Assessing rake mark ontogeny to investigate social aggression in common dolphins (*Delphinus delphis*) in Aotearoa New Zealand

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Abstract

Aggressive competition can impact resource allocation, social structure, and reproductive success in social species. Rake marks, semi-permanent parallel scars from teeth raking across the dermis of another individual, indicate delphinid social aggression. When examined alongside ontogeny, demographic traits, and position, rake marks can inform social dynamics, and potentially health, in delphinids. The majority of existing rake mark studies have been field based and often lack sex, age, total body length (TBL), body condition and reproductive context. Here, I analysed rake marks on common dolphins (*Delphinus delphis*) examined postmortem between 2006-2024 (n = 102) in Aotearoa New Zealand. To account for skin loss and surface area variation, a zero-inflated generalised linear mixed model assessed rake mark occurrence (probability of rake density > 0) and prevalence (rake density, rm/dm^2) across the body (n = 89; dorsal/ventral, cranial/caudal, left/right), inferring potential confrontation, avoidance, and lateralisation. Zero-inflated generalised linear model was used to assess rake mark occurrence and prevalence with sex, age, TBL, sexual maturity, and body condition (n = 89), as well as female reproductive status (n = 51). Females demonstrated higher rake mark prevalence, but lower occurrence than males, possibly due to infrequent but severe aggressive sexual coercion. Males may engage in frequent intrasexual competition for mates. Resting mature females exhibited higher rake mark prevalence and occurrence than immature and pregnant and/or lactating females, likely attributed to reproductive availability and heightened sexual coercion. Rake mark occurrence and prevalence increased with greater TBL, possibly due to the increased surface area available to receive rake marks. Larger male body size, with a pronounced post-anal hump, may signal dominance, resulting in frequent severe aggression. Sexual maturity, age, and body condition displayed no relationship with rake occurrence or prevalence. However, biotic and abiotic factors may influence dolphin skin healing and rake mark longevity, which potentially inhibited the detection of existing relationships. These results provide first insights to how ontogeny may influence rake mark scarring in common dolphins, and the inferred context of the interactions that led to these rake marks.

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1.1 Socially complex mammals

The social behaviour of complex mammals, including humans (*Homo sapiens*) (Schill et al., 2019), great apes (Graham et al., 2022), and cetaceans (Syme et al., 2021), has been the subject of extensive study. Understanding their social dynamics is particularly complicated, as discrete behaviours can often be underpinned by factors such as external threats and social competition (Connor, 2007). Additionally, the level of understanding of social behaviours of complex mammals varies depending on the species. Human social behaviour has been highly studied, due to biased interest in the subject species (Campbell, 2010; Ebstein et al., 2010; Siracusa et al., 2022; Vermande & Sterck, 2020). Great apes, given their close ancestral link to humans, have also been comprehensively studied, particularly in the context of grooming (Morales Picard et al., 2020), infanticide (Colchero et al., 2021) and other socially driving behaviours (Kret et al., 2020; Lewis, 2005).

Cetaceans have not been studied as well as their terrestrial counterparts, largely due to their submerged aquatic lifestyle which complicates direct behavioural observations (King & Jensen, 2022). While the emergence of new technologies, including drones (Fettermann et al., 2022) and omics tools (Monteiro et al., 2021), increasingly offer novel insights to cetacean social behaviour, these animals remain ambiguous in many aspects of their social biology. Nonetheless, Aihe (common dolphins, *Delphinus delphis*) are socially complex cetaceans that engage in a range of interactive events, including cooperative hunting and social bonding (Hupman, 2016; Stockin et al., 2008a; Zanardo et al., 2016). Common dolphins tend to live offshore in large groups, forming a fluid fission-fusion society with weak social bonds (Bruno et al., 2004; Castro et al., 2022; Hupman, 2016; Neumann, 2001b). However, some populations form small groups with strong associations among individuals, indicating plasticity in social structure similar to associations expected for inshore delphinids (Mason et al., 2021; Mason et al., 2016; Möller, 2012). In Aotearoa New Zealand, herein referred to as New Zealand, common dolphins display high variability in group size (Dwyer et al., 2016; Hupman, 2016; Neumann & Orams, 2006; Stockin et al., 2008b). They also exhibit social bonds, evidenced through patterns of long-term preferred associations among individuals (Hupman, 2016).

