 3.13 years for the two pregnancy rate estimates.



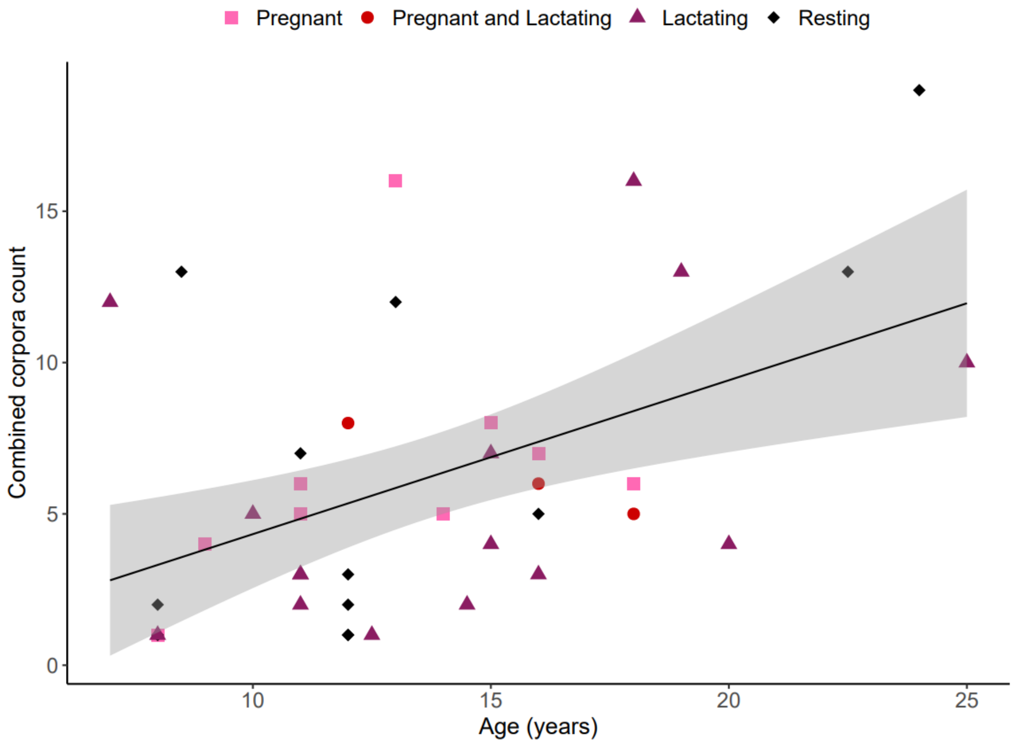


Figure 4.5. Linear regression of combined *corpora* count (ovarian activity) as a function of (a) total body length (TBL; $y = 0.043x - 2.109$, $r^2 = 0.008$, $n = 49$) and (b) age ($y = 0.5085x - 0.7539$, $r^2 = 0.2245$, $n = 44$) for mature female common dolphins (*Delphinus delphis*) stranded and bycaught on the Aotearoa New Zealand coast between 1997 and 2019. The black solid line represents the regression, and the shaded area is the 95% confidence interval.

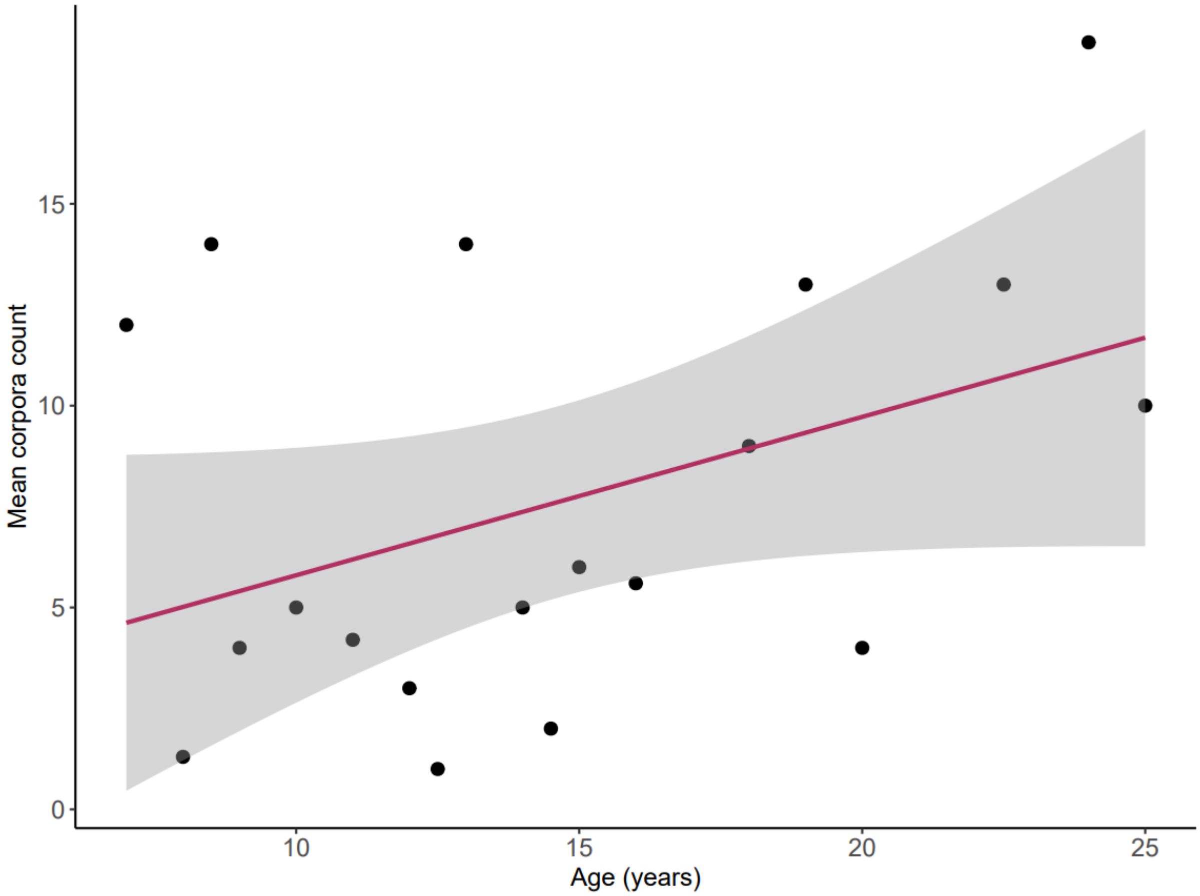


Figure 4.6. Linear regression of mean *corpora* count on age for Aotearoa New Zealand female common dolphins (*Delphinus delphis*) stranded and bycaught on the Aotearoa New Zealand coast between 1997 and 2019 ($y = 0.3924x + 1.8754$, $r^2 = 0.1692$, $n = 18$). The solid line represents the linear regression, and the shaded area indicates the 95% confidence interval.

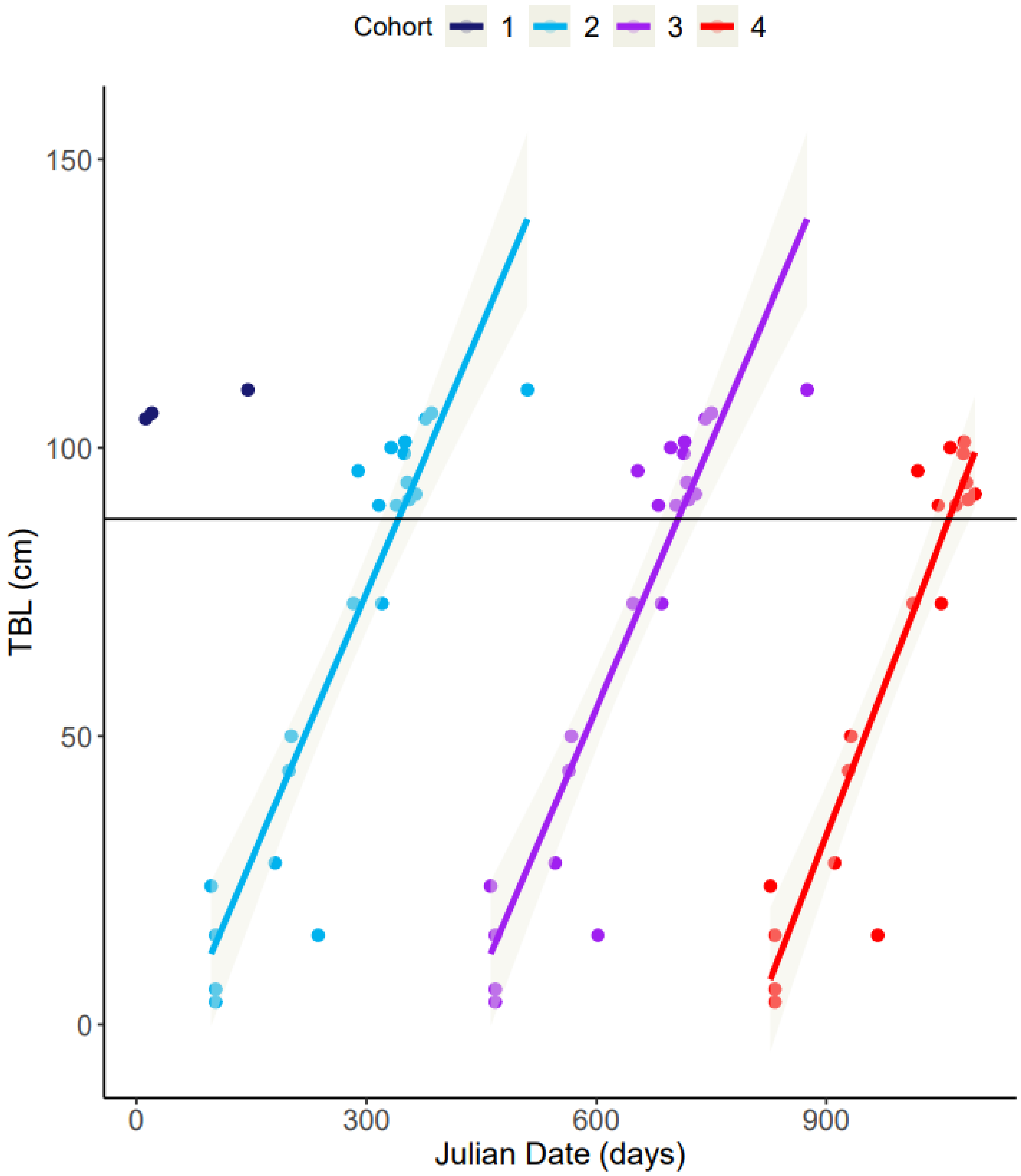


Figure 4.7. Three repetitions of assigned cohorts of a plot of foetal and neonatal total body length (TBL) against day of year sampled (Julian date) for common dolphins (*Delphinus delphis*) stranded and bycaught on the Aotearoa New Zealand coast between 1997 and 2019 (*n* = 22). The diagonal solid line indicates the growth trajectory for a 'nominal' cohort and is fitted by a linear regression. The horizontal solid line is the estimated length at birth (85.4 cm). The grey shaded areas represent the 95% CI for the linear regression.

4.4.10 Reproductive seasonality

Of the 27 females with a CL present, 12 were likely ovulating (based on the presence of a CL but no detectable foetus), with the majority observed over austral spring (September to November, *n* = 4) and summer (December to February, *n* = 4). However, instances in March (austral autumn, *n* = 1) and August (austral winter, *n* = 2) also occurred. Macroscopic follicles were observed in February, April, June, July, August and December (Figure 4F in Appendices), with the largest follicle (> 6mm) recorded in December.

Conception and birth dates were back-calculated for each foetus (*n* = 12) and yearling calf (*n* = 32). Using the Huggett and Widdas method for gestation, estimated conception dates were recorded in all months. There were peaks in October and November, and secondary peaks in August and May (Figure 4Ga in Appendices). Estimated birth dates were also recorded in all months of the year with peaks in October and November (Figure 4Ga in Appendices). By season, austral spring (September to November) had the highest conception and birth dates (40.9% and 45.5%, respectively) and austral summer (December to February) the lowest (both 15.9%).

Using the logistic regression method for gestation, estimated conception dates were recorded in every month of the year, with the biggest peak in October and secondary peaks evident in September and July (Figure 4Gb in Appendices). Estimated birth dates were also recorded in all months with the biggest peak in November and secondary peaks in October and August (Figure 4Gb in Appendices). When observing seasons, austral spring (September to November) had the highest proportion of conception dates (40.9%) and austral summer (December to February) the lowest (15.9%). For birth dates, austral spring had the highest (45.5%) and austral summer the lowest (13.6%).

4.5 Discussion

4.5.1 Age and length at attainment of sexual maturity

Our LSM estimates for female common dolphins in Aotearoa New Zealand waters were 183.5 cm (*n* = 104) and 188.9 cm (*n* = 27) for the logistic regression and SOFI methods, respectively (Figure 4H in Appendices). These estimates both align with common dolphin populations in the eastern tropical Pacific (186.5 cm, *n* = 700; Danil and Chivers 2007) and eastern North Atlantic (ca. 188 cm, *n* = 453; Murphy et al. 2009), which used the SOFI and logistic regression methods, respectively. In the western North Atlantic, females attain sexual maturity at approximately 200 cm, which is over 10 cm larger than any other population (*n* = 69; Westgate and Read 2007). However, Westgate and Read (2007) do not report how the LSM for the western North Atlantic population was estimated. In the southwestern Atlantic, off the coast of Argentina, an overlap between immature and mature female TBL was noted, with the largest immature female measuring 191 cm and the smallest mature female measuring 178 cm (*n* = 35; Grandi et al. 2022). Due to a small sample size, the LSM was not estimated for the Argentine population. In contrast, the estimated LSM for female common dolphins in the North Pacific is at least 10 cm less than any other population for which estimates exist (ca. 172 cm, *n* = 43; Ferrero and Walker 1995).

Our estimated ASM of 7.5 years (*n* = 88) based on logistic regression for female common dolphins in Aotearoa New Zealand waters represents the youngest ASM reported for females in any international population (Table 4H in Appendices). The ASM was also calculated using the SOFI method, 8.39 years (*n* = 17), and this was closer to previously reported common dolphin ASMs. For example, females in the North Atlantic are estimated to obtain sexual maturity at 8.22 years (regression method [Generalised Linear Model], *n* = 108; SOFI method = 8.66 years, *n* = 379; Murphy et al. 2009) and 8.3 years (SOFI method, *n* = 69; Westgate and Read 2007) for the eastern and western populations, respectively. In the North Pacific and eastern tropical Pacific, the estimated ASM is 8 years (SOFI method, *n* = 43) and 7.9 years (regression method [maximum likelihood], *n* = 405), respectively (Danil and Chivers 2007; Ferrero and Walker 1995). In the southwestern Atlantic, the oldest immature female and youngest mature female sampled were 6 years and 7 years of age, respectively (*n* = 35; Grandi et al. 2022). ASM was not estimated in that study due to the small sample size. The estimate of ASM for the Aotearoa New Zealand population is at the lower end of what has been observed for this species (Table 4H in Appendices), though any differences may be due to sampling variation (and available sample size). Further research with combined datasets is required to determine the extent of any differences among populations. Aotearoa New Zealand samples were acquired from both stranded and bycaught individuals with an approximate 50:50 split of immature and mature females, as is consistent with other studies (e.g., Murphy et al. 2009, Westgate and Read 2007).

Age was a better indicator of sexual maturity than TBL. This has important management implications as it confirms that TBL (the easiest parameter to obtain in the field by the management agency) is not the best predictor of sexual maturity. Instead, to accurately predict sexual maturity, post-mortem collection of teeth is required from stranded or bycaught dolphins (when cultural consent from hapū is given) to enable accurate age estimation. If TBL is the only parameter able to be collected, accurate linear measurements are required. While there is a possibility that our study underestimated the age of older individuals due to the potential occlusion of the pulp cavity (Murphy et al. 2014), the standardised methods that were employed including the use of blind readings and at least two experienced readers per individual (Murphy et al. 2014; Perrin and Myrick Jr 1980) mitigates such concerns.

4.5.2 Ovarian asymmetry

In Aotearoa New Zealand female common dolphins, 3.7 times more *corpora* scars were observed on the left ovary compared to the right. Such asymmetry has been observed in other common dolphin populations (Danil and Chivers 2007; Murphy 2004), as well as spinner dolphins (*Stenella longirostris*, Perrin et al. 1976, 1977), harbour porpoises (*Phocoena phocoena*, Murphy et al. 2010), Indo-Pacific bottlenose dolphins (*Tursiops aduncus*, Kemper et al. 2019) and long-finned pilot whales (*Globicephala melas*, Betty 2019; Soto et al. 2017). While such asymmetry exists for many species, there have been no conclusive reasons as to why this is the case in odontocetes, though ovarian asymmetry has also been observed in birds and linked to egg protection during the final stage of development (Guioli et al. 2014).

4.5.3 Persistence of corpora and ovulation rate

The variability in ovulation rate as determined by *corpora* count (Figure 4.5) may suggest that some females ovulate more often than others. This has been previously observed in common dolphins (Danil and Chivers 2007) and other species including harbour porpoises (Murphy et al. 2010), long-finned pilot whales (Betty 2019; Soto et al. 2017) and Indo-Pacific bottlenose dolphins (Kemper et al. 2019). In this study, this is seen in the two young females that have unusually high *corpora* count. These females could represent a biological anomaly or may be the result of variation in ovulation rates where certain females hyper-ovulate, therefore leading to scars, before they become pregnant. In common dolphins and harbour porpoises, the onset of sexual maturation can be marked by a variable number of successive infertile ovulations (Collet and Harrison 1981; Gaskin et al. 1984; Murphy et al. 2010). While such variation in ovulation exists, evidence across various odontocete species still supports the theory that *corpora* persist temporally (Betty 2019; Danil and Chivers 2007; Perrin and Reilly 1984; Westgate and Read 2007). This aligns with our findings that, beyond sexual maturity, the mean number of *corpora* marginally increases. In contrast, Dabin et al. (2008) suggested most CAs heal quickly, with a half-life of less than one year, and that *corpora* may not persist over time as the number of CAs did not increase with age past age at sexual maturity in short beaked common dolphins (Dabin et al. 2008). However, recent research supports our findings as Inbaraj et al. (2021) found through an extensive literature review that most reports of *corpora* persistence in cetaceans record long-lived *corpora*. *Corpora* scars have previously been used as an index of reproductive activity over a female's lifetime (Murphy et al. 2010; Murphy et al. 2018; Perrin and Donovan 1984). However, future research is required to distinguish scars of ovulation from scars of pregnancy (Danil and Chivers 2007) and the rate of accumulation (Marsh et al. 1984a).

4.5.4 Gestation, lactation, and resting periods

The gestation period estimated here at 12.6 to 12.8 months for the Aotearoa New Zealand population based on the Hugget and Widdas equation and the regression equation, respectively. This is a slightly protracted gestation period compared with international populations of common dolphins, which range between 10 to 12 months for the North Pacific (Ferrero and Walker 1995), North Atlantic

(Murphy et al. 2009; Westgate and Read 2007), and eastern tropical Pacific (Danil and Chivers 2007). An extended gestation period intuitively signals a longer time for growth and development, however the reported length-at-birth for Aotearoa New Zealand common dolphins is 85.4 cm (95% CrI: 78.0–91.5 cm). Alongside eastern tropical Pacific length at birth estimates (83.7 and 87 cm), Aotearoa New Zealand is one of the smallest estimated for common dolphin populations, which somewhat contradicts this theory. The rate of maternal energy turnover can influence foetal brain and body growth in mammals (Barton and Capellini 2011), meaning slower growth would result in an extended gestation period. Foetal growth appears slower in Aotearoa New Zealand (6.84 to 6.95 cm/month) compared to other international (7.6 and 8.2 cm/month) common dolphin populations (Danil and Chivers 2007; Westgate and Read 2007; Murphy et al. 2009). Lack of reproductive seasonality and slower rates of population increase can also increase gestation length (Clauss et al. 2014; Clauss et al. 2021). Resources must be available year-round for female common dolphins in Aotearoa New Zealand waters as births occur year-round, akin to what has been observed for the species in the eastern tropical Pacific (Danil and Chivers 2007). This contrasts with the North Atlantic populations where there is a distinct unimodal calving period (Murphy et al. 2009; Westgate and Read 2007). The small sample size of foetuses and neonates (*n* = 22) within the current study produces a degree of error. Additionally, small changes to the estimated length at birth may result in profound changes to the estimated length of gestation. It cannot be ruled out that other factors, such as exposure to persistent pollutants, may impact foetal development and therefore result in an extended gestation period (Murphy et al. 2018).

Contaminants can pose a threat to reproduction and may affect gestation and foetal development (Murphy et al. 2015; Nabi et al. 2018; Nawrot et al. 2018). For example, a high proportion of lipophilic pollutant offload occurs from mother to offspring during pregnancy and lactation (Cadieux et al. 2016; Mongillo et al. 2016; Stockin et al. 2007). In cetaceans, transfer of organochlorides during gestation is between 3% and 15% compared to 67–99% during lactation (Mongillo et al. 2016). Transfer of contaminants from mother to calf has been documented for several odontocete species including killer whales (*Orcinus orca*, Desforges et al. 2018; Lundin et al. 2016) and beluga whales (*Delphinapterus leucas,* Béland et al. 1993; Cadieux et al. 2016). Within an Aotearoa New Zealand context, such maternal offloading has been recorded in bottlenose (*Tursiops truncatus*; Tezanos-Pinto et al. 2015) and common dolphins (DDTs [dichlorodiphenyltrichloroethane] and PCBs [polychlorinated biphenyls]: 42–46% lactational transfer; Stockin et al. 2007).

The lactation period of Aotearoa New Zealand common dolphins (12.6 to 12.8 months) is within the range of lactation periods estimated from previous studies; 10.35 months for the eastern North

Atlantic population (Murphy et al. 2009), and 16.5 months for the eastern tropical Pacific population (Danil and Chivers 2007). Lactation periods are generally associated with body size and other life history traits (Gowans 2019). Therefore, it is common for there to be variation in reproductive parameters, such as lactation, within as well as between populations (Karniski et al. 2018).

The length at weaning estimate for the Aotearoa New Zealand population is 128.3 cm using the Huang et al. (2009) equation. This equation is curated with generalised linear models and based on data collected across 79 species of cetaceans including common dolphins. The length at weaning for the Aotearoa New Zealand population corresponds to between 10 and 11 months of age (Chapter 2). While less than the estimated lactation period of ca. 12.5 months reported here, this likely represents the transition period where consumption of both solids and milk occurs. Peters et al. (2020) reported a decrease in δ15N values (an indication of trophic position) at a body length of 160 cm for common dolphins in Aotearoa New Zealand, which may indicate the transition from milk to live prey. This also aligns with the estimated lactation period within our dataset; the largest 1-year old was 160 cm in length. Similarly, Chivers et al. (2016) reported calves swimming independently of their mothers at a TBL of 140.5cm, which is approximately 14 months of age (Danil and Chivers 2007). Swimming independently refers to their ability to forage and consume live prey, independent of lactation. Additional age-at-length data for females would provide a more robust estimate of weaning period as the equation is based on asymptotic length. Stomach contents for individuals around the estimated weaning age would also be useful.

The resting period observed for Aotearoa New Zealand female common dolphins ranged from 12.6 to 12.8 months, for the Hugget and Widdas and the regression methods, respectively. Considerable variation in resting periods has been noted across other studies of common dolphins, ranging from 2.8 months in the eastern tropical Pacific (Danil and Chivers 2007) to 20.7 months in the eastern North Atlantic (Murphy 2004; Murphy et al. 2009). Such variation could be driven by differences in habitat and resource availability, the success of previous pregnancies, and whether breeding seasonality is present in the population (Beauplet et al. 2006; Mann et al. 2000; New et al. 2013).

4.5.5 Annual pregnancy rate and calving interval

The estimated APR for female Aotearoa New Zealand common dolphins is 30–33%, which is consistent with estimates for common dolphin populations from the North Atlantic (Murphy et al. 2009; Westgate and Read 2007; Read et al. 2019). For example, the estimated APRs for the eastern and western North Atlantic populations are 26% and 28%, respectively (Murphy et al. 2009; Westgate and Read 2007). In the temperate eastern North Pacific, a birth rate of 13% was reported by converting the estimated proportion of calves assuming a 1:1 male:female sex ratio in the population

(Chivers et al. 2016). This is much lower than a previous study in the region where the APR was recorded as 28% using steroid hormones to assess pregnancy (Kellar et al. 2006; Kellar et al. 2014). In the eastern tropical Pacific, a higher APR of 47% has been recorded using the same methodology as used in this study (Danil and Chivers 2007).

The estimated calving interval of 3.2 years (*n* = 56) for the Aotearoa New Zealand population is almost half a year shorter than that recorded for the eastern North Atlantic (3.79 years, *n* = 248; Murphy et al. 2009). The shorter calving interval observed in Aotearoa New Zealand waters is a result of the slightly higher APR, in comparison to the eastern North Atlantic. A factor that may influence the population calving interval estimate (through impacting the pregnancy/newborn survival rate) is a female's pollutant load. This has been suggested for the eastern North Atlantic population, which is reported to have higher levels of organochlorines compared to other common dolphin populations, as well as higher rates of observed cases of reproductive pathologies and dysfunction (Murphy et al. 2018). Variation in calving intervals may also be driven by the differing environments of Aotearoa New Zealand waters in comparison to North Atlantic waters. Geographic variation in life history traits within a species can be driven by population-specific adaptations to local habitats (Danil and Chivers 2006; Ferguson and Higdon 2013). Differences in these parameters could also be driven by seasonal (Murphy et al. 2009; Westgate and Read 2007) or year-round reproduction (Danil and Chivers 2007).

In Aotearoa New Zealand, 7% (*n* = 4 out of 56) of sexually mature females were simultaneously pregnant and lactating. In the eastern North Atlantic this was 6% (*n* = 18 out of 302; Murphy et al. 2009), and in the western North Atlantic only one female in the dataset was pregnant and lactating (3%, out of 39 mature females; Westgate and Read 2007). In comparison, 30.4% (*n* = 65 out of 333) of mature females in the eastern tropical Pacific were both pregnant and lactating (Danil and Chivers 2007). The high proportion of simultaneously pregnant and lactating females in the eastern tropical Pacific could be explained by their elongated lactation period (16.5 months). It could also reflect a higher intrinsic reproductive rate for this population (Danil and Chivers 2007) due to the abundant resources available which enable them to maintain this energetically costly condition (Fiedler and Reilly 1994). Another explanation may be density-dependent responses exhibited by the population following a decline from decades of fisheries impacts (Cramer et al. 2008; Gerrodette 2008; Gerrodette and Forcada 2005). The Aotearoa New Zealand population also experiences notable levels of fisheries bycatch (Abraham et al. 2017; Abraham et al. 2021; Stockin and Orams 2009), with 220 common dolphins reported bycaught between 2002 to 2020 (Ministry for Primary Industries 2022), noting further that <20% of the fishery was independently observed during this period. Continued monitoring will be important to identify any potential increase in the proportion of sexually mature females that are simultaneously pregnant and lactating. Populations that are at a low density tend to reproduce at a faster rate due to the availability of resources per capita (Murphy et al. 2018). This may be the case for the Aotearoa New Zealand population, and the idea is supported by a comparatively lower ASM. There is also the possibility that this is the baseline/natural pregnancy rate for the Aotearoa New Zealand population, as no previous data exists.

APR is typically calculated by excluding females in the mating season since it is easy to overlook early embryos and subsequently underestimate pregnancy rate. The APR was calculated with and without females during the weak calving season (October and November) and very similar outputs were found. Therefore, it is considered that the APR is reflective of the population. Future studies with an increased sample size are recommended to facilitate greater precision on reproductive seasonality, and specifically, ovulation rate. In the field, pregnancy assessment of free-ranging common dolphins via progesterone concentration from blubber biopsies (Kellar et al. 2014; Trego et al. 2013) would also be of notable benefit to our understanding of the APR within the Aotearoa New Zealand population.

4.5.6 Reproductive seasonality

Weak seasonality was observed in the reproduction of female common dolphins in Aotearoa New Zealand waters. In comparison, strong seasonality is observed with a clear breeding season during the boreal summer months of May to September in the Northern Hemisphere (Murphy et al. 2009; Westgate and Read 2007). Reproduction is seasonal and synchronised in these populations, which allows mothers and calves to take advantage of seasonally abundant food and resources, and warm temperatures (Henderson et al. 2014; Rutberg 1987; Thayer et al. 2003; Westgate and Read 2007). Reproductive seasonality is also observed in the North Pacific with calving peaking in boreal summer months of May and June (Ferrero and Walker 1995). Alternatively, in the eastern tropical Pacific, breeding has been documented as year-round (Danil and Chivers 2006, 2007), although further findings from the eastern North Pacific revealed calving peaks in boreal winter, which corresponds with high productivity and prey biomass (Chivers et al. 2016). In Aotearoa New Zealand, temporal changes to primary productivity are known to affect the diet of common dolphins (Peters et al. 2020; Stockin et al. 2022). These temporal changes may also be impacting reproduction and resulting in the weak seasonality observed in the Aotearoa New Zealand population.

Conception and birth dates for Aotearoa New Zealand common dolphins were recorded in all months of the year (Figure 4G in Appendices) with peaks noted between August and December (late austral winter, austral spring, and early austral summer). This indicates that while the breeding occurs year-round, there is a marginal bias with 59% of births occurring between August and December. This is supported by field evidence, where a high prevalence of neonates is observed off the eastern coast of the North Island of Aotearoa New Zealand, specifically the Hauraki Gulf, Bay of Islands and Bay of Plenty during austral spring and summer (Neumann 2001a; Schaffar-Delaney 2004; Stockin et al. 2008b). The presence of calves (including neonates) year-round in the Hauraki Gulf, Auckland (Schaffar-Delaney 2004; Stockin et al. 2008b) also supports the idea of weak reproductive seasonality for females in the region.

4.6 Conclusions

Female reproductive parameters such as ASM, LSM, reproductive phases, pregnancy rates, calving intervals and reproductive seasonality play an important role in understanding the life history of a species. Here, data from 106 female common dolphins is presented, comprising of 50 sexually immature and 56 sexually mature individuals. As with all opportunistic datasets, our sample size was limited and there is a possibility that this sample may not be fully representative of the population. However, our sample comprised of females from three different sources (single strandings, mass strandings, and fisheries bycatch) spanning a range of ages and maturity levels, giving us confidence in our inferences. With a baseline of reproductive parameters now established, monitoring and management can occur to allow for conservation priorities to be identified.

Chapter 5

General Discussion

Common dolphins in the Hauraki Gulf, Auckland, April 2021.

Photograph credit: Emily Palmer

In the final chapter of this thesis, I synthesise age, growth and reproductive findings from data chapters for common dolphins (*Delphinus delphis*) in Aotearoa New Zealand waters. This is in the context of known threats and current management plans. Specifically, I address the following: (1) outline the contribution to knowledge that the thesis overall provides, (2) evaluate what conservation and management exists for the species currently and what this thesis provides in this context, and (3) highlight aspects of future research.

5.1 Contribution to knowledge

Despite their cosmopolitan distribution (Perrin 2018; Saavedra et al. 2021), it is globally recognised that several sub-populations of common dolphins are under threat and/or in decline (Murphy et al. 2021; Mussi et al. 2019; Saavedra et al. 2014; Vella et al. 2021). This is in part due to the wide variety of anthropogenic impacts experienced by the species including but not limited to, fisheries bycatch (de Boer et al. 2012; Hamer et al. 2008; Mannocci et al. 2012; Peltier et al. 2016; Rouby et al. 2022; Thompson et al. 2013; Tudela et al. 2005), vessel and tourism interactions (Fumagalli et al. 2021; Martinz and Stockin 2013; Meisnner et al. 2015) and pollution (Borrell et al. 2001; Hernandez-Gonzalez et al. 2018; Murphy et al. 2010; Pierce et al. 2008; Stockin et al. 2021a; Stockin et al. 2021b). To understand population level impacts of these pressures, baseline growth and reproductive parameters are required for future population viability analysis. Population changes can occur without detection unless key reproductive parameters are monitored, as was the case for Mediterranean Sea common dolphins (Bearzi et al. 2003; Piroddi et al. 2011). Overfishing, pollution and fisheries bycatch are some of the threats faced by the species in the region which have led to their decline (Pirroddi et al. 2011; Vella et al. 2020). Parameters have now been established for the population meaning that the species can now be monitored effectively in the region (Vella et al. 2021). This is critical for so called ‘abundant’ species, where the general assumption is that the population is stable until such a point where it crashes (Gaston 2011; Winfree et al. 2015).

Common dolphins are widely distributed in Aotearoa New Zealand (Stephenson et al. 2020) and have an extensive stranding record (Chapter 2). They also continue to be the most bycaught cetacean within Aotearoa New Zealand waters (Mackenzie et al. 2022). Despite this, they are not a conservation priority in Aotearoa New Zealand (Baker et al. 2019) and only recently has the first fisheries risk assessment been carried out for the species (Mackenzie et al. 2022). The designation of the ‘Not Threatened’ conservation status has occurred in the absence of growth and reproductive data. This thesis provides a baseline on growth and reproductive parameters for the population within Aotearoa New Zealand waters. There is now the ability to build from this important data and allow for the possibility to make more informed conservation management decisions for the species.

As acknowledged by Möller et al. (2020), relatively little is known about the biological parameters of common dolphins in Aotearoa New Zealand, especially compared to international populations. Considering life history traits now obtained for the species, management agencies for conservation and fisheries need to review current management policies in the context of biological data identified here. Here, reported growth and reproductive parameters for Aotearoa New Zealand align with international populations that are heavily impacted by fisheries bycatch and other anthropogenic impacts. This has significant implications for the conservation and management of common dolphins in Aotearoa New Zealand waters.

This thesis examined the life history of common dolphins (*D. delphis*) in Aotearoa New Zealand waters. Knowledge garnered especially on growth and reproductive parameters, provides conservation managers with critical baseline data for a species impacted by commercial fisheries, both nationally and across the Tasman Sea (Abraham et al. 2017; Bilgmann et al. 2008; Du Fresne et al. 2007; Goldsworthy et al. 2019; Mackay and Goldsworthy 2017; Parra et al. 2021; Thompson et al. 2013; Tulloch et al. 2020). Such data will enable population viability analyses (PVA) to be conducted.

5.1.1 Age, growth and sexual dimorphism of common dolphins in Aotearoa New Zealand

In Chapter 2, the first descriptions of age, growth, and sexual dimorphism of common dolphins in Aotearoa New Zealand waters are presented. Both males and females obtained physical maturity at a similar age and length than that of international populations (Danil and Chivers 2007; Grandi et al. 2022; Murphy et al. 2005; Murphy and Rogan 2006; Murphy et al. 2009; Westgate 2005). Males obtained asymptotic length at a greater size than females, which is consistent with the species internationally (Grandi et al. 2022; Murphy and Rogan 2006; Westgate 2005). The growth patterns of the species within Aotearoa New Zealand waters align with common dolphins globally, though less sexual dimorphism is observed for common dolphins in this region. Understanding aspects of growth has important implications for knowledge obtained for sexual maturity of male (Chapter 3) and female (Chapter 4) common dolphins in Aotearoa New Zealand waters. Estimated length-at-birth aligned with recorded estimates for global populations (Ferrero and Walker 1995; Grandi et al. 2022; Murphy and Rogan 2006; Westgate and Read 2008). Parameters estimated here are likely influenced by variation in environmental factors and availability of resources. Age and growth parameters calculated for this chapter, such as length at birth and length at physical maturity, align with numerous at-risk international populations that are heavily impacted by anthropogenic pressures. Given this study represents the first assessment of age and growth parameters for the population, there needs to be careful monitoring from herein to determine whether this reflects the baseline for the population or whether these parameters are changing.

5.1.2 Reproductive biology of male common dolphins in Aotearoa New Zealand waters

The first descriptions of immature, pubescent and mature males using histological and morphological data were presented in Chapter 3. Testicular variables were better indicators of sexual maturity than demographic variables. The length at attainment of sexual maturity for males in Aotearoa New Zealand waters aligned with international populations, although the age at attainment of sexual maturity was at the younger end of previously reported estimates. This geographical variation in attainment of sexual maturity may be driven by factors such as habitat, diet, anthropogenic impacts and other environmental factors. Reproductive seasonality is observed for Aotearoa New Zealand males, as it is with other global populations. Alongside knowledge of sexual dimorphism (Chapter 2), this gives insight into male mating strategy and the overall promiscuous mating system for the species, where males invest heavily in reproductive tissues and have large testes relative to body size. This chapter provides a first step toward more effective management for the species in Aotearoa New Zealand waters.

5.1.3 Reproductive biology of female common dolphins in Aotearoa New Zealand waters

Critical reproductive parameters such as age and length at attainment at sexual maturity, gestation and lactation period, foetal growth rate, annual pregnancy rate and calving interval were estimated for female common dolphins in Aotearoa New Zealand waters in Chapter 4. Average age and length at attainment of sexual maturity aligned with international populations, though as with males (Chapter 3), age at sexual maturity was at the younger end of the international spectrum. Females have a marginally longer gestation period than that of females from other regions, though foetal growth was slightly slower than that reported in international populations. Annual pregnancy rate was higher than that of temperate North Atlantic common dolphins but lower than the eastern tropical Pacific population. Additionally, there appears to be limited seasonality to female reproduction, with births occurring year-round, though peaking in austral spring. It is yet to be determined whether these parameters are a natural baseline for the population or whether these are changing or have changed over time.

Table 5.1: Biological information on common dolphins (*Delphinus delphis*) in Aotearoa New Zealand waters.

	Male	**Female**
Min TBL	89 cm	83 cm
Max TBL	244 cm	233 cm
Min age	0 yrs	0 yrs
Max age	26 yrs	29 yrs
Length at birth	85.4 cm*	
TBL range of sexually immature individuals	89 – 200 cm	82 – 193 cm
TBL range of sexually mature individuals	190 – 244 cm	183 – 233 cm
Age range of sexually immature individuals	0 – 9 yrs	0 – ≥ 9 yrs
Age range of sexually mature individuals	7.5 – 26 yrs	7 – 29 yrs
Average TBL at attainment of sexual maturity	198.3 cm	183.5 cm
Average age at attainment of sexual maturity	8.8 yrs	7.5 yrs
Average TBL at attainment of physical maturity	212.1 cm	198.3 cm
Average age at attainment of physical maturity	20 yrs	18 yrs
Combined testes weight range in mature males	492 – 5796.5 g	NA
Reproductive seasonality?	Yes	No
Gestation period	NA	12.6 – 12.8 m
Annual pregnancy rate	NA	0.30 yr^{-1}
Calving interval	NA	3.15 – 3.2 yrs
Lactation period	NA	12.6 – 12.8 m
Resting period	NA	12.6 – 12.8 m

*Sex differences were not calculated

5.2 Conservation and management

Species-led conservation management tends to focus primarily on species with a high and/or imminent risk of extinction. This usually results in prioritising species with small populations and/or geographical ranges (Stockin 2008). Efforts are also generally focused on those that are recognised as flagship (Bennett et al. 2015), keystone (Sinclair 2003) or indicator species (Lindenmayer 1999), with the idea that these ‘surrogate’ species may safeguard more biodiversity via proxy over long periods of time (Caro 2010). Common and widespread species are also of significant conservation importance (Gaston 2011, Winfree et al. 2015), yet they typically receive less attention. They are important for three reasons: (1) many species currently threatened or extinct could have previously been described as common and widespread; (2) there is mounting evidence that large numbers of currently common and widespread species are undergoing massive declines which are having subsequent ramifications for ecosystem functions and services, and (3) processes that underline such declines seem likely to intensify with time (Gaston and Fuller 2007). As a result, there is a need for conservationists to pay more attention (i.e., long-term monitoring) to species considered abundant and widespread (Stockin 2008).

Aotearoa New Zealand is an important biodiversity hotspot (Myers et al. 2000) and home to many endemic species that are threatened with extinction. The country has experienced massive biodiversity loss, with nearly one-third of terrestrial and freshwater bird species going extinct due to anthropogenic activity in the last ~700 years (Wilson 2004). Loss of indigenous cover from terrestrial landscapes is also an issue, with over 70% loss occurring for almost two-thirds of land environments (Proce et al. 2006). However, little is comparatively known about the loss of diversity in the marine environment, despite the marine environment being 21 times larger than the terrestrial environment (MacDiarmid et al. 2013). Marine research efforts are typically focused on commercially important (e.g., snapper, *Pagrus auratus*) or threatened endemic species such as Hector's (*Cephalorhynchus hectori hectori*) and Māui's (*C.h. maui*) dolphins. Protecting biodiversity and preventing extinction remain critical parts of the Aotearoa New Zealand Government's Biodiversity Strategy (Department of Conservation 2020), which is primarily facilitated by the Aotearoa New Zealand Threat Classification System (Townsend et al. 2008). This strategy is administered by the Aotearoa New Zealand Department of Conservation (DOC), with reference to the International Union for Conservation of Nature (IUCN) Red List of Threatened Species.

5.2.1 Threat classification

Life history knowledge must inform threat status as it is one of the most critical aspects for assessing population viability. Population viability analysis is the estimation of the probability of extinction of a population (Lacy 1993), of which reproduction plays a vital role. Reproduction can be more influential to population dynamics than adult survival and therefore, a feasible way to reverse potential declines in the population is to increase reproductive rates (Manlik et al. 2016). Ashe et al. (2021) used population viability analysis to assess the sensitivity of four species of oceanic dolphins, one of which was common dolphins. It was identified that projected declines of the species would not be detected in the current monitoring system which is of concern as the US system is one of the most data-rich systems internationally. Again, this demonstrates the importance of monitoring species we deem to be 'common' and 'abundant', and that proactive management and monitoring are critically important (Ashe et al. 2021).

Parsons (2016) stated there is also a need for species that are data deficient/poor to be more accurately classified as "assumed threatened". The management of a species, which is generally based on threat status, means that those listed as data deficient/poor do not allow for precautionary approaches in conservation as it is not seen "category of threat" (IUCN 2001; Parsons 2016). Within the Southern Hemisphere specifically, little knowledge is available on any biological parameters of the species which limits the effectiveness of potential conservation management. There are few abundance estimates for common dolphins conducted off South Africa (Cockcroft and Peddemors 1990), and more recently from localised regions off southern Australia (Bilgmann et al. 2018; Parra et al. 2021) and here in Aotearoa New Zealand (Abraham et al. 2017). Despite the recognition of vulnerable and declining subpopulations with numerous anthropogenic threats, the 'Least Concern' IUCN conservation status has been given to common dolphins globally as there is "no evidence that threats are resulting in a global decline" (Braulik et al. 2021).

5.2.2 Management

Marine mammal populations are challenging to manage, especially when there is limited biological information available on the population or species (Stockin 2008). Effective management requires accurate biological information, such as life history knowledge (Betty 2019; Danil and Chivers 2007; Slooten 1991). This thesis provides critical life history knowledge of age and growth (Chapter 2), and male (Chapter 3) and female (Chapter 4) reproductive parameters. Such data can help inform accurate and effective conservation management. Changes to the demographic structure of a population can be monitored by changing reproductive parameters. Such changes may lead to a lack of mature individuals which can ultimately lead to a rapid decline in the population (Jackson et al. 2020). Actual and potential anthropogenic impacts can either be reduced or increased based on a species conservation status within a region (Peltier et al. 2016). A more comprehensive understanding of the species management needs has been achieved through the knowledge presented by this thesis.

DOC is the government agency responsible for marine mammal management within Aotearoa New Zealand waters. Möller et al. (2020) published the most recent summary on the genetics, population structure and demography of common dolphins in Aotearoa New Zealand waters. More recently, focused studies on reproduction (Palmer et al. 2022; 2023), diet (Peters et al. 2020; Stockin et al. 2022) and contaminants (Stockin et al. 2021a; Stockin et al. 2021b) have been published. When looking at ways to manage common dolphin populations across the Australasian region, new taxonomy data suggests the Australasian population should be managed as one management unit (Barceló et al. 2021). Currently, multiple management units of common dolphins in Southern and South-Eastern Australia exist (Bilgmann et al. 2014). Meanwhile in Aotearoa New Zealand, no management units have been defined as they are not considered a threatened species. Parra et al. (2021) recently assessed the abundance and potential removal of common dolphins in South Australia and found that historically estimated bycatch exceeded the potential biological removal limits. More recent estimates highlight this limit is no longer being exceeded, however, there is uncertainty due to low observer coverage and underreporting of mortality meaning that estimates of bycatch are not robust (Parra et al. 2021). Low observer coverage is also an issue in Aotearoa New Zealand but potential removal estimates cannot be calculated due to the lack of abundance estimates. Marine Mammal Risk Assessments (MMRAs) have been carried out on the species due to their historically high levels of bycatch in certain regions (Abraham and Berkenbusch 2019a; Abraham et al. 2017; Abraham et al. 2021; MacKenzie et al. 2022).

5.2.3 Fisheries Bycatch

In the most recent risk assessment by MacKenzie et al. (2022), common dolphins were the most bycaught cetacean within Aotearoa New Zealand waters. Between 1995 and 2019, 225 total observed captures of common dolphins were recorded in commercial fisheries. Modelled observed captures between 2016 and 2019 using mean commercial fisheries effort estimated ca. 60 bycaught individuals in these 3 years. As many fisheries in Aotearoa New Zealand waters are underreported and have little to no observer coverage, this makes it difficult to determine incidental capture rates (Möller et al. 2020). Historically, the jack mackerel fishery on the west coast of the North Island has had high reported bycatch of common dolphins (Du Fresne et al. 2007; Thompson et al. 2013) but with increasing observer coverage and changes to fishing operations, bycatch was reduced to negligible between 2016 and 2019 (Möller et al. 2020). In somewhat of a contrast, between 2019 and 2022, a total of 34 common dolphins were bycaught in Aotearoa New Zealand fisheries from self-reporting on fishing boats (Ministry for Primary Industries 2022). This information was released in a report associated with a landmark case launched against the Aotearoa New Zealand Government (Ministry for Primary Industries 2022). As with all marine mammal species, common dolphins are protected under the Marine Mammal Protection Act 1978 and yet there has been little evidence of success in reducing bycatch of this species. Further monitoring and extending observer coverage (Allen et al. 2017; Jaiteh et al. 2013) to other fisheries within Aotearoa New Zealand waters would allow a better understanding of the full extent of bycatch on common dolphins within the region.

The knowledge garnered from this thesis will aid in determining the vulnerability of the population to fisheries bycatch. Knowledge of population structure and distribution alongside reproductive parameters, such as age at maturity (estimated in Chapter 3 and Chapter 4) are used in calculations for assessments such as Population Viability Analysis (PVA; Verborgh et al. 2021; Wade et al. 2012). Bycatch reference point is another calculation that is used to assess the impact of bycatch on marine mammal populations (Wade et al. 2021). This calculation requires the minimum estimate of abundance, the maximum reproductive rate, and the recovery factor of a population (Wade et al.

2021). This thesis contributes to understanding with reproductive knowledge (Chapter 3 and Chapter 4), age class knowledge and growth models (Chapter 2). Bycatch data has been collected consistently since the late 1990s for common dolphins, especially in specific areas around Aotearoa New Zealand. The next step will be to systematically assess the abundance of common dolphins in Aotearoa New Zealand waters as almost all assessments require this knowledge. The impact of fisheries bycatch of common dolphins, along with all marine mammals, will likely be exacerbated by climate change in the form of altering fish recruitment, range shifts, and prey availability which may lead to more aggressive interactions between marine mammals and fisheries gear, especially in times of low prey abundance (Roberts and Hendricks 2022).

5.2.4 Climate Change

Climate change is altering the marine environment in numerous ways including increasing sea level and warming and acidification of the oceans. The two major impacts of climate change (so far) on marine mammals are geographical range shifts and habitat loss (Evans and Waggit 2020). Other documented impacts also include altering migration patterns (Huntington et al. 2017; Nagelkerken and Munday 2016), timing of breeding (Sydeman et al. 2015) and overall demographic rates that drive population change (Roberts and Hendricks 2022). Climate change has been recognised as a major threat to common dolphins in some parts of the Northern Hemisphere such as in the Mediterranean (Vella et al. 2021).

Roberts and Hendricks (2022) recently assessed the potential effect that climate change will have on marine mammals in Aotearoa New Zealand. It is suggested that the areas that common dolphins are abundant in currently (North Island and west coast South Island; Stephenson et al. 2020) will likely become less productive by the end of the century due to changing prey availability and distribution (Albouy et al. 2020; Allan et al. 2013; Ono 1996).

Climate change models and forecasting have historically tended to leave out important biological mechanisms, such as physiology, demography, and life history, which have demonstrated importance in determining species and ecosystem responses to climate change (Urban et al. 2016). Good-quality long-term data sets are required to quantitatively assess the impact of climate change on marine mammal species (Fleishman et al. 2016) as well as detecting and understanding trends in life history. This thesis provides an important baseline of life history knowledge for Aotearoa New Zealand common dolphins from which trait-based modelling can be used to assess climate change impacts on the species.

5.3 Study limitations

This study used an opportunistic dataset of both stranding and bycatch events. Opportunistic data sets tend to have several limiting factors. For example, stranding events can have a bias towards a certain age class, sex, season and location (Lanyon and Burgess 2014). In bycaught individuals, capture probability varies with age and sex (Brown et al. 2014; Fernández-Contreras et al. 2010; Fruet et al. 2012). When collecting samples from stranded individuals, exposure to air, sun and water can impact sample quality. Determination of sexual maturity can be affected by this as gonadal samples are quick to decompose. Additionally, freezing can impact tissue quality with stranded individuals, and carcasses are transported from stranding location to post-mortem frozen. Another limitation of this study is that there is a lack of larger and older individuals. This may have influenced the growth models and asymptotic values calculated in this study. This can be improved with the addition of larger and older individuals in the data set as there were very few individuals above 20 years of age.

Age at sexual and physical maturity underpins life history and age is the basis for many parameters calculated in this study. Aging via GLGs in teeth can come with numerous challenges, especially in older individuals, including the wearing down of the tooth, the tooth curving, compression of GLGs and accessory layers (Barratclough et al. 2023). To mitigate such issues, best practice and standardised methods were implemented in this study such as blind readings, no *a priori* knowledge, and three experienced readers.

Previous international studies have used opportunistic datasets (Danil and Chivers 2007; Murphy et al. 2009; Westgate and Read 2007) and this dataset has a wide latitudinal spread of samples across the North and South Island of Aotearoa New Zealand which minimises certain biases. Additionally, this thesis also avoids the caveats of single strandings which tend to bias older and/or diseased individuals (Cordes 1982; IJsseldijk et al. 2020). Mass strandings tend to have a mix of ages and usually contain healthy individuals (Brabyn and McLean 1992; Evans et al. 2005; Pugliares-Bonner et al. 2021), of which this dataset contains nine mass stranding events.

While these limitations exist, protocols and procedures have been put in place to minimise the impact they have on the study. Despite the dataset spanning more than a quarter of a century, the sample size can always be increased. This will allow improved estimates of parameters and monitoring of the population to identify any changes.

5.4 Future Research

There are still critical knowledge gaps that remain to better understand common dolphins in Aotearoa New Zealand waters. Further insights of growth and reproduction are required to monitor any changes to the parameters assessed in this thesis. This has important implications for the conservation management of common dolphins in Aotearoa New Zealand waters. Other important areas of proposed research include:

5.4.1 Age and growth

Knowledge of age structure and growth is important for answering species-related biology, ecology, and conservation questions (Evans et al. 2010; Fortune et al. 2012). Growth models, allometry and sexual dimorphism are first described here for both male and female common dolphins. This allows an understanding of morphological diversity between sexes and geographical variation within a species (Murphy et al. 2006; Weckerly 1998), offering important insights into growth variability (Betty et al. 2022). The inclusion of more older individuals will be important to clarify the length and age at asymptotic lengths for males and females. Additionally, as the length-at-birth parameter is not separated by sex, the inclusion of more foetal data will be important to determine sex-specific length-at-birth estimates. As this dataset is built upon, it will be important to re-assess these parameters to monitor any changes in the Aotearoa New Zealand population of common dolphins.

5.4.2 Reproductive biology

Future studies would benefit from the addition of more pubescent and mature males across all seasons, which would aid in refining estimates of ASM, LSM and the understanding of indicators of sexual maturity for male common dolphins. The distinction between ovarian scars from ovulation or pregnancy would allow for more definite conclusions to be made about the persistence of scars and the rate of accumulation in females. Further sampling of females will also allow for a better idea of reproductive seasonality as currently, the seasonality of males and females does not align. Alternative methods of determining sexual maturity could also be assessed which may include biopsies from free-ranging animals (Kellar et al. 2006; Kellar et al. 2009; Kellar et al. 2014) or using other distinguishing features such as the postanal hump in mature males (Heyning and Perrin 1994; Murphy 2004; Neumann et al. 2002; Ngqulana et al. 2017).

Further assessment of reproductive dysfunction and disease is required, especially in the context of legacy and emerging contaminant burdens reported in Aotearoa New Zealand (Stockin et al. 2007; Stockin et al. 2021a; Stockin et al. 2021b). This is because in the North Atlantic, reproductive failure in female common dolphins has been associated with higher contaminant burden (Murphy et al. 2018).

Continued collection of data and future re-estimation of parameters, especially with larger sample sizes, will be beneficial to assess any changes to the population.

5.4.3 Survivorship

Survivorship and mortality rates are other important aspects of understanding population dynamics. Being able to assess survivorship curves, sex and age specific survivorship, life tables, and spatial and temporal patterns of survivability underpins the ability to determine whether certain age classes are more susceptible to anthropogenic impacts such as bycatch. It would be useful to obtain abundance estimates to use the knowledge gained here more effectively.

5.5 Conclusion

This thesis provides critical first insights into the life history of common dolphins in Aotearoa New Zealand waters. Age, growth and reproductive parameters such as age and length at physical and sexual maturity, reproductive phases and growth rates are now described for the first time in this population. Life history parameters allow us to accurately determine population-level impacts and/or changes from influences such as fisheries bycatch. Certain parameters also allow us to understand which individuals are being lost from the population and assess the viability and sustainability of the population. These crucial first insights to life history of the Aotearoa New Zealand population will allow improved assessment and management of common dolphins in Aotearoa New Zealand waters. Specifically, this thesis provides practical, important data to assess and measure potential anthropogenic impacts to the population i.e., reproductive parameters accurately indicate the viability of a population. Though common dolphins are neither endemic nor ‘threatened’ in Aotearoa New Zealand, they are subject to genetic and morphological differentiation, and as a highly gregarious species, they need to be conserved in large biomasses. Accordingly, long-term longitudinal monitoring will be crucial to assess any changes in these parameters and avoid the same demise seen in international populations of common dolphins.

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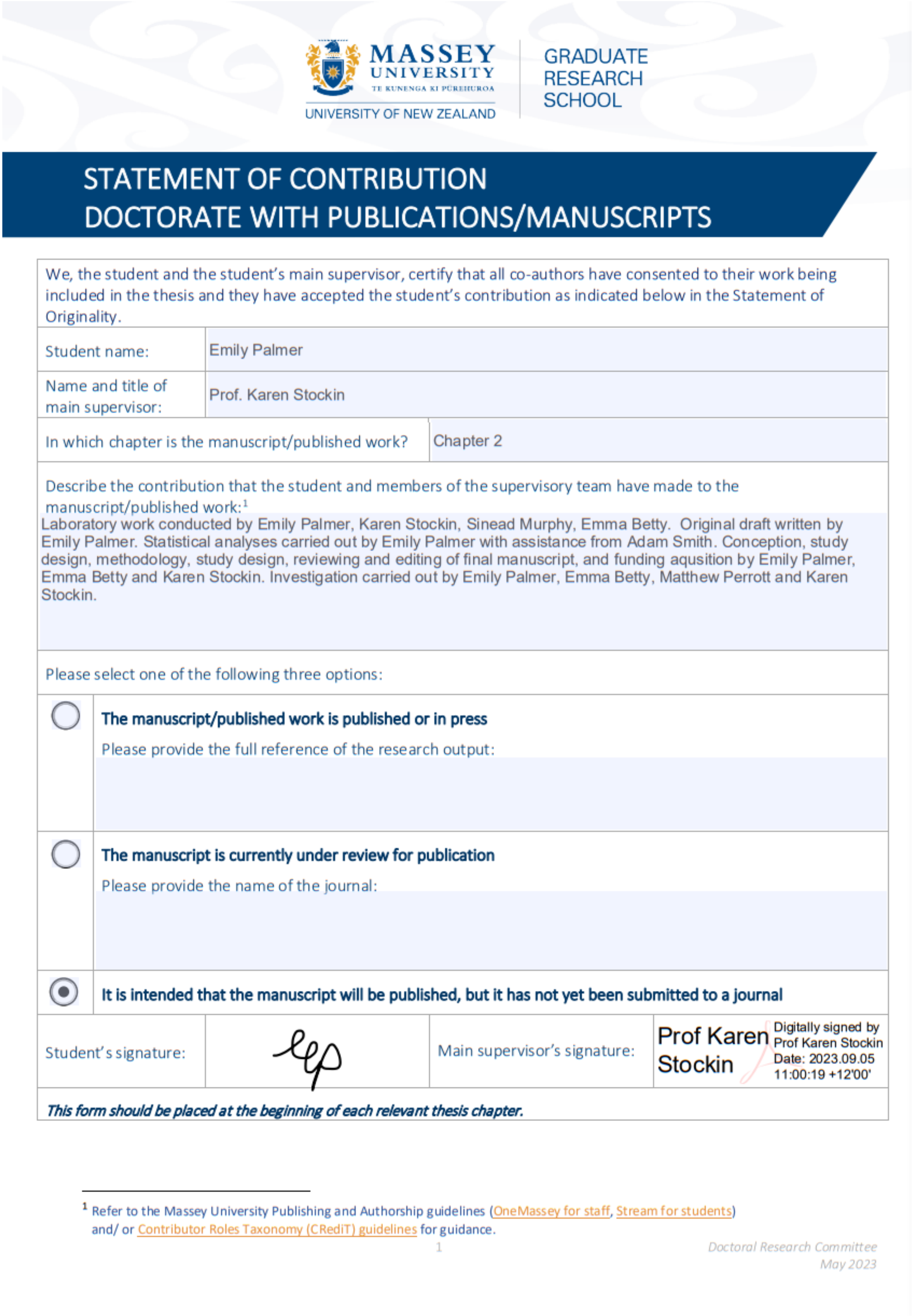
Appendices



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Equation 2A, 3A, 4A. sum-of-fractions immature method

The sum-of-fracture of immature method for estimating the average age at attainment of sexual maturity (ASM) was used as follows:

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

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

J is the first indeterminate age class, k is the last indeterminate age class, p_i is the proportion of immature specimens in age class i, q_i is the proportion of mature specimens in age class i ($p_i + q_i = 1$), x_i is the number of age classes combined to obtain a sample size of >2 in age class i, I_i is the number of immature specimens in age class i, M_i is the number of mature specimens in age class i, and N_i is the number of specimens in age class i ($N_i = I_i + M_i$). Where, if $I_i \neq N_i$, p_i = Ii / N_i, and $q_i = (M_i)/N_{i;}$ if I_i = Ni, $p_i = (I_i - ½)/N_i$, and $q_i = (M_i + ½)/N_i$, and if $M_i = N_i$, $p_i = (I_i + ½)/N_i$, and $q_i = (M_i - ½)/N_{i.}$

The average length at attainment of sexual maturity (LSM) was estimated by modifying the SOFI method, using constant length intervals (5 cm) instead of age (after Danil and Chivers, 2007).

$$\text{LSM} = j + \sum_{i=i_{min}}^{i_{max}\Sigma} p_i x_i$$

$$\text{Variance } (s^2) = \sum_{i=i_{min}}^{i_{max}\Sigma} \frac{p_i(1-p_i)x_i}{n_i-1}$$

J is the lower limit of the length class with the smallest mature animal, i_{min} is the length class with the shortest mature animal, i_{max} is the length class the longest mature animal, p_i is the proportion of immature animals in length class i, x_i is the proportion of length classes combined in length class i, n_i is the total number of animals in the ith length class.

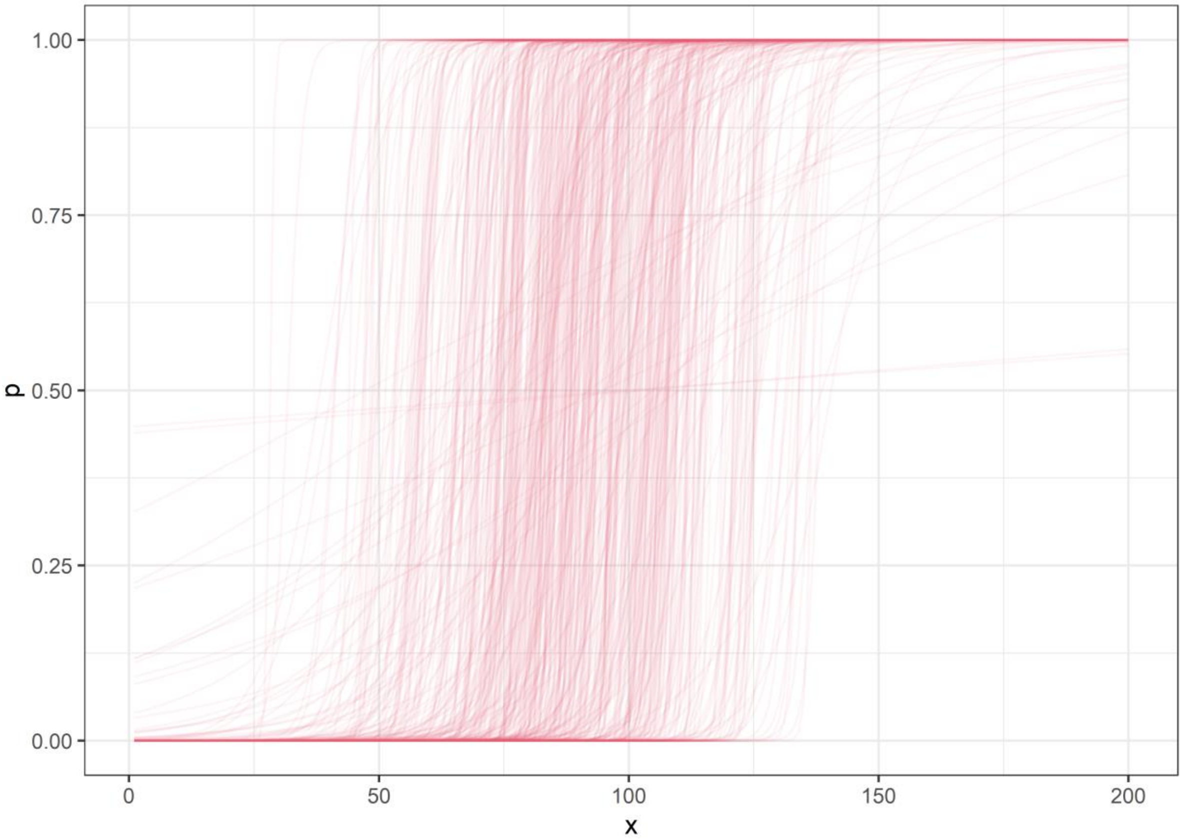


Figure 2B. Prior predictive simulation of p (probability of birth) given x (total body length) for common dolphins stranded along the Aotearoa New Zealand coast and bycaught in Aotearoa New Zealand waters. This is based on prior predictions for Bayesian logistic regression model parameters m = Normal (90, 20) and w = Normal^{+} (0,1). Simulation was fitted using Stan in R (Stan Development Team 2021).

R code:

```
# Function for calculating P(y = 1) given x, w, and m
sim_hof2 <- function(x, m, w) {
  eta = w * ( x - m )
  inv_logit (eta)
}
#set number of simulations
nsim = 500
# draw values of m and w from priors, calculate P, and make plot
expand_grid( x = 1:200,
             data.frame(m = rnorm(nsim, 90, 20),
                        w = abs(rnorm(nsim, 0, 1)),
                        group = 1:nsim)) %>%
```

```
mutate(p = sim_hof2(x = x, m = m, w = w)) %>%
# group_by(group) %>%
ggplot() +
  aes(x = x, y = p, group = group) +
  geom_line(alpha = 3/50, col =2)
```

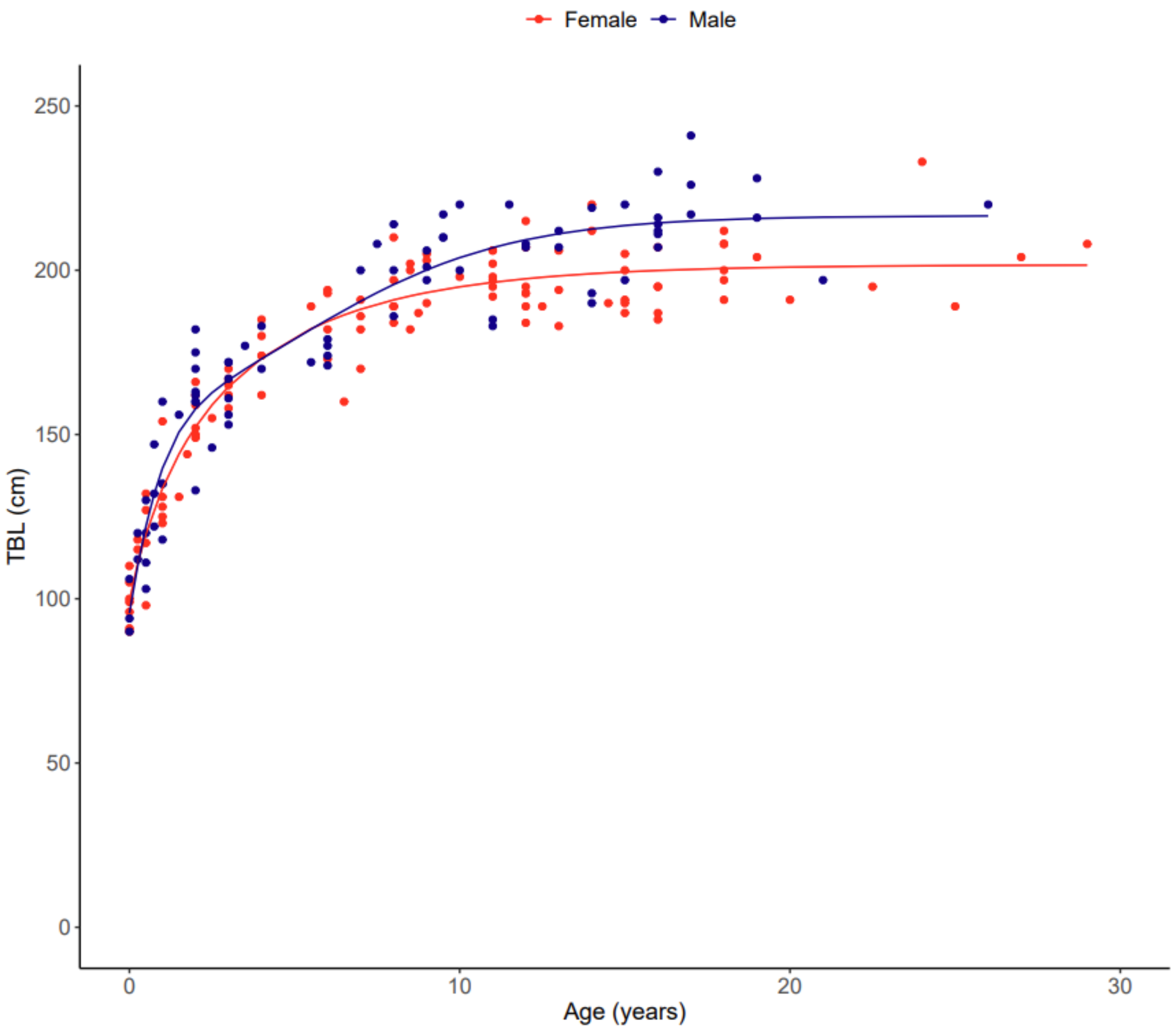


Figure 2C. Growth curves superimposed on length-at-age data for female (Richards growth model) and male (Double-Richards growth model) common dolphins (*Delphinus delphis*) stranded and bycaught in New Zealand from 1997 to 2020 (*n* = 182). The coloured dots represent the length-at-age data and the solid lines represent the sex-specific growth curves.

Table 2D. Summary of male and female common dolphin (*Delphinus delphis*) estimates of average age (APM, in years), length (LPM, in cm), and length at birth (cm) from published studies.

Location	**Eastern North Atlantic**	**Eastern North Atlantic – North West Spain**	**Western North Atlantic**	**Eastern Tropical Pacific**	**North Pacific**	**Western South Atlantic**	**Aotearoa New Zealand**
Reference	Murphy and Rogan 2006	Read et al. 2019	Westgate 2005; Westgate and Read 2007	Danil and Chivers 2007	Ferrero and Walker 1995	Grandi et al. 2022	Chapter 2
Source	Strandings and bycatch	Strandings and bycatch	Strandings and bycatch	Bycatch	Bycatch	Strandings and bycatch	Strandings and bycatch
APM	Male = 11 Female = 9	Male = 10.5 Female = 8.4	Not reported	Not reported	Not reported	Male = 15 Female = 14	Male = 20 Female = 18
***n* APM**	Male = 107 Female = 78	Male = 216 Female = 168	Not reported	Not reported	Not reported	Male = 53 Female = 36	Male = 78 Female = 104
LPM	Male = 211.6 Female = 197.4	Male = 214 Female = 199	Male = 221.5 Female = 202.2	Male = not reported Female = 197.2	Male = 188.1 Female = 179.4	Male = 210.75 Female = 196	Male = 212.1 Female = 198.3
***n* LPM**	Male = 107 Female = 78	Male = 331 Female = 224	Male = 161 Female = 74	Female = 405	Male = 93 Female = 59	Male = 53 Female = 36	Male = 78 Female = 104
Method used	Gompertz growth curve	Not reported	Gompertz growth curve	Regression (logistic)	Gompertz growth curve	Gompertz growth curve	Gompertz growth curve
Length at birth	Male = 108.8 Female = 104.1	Not reported	92.7 cm	83.7 - 87	82	91.4	85.4
Length at birth method	Mean overlap statistic	Not reported	Mean neonatal length	Logistic regression	Mean neonatal length	Mean neonatal length	Logistic regression
***n* length at birth**	18	Not reported	6	Not reported	3	3	19

Table 2E. Summary table of allometric growth type in the Aotearoa New Zealand (NZ), South African (SA) and eastern North Atlantic (ENA) populations of common dolphins (*Delphinus delphis*).

	FEMALE			**MALE**		
	NZ	**SA**	**ENA**	**NZ**	**SA**	**ENA**
Snout_anus	=1	=1	=1	=1	=1	=1
Snout_genital slit	=1	=1	<1	=1	=1	=1
Snout_navel	=1	>1	<1	=1	=1	<1
Snout_originflipper	=1	>1	<1	=1	>1	<1
Snout_origindorsalfin	=1	=1	<1	=1	>1	<1
Snout_tipdorsalfin	=1	>1	<1	=1	<1	<1
Snout_blowhole	=1	=1	=1	=1	=1	=1
Snout_cnrmouth	>1	<1	=1	=1	<1	=1
Genitalslit	<1	NA	NA	<1	NA	NA
Rostrum	<1	<1	NA	<1	<1	NA
Cnrmouth_eye	<1	<1	NA	=1	<1	NA
Eye_blowhole	=1	<1	NA	=1	>1	NA
Dorsalfinheight	<1	<1	<1	<1	<1	P
Dorsalfinlatbase	<1	<1	=1	=1	<1	=1
Flukewidth	<1	<1	>1	<1	<1	=1
Flukelength	=1	NA	NA	=1	NA	NA
Flukenotch	<1	<1	NA	<1	<1	NA
Flipperinternal	<1	<1	<1	<1	<1	<1
Flipperexterior	=1	=1	<1	=1	=1	<1
Flipperwidth	<1	<1	<1	<1	=1	<1
Girthflippers	=1	<1	<1	=1	<1	<1
Girthnavel	=1	NA	NA	=1	NA	NA
Girthanus	=1	=1	=1	=1	<1	=1

"=1" refers to isometric growth, ">1" refers to positive growth, "<1" refers to negative growth. NA = not assessed.

Table 3B. Summary of male common dolphin (*Delphinus delphis*) estimates of average age (ASM, in years) and length (LSM, in cm) at attainment of sexual maturity from published studies. Where available, 95% confidence intervals(CI), credible (CrI) intervals or standard error (SE) are also presented.

Location	**Eastern North Atlantic**	**Eastern North Atlantic – North West Spain**	**Western North Atlantic**	**Eastern tropical Pacific**	**North Pacific**	**Western South Atlantic**	**Aotearoa New Zealand**
Reference	(Murphy 2004; Murphy et al. 2005)	(Read et al. 2019)	(Westgate 2005; Westgate and Read 2007)	(Oliver 1973)	(Ferrero and Walker 1995)	(Grandi et al. 2022)	Chapter 3
Source	Strandings and bycatch	Strandings and bycatch	Strandings and bycatch	Bycatch	Bycatch	Strandings and bycatch	Strandings and bycatch
ASM (95% CI or CrI)	11.86 (SE = 0.62)	10.5	9.45 (SE = 0.19)	Not reported	10.5 (SE = 0.5)	Immature: 0-9 Mature: 6-23	Regression = 8.77 (7.81 – 9.84) SOFI = 8.75 (SE = 0.16)
***n* ASM**	Immature = 136 Mature = 38	Total = 216	Immature = 57 Mature = 98	Not reported	Immature = 50 Mature = 21	Immature = 12 Mature = 40	Immature = 30 Mature = 21
LSM (95% CI or CrI)	~200	204	215	202	~180 Immature = 179 Mature = 182	Immature: 97.5 - 209 Mature: 184 - 228	Regression = 198.33 (191.39 – 204.89) SOFI = 200 (SE = 0.15)
***n* LSM**	Immature = 140 Mature = 45	Total = 266	Immature = 57 Mature = 98	Total = 405	Immature = 50 Mature = 21	Immature = 12 Mature = 40	Immature = 37 Mature = 24
Method used	SOFI	Not reported	SOFI	Not reported	SOFI	Not calculated	Bayesian (regression) and SOFI

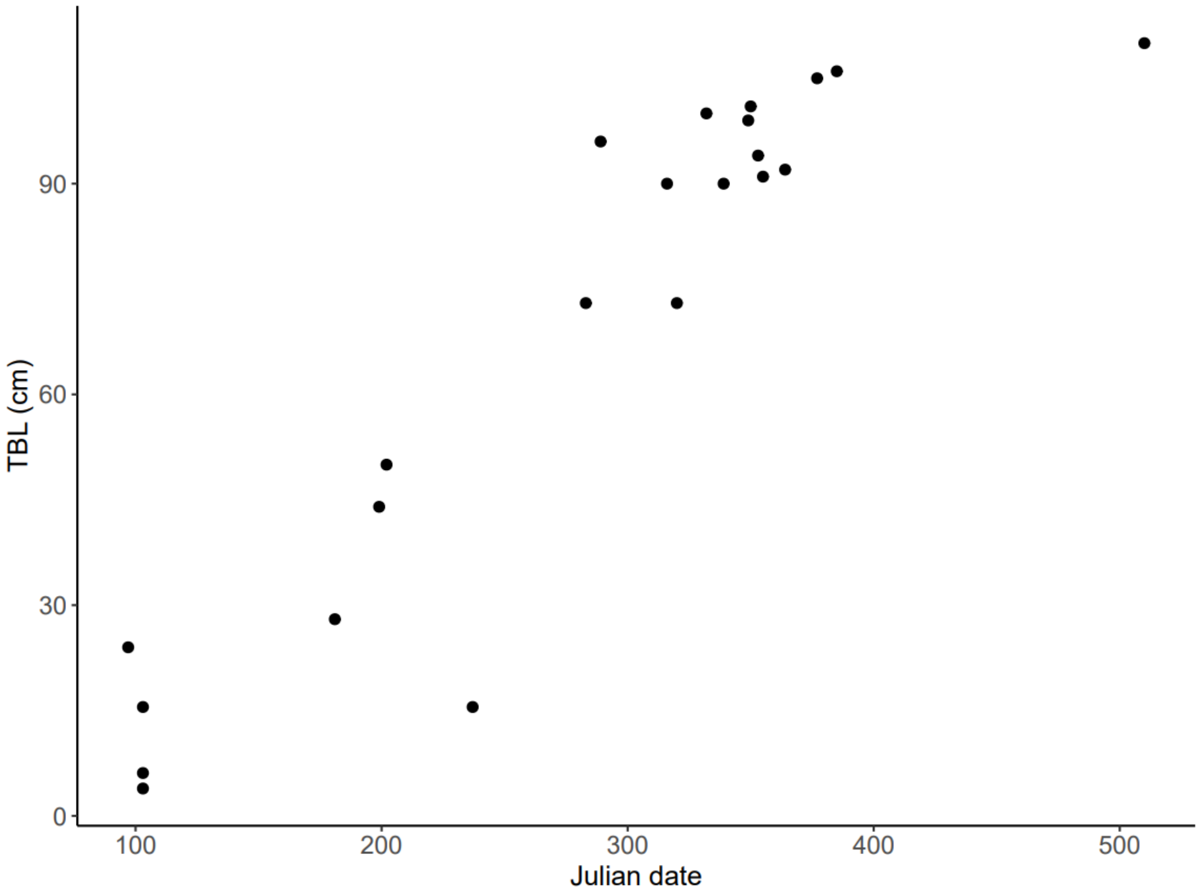


Figure 4B. Crown to rump measurement (cm) of foetuses and total body length (TBL) of neonates (cm) of foetuses and neonates against day of year of collection (Julian date) for common dolphins examined from Aotearoa New Zealand waters between 1997 and 2019.

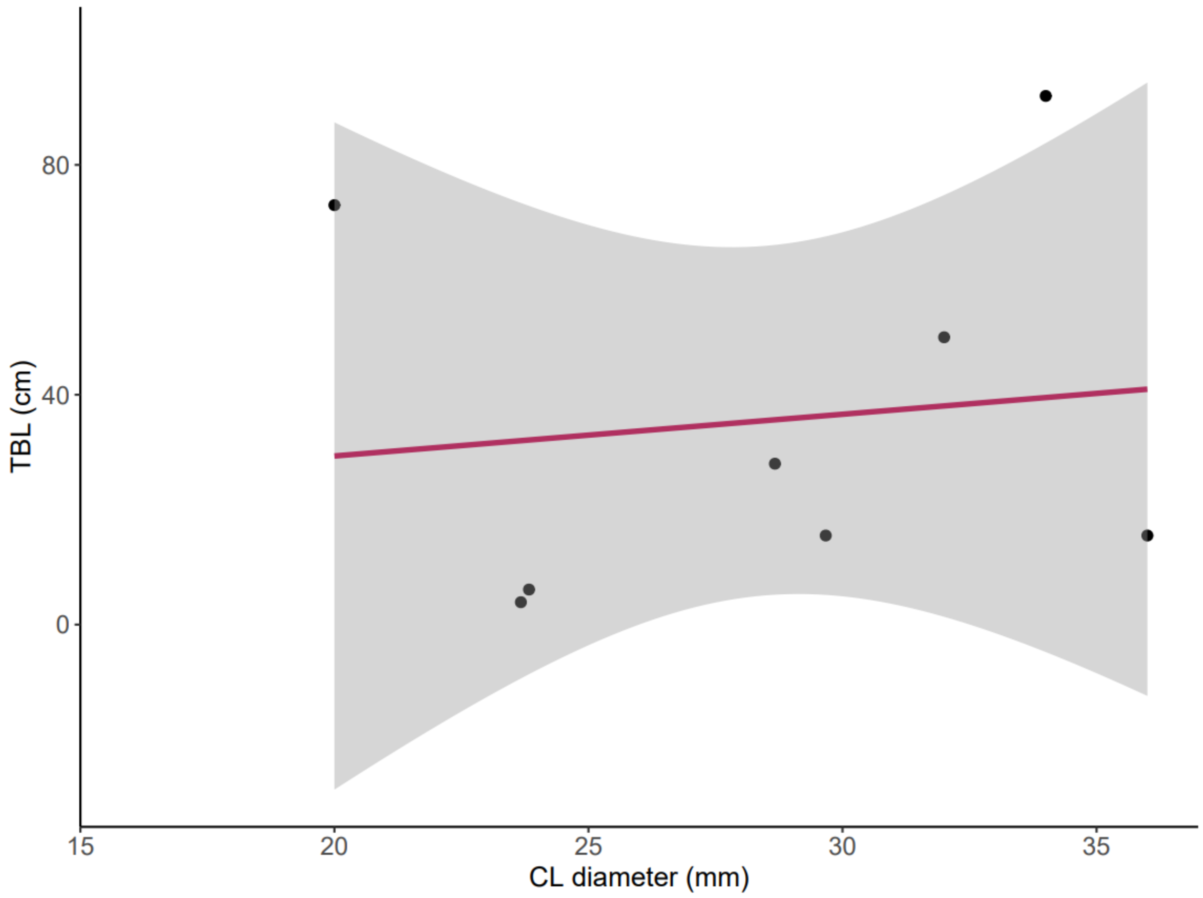


Figure 4C. Linear regression of foetal crown to rump measure (cm) as a function of *corpus luteum* (CL) diameter (mm) for female common dolphins examined from Aotearoa New Zealand waters between 1997 and 2019. The solid pink line indicates the linear regression (Y = 0.7263x + 14.814, r^2 = 0.01524, *n* = 8). The shaded area represents the 95% confidence interval for the regression.

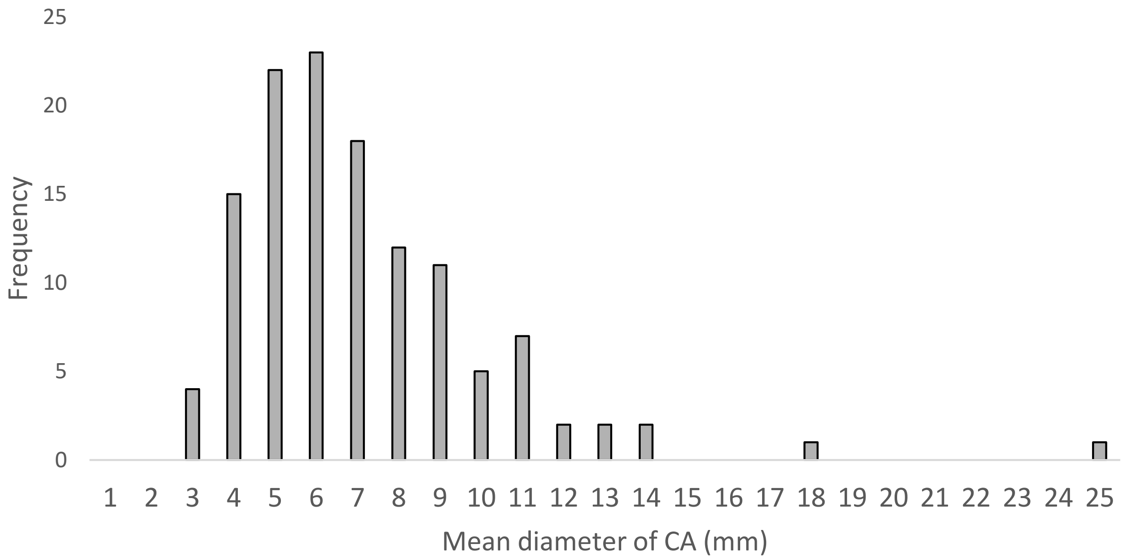


Figure 4D. Size frequency distribution of *corpora albicantia* (CAs) on the ovaries of female common dolphins (n = 123 from 49 individuals) examined from Aotearoa New Zealand waters between 1997 and 2019.

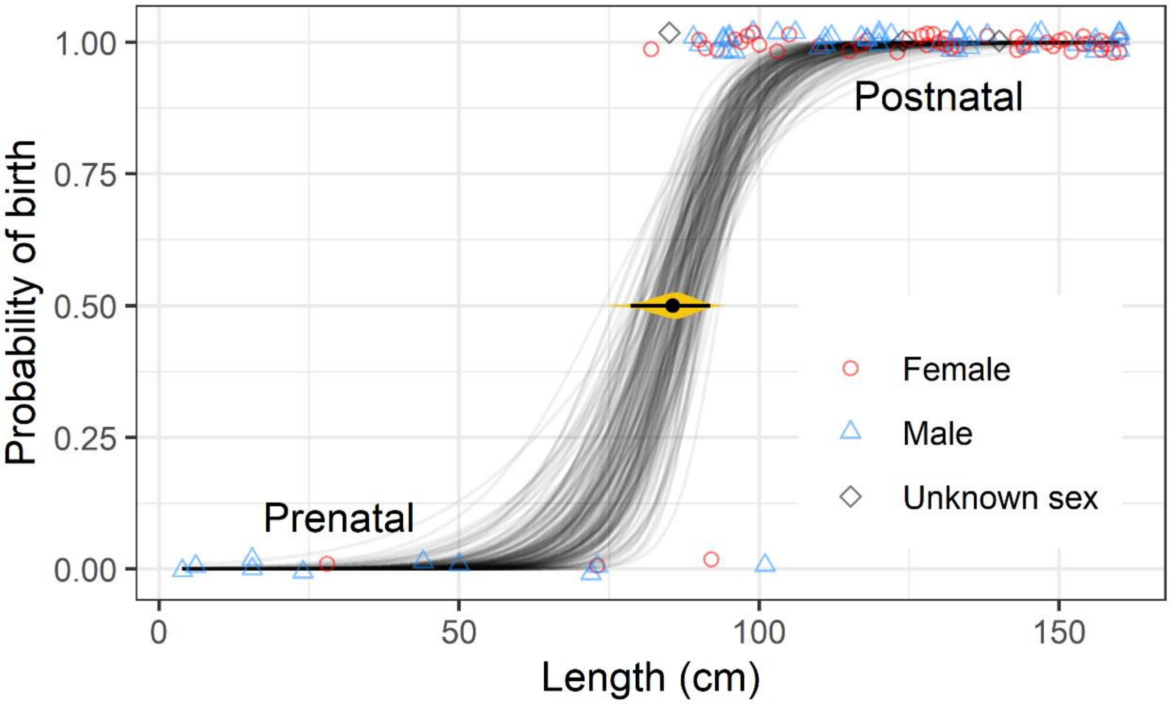


Figure 4E. The total body lengths of prenatal and postnatal common dolphins examined in Aotearoa New Zealand from 1997 to 2019 (n = 103). Logistic curves show the mean probability of birth as a function of length (thin grey lines) using the partially weighted model that disregards sex and is fitted to n = 103 cases. 'Jitter' and a small amount of transparency was used to aid in the visualisation of the overlapping points. The small centre point and thin horizontal line show the mean and 95% highest posterior density interval for the length at which the probability of birth is 50% i.e., the estimated median length-at-birth. The gradient plot is highlighted in yellow (Kay, 2021).

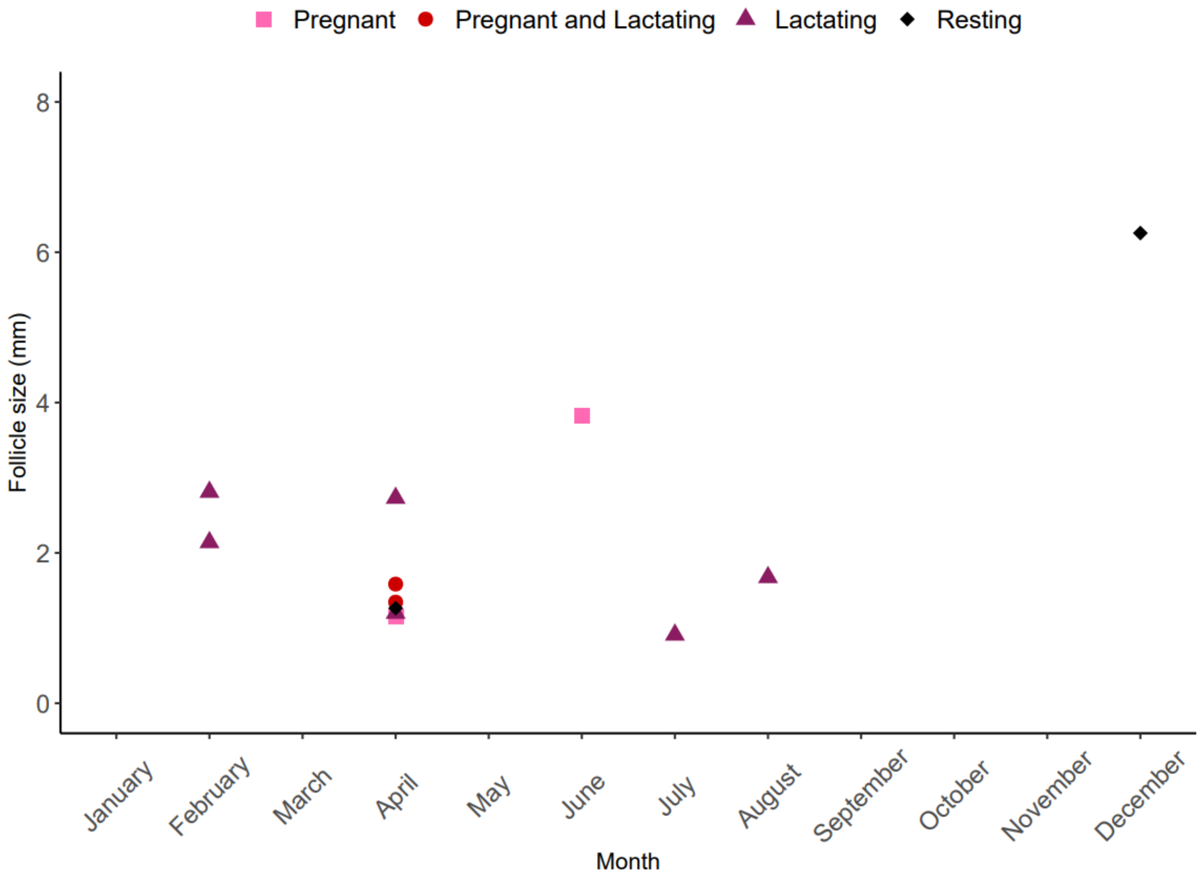
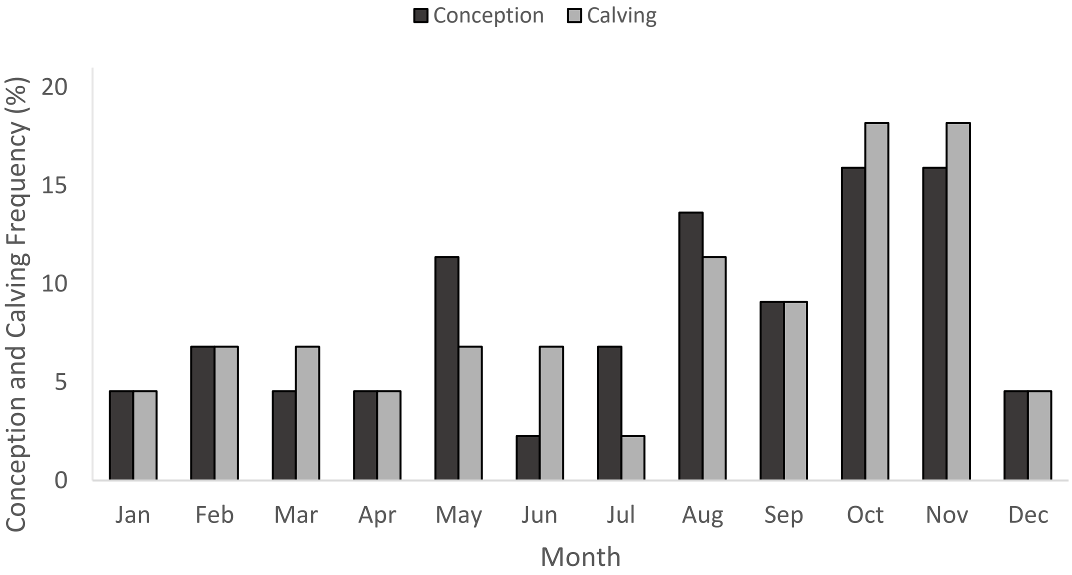
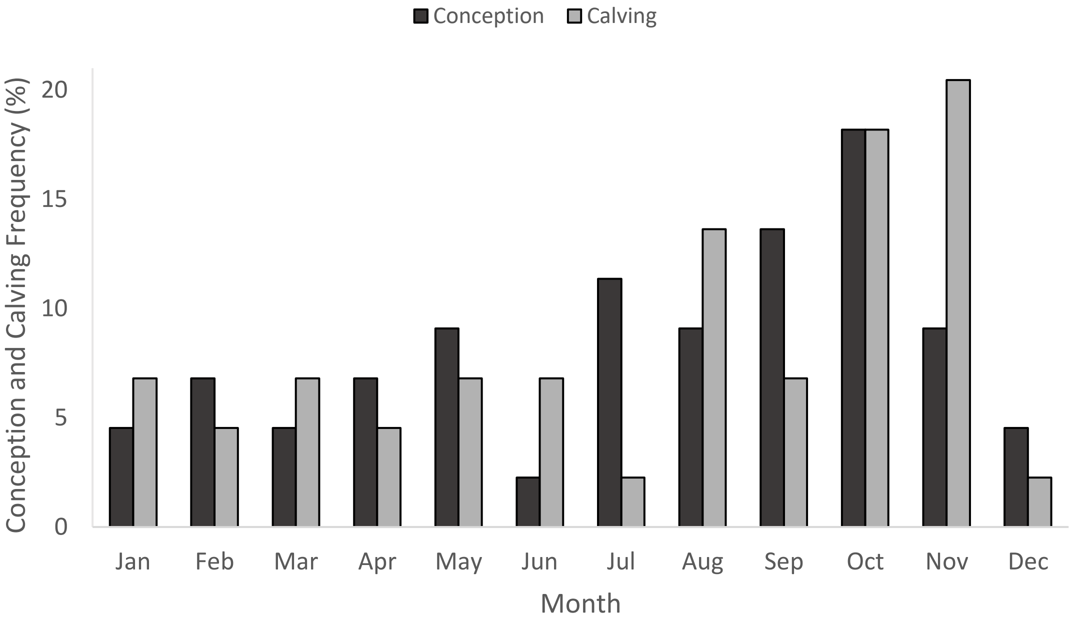


Figure 4F. Mean diameter of the largest follicle on either ovary for mature female common dolphins (pregnant, pregnant and lactating, lactating, resting mature, *n* = 12) examined from Aotearoa New Zealand waters between 1997 and 2019.



(a)



(b)

Figure 4G. Monthly distribution of estimated conception and birth dates for foetuses (*n* = 12) and calves < 1 year of age (*n* = 32) using the (a) Huggett and Widdas (1951) method and the (b) regression method for calculating gestation period (Perrin et al. 1977) for common dolphins examined from Aotearoa New Zealand waters between 1997 and 2019.

Table 4H. Summary of female common dolphin (*Delphinus delphis*) estimates of average age (ASM, in years) and length (LSM, in cm) from published studies. Where available, 95% confidence (CI) or credible (CrI) intervals are also presented.

Location	**Eastern North Atlantic**	**Eastern North Atlantic – North West Spain**	**Western North Atlantic**	**Eastern Tropical Pacific**	**North Pacific**	**Western South Atlantic**	**Aotearoa New Zealand**
Reference	(Murphy 2004, Murphy et al. 2009)	(Read et al. 2019)	(Westgate 2005; Westgate and Read 2007)	(Danil and Chivers 2007)	(Ferrero and Walker 1995)	(Grandi et al. 2022)	Chapter 4
Source	Strandings and bycatch	Strandings and bycatch	Strandings and bycatch	Bycatch	Bycatch	Strandings and bycatch	Strandings and bycatch
ASM (95% CI or CrI)	Regression = 8.2 (7.7 – 8.7) SOFI = 8.7 (SE = 0.03)	8.4	8.3 (7.9 – 8.8)	Regression = 7.9 (7.3 – 8.3) SOFI = 7.8 (SE = 0.02)	~8 Immature: 0 – 7.2 Mature: 8.5+	~ 7 Immature: 0 – 6 Mature: 7 – 21	Regression = 7.5 (6.7 – 8.3) SOFI = 8.4 (7.3 – 9.5)
***n* ASM**	Immature = 36 Mature = 72	Total = 168	Immature = 32 Mature = 37	Total = 405	Total = 43	Immature = 10 Mature = 25	Immature = 42 Mature = 46
LSM (95% CI or CrI)	Regression = 188.8 (SE = 0.02)	187	202 (200.1 – 204.4)	Regression = 186.5 (185.5 – 187.4) SOFI = 187 (SE = 0.01)	Regression = 170.7 (SE = 2.74) SOFI = 172.8 (SE = 0.56)	Immature: 82 – 191 Mature: 178 – 210	Regression = 183.5 (179.5 – 186.5) SOFI = 188.9 (187.9 – 189.9)
***n* LSM**	Immature = 172 Mature = 281	Total = 224	Immature = 32 Mature = 37	Immature = 349 Mature = 351	Total = 43	Immature = 10 Mature = 25	Immature = 49 Mature = 55
Method used	Regression (generalised linear model) and SOFI	Not reported	SOFI	Regression (logistic) and SOFI	Regression (logistic) and SOFI	Not reported	Regression (Bayesian logistic) and SOFI