1.1.1 Aggression in social species

Aggression is a social behaviour that often arises due to conspecific competition in both terrestrial and marine socially complex mammals, including humans (Georgiev et al., 2013; Wu et al., 2023), chimpanzees (*Pan troglodytes*) (Pougnault et al., 2022), killer whales (*Orcinus* orca) (Grimes et al., 2022; Robeck et al., 2019), common bottlenose dolphins (*Tursiops truncatus*) (Scott et al., 2005; Volker & Herzing, 2021), and common dolphins (Murphy et al., 2005). Aggression is typically a response to intra-specific competition for territory and food (Curcio et al., 2023; Gómez et al., 2021; Niu et al., 2020), between males for mates (Lee et al., 2019; Murphy et al., 2005; Orbach et al., 2015), in defence of themselves and offspring (Agrell et al., 1998; Maestripieri, 1992; Reinhart et al., 2013; Robinson, 2014), and/or to determine and sustain their dominance hierarchies (Scott et al., 2005).

Social living provides a range of individual benefits (Dantzer et al., 2017a). However, it is also associated with potentially harmful aggressive behaviour between group members, including competition for status (Creel et al., 2013; Dantzer et al., 2017a; Dantzer et al., 2017b; Drea & Davies, 2022; Hobson et al., 2021; Honess & Marin, 2006; Šabanović et al., 2020), resources (Milewski et al., 2022; Waples & Gales, 2002), and mates (Beaulieu et al., 2014; Lemonnier et al., 2022). Aggressive interactions can interfere with beneficial social relationships (Snyder-Mackler et al., 2020). They are also energetically, physically and physiologically costly, particularly for the receivers of aggression (Georgiev et al., 2013; Grimes et al., 2022). Such aggression within social groups can also contribute to social stress, impacting overall health and well-being (Burgess et al., 2013; Honess & Marin, 2006; Šabanović et al., 2020).

Repeated and sustained chronic stress responses can lead to the deterioration of animal health (Gonzalez-Rivas et al., 2020; Honess & Marin, 2006; Karaer et al., 2023; Kellar et al., 2015; Waples & Gales, 2002; Wittig et al., 2016). This occurs specifically in the context of accelerated aging (Milewski et al., 2022; Wright et al., 2007), increased susceptibility to and symptoms of disease (Aich et al., 2009; Paital et al., 2016; Wright et al., 2007), as well as impairment of reproduction, wound healing, and development (Christian et al., 2007; Dantzer et al., 2017b; Moberg & Mench, 2000; Waples & Gales, 2002; Wright et al., 2007).

Given the adverse health effects associated with stress from aggression, consideration of these interactions is important from both an animal welfare (Beausoleil et al., 2018; Boys et al., 2023; Boys et al., 2022a, 2022b; Clegg et al., 2017) and a conservation biology (Kaisin et al., 2021; Kophamel et al., 2022; Schweinfurth, 2020) perspective. Health impacts both animal fitness and quality of life, which are key factors to animal welfare (Beausoleil et al., 2018; Clegg et al., 2021; Mellor et al., 2020). Both welfare and conservation evaluate how animals respond to their environment (Beausoleil, 2020; Beausoleil et al., 2018; Clegg et al., 2021). However, conservation typically focuses on the survival of populations or species as a whole, while welfare is concerned with the experience of individual animals (Beausoleil, 2020; Beausoleil et al., 2018; Clegg et al., 2021). Therefore, it is key that the welfare of individuals within a population is considered when evaluating the conservation status of populations or species, due to the ramifications for the welfare of individuals within them

(Beausoleil, 2020). Addressing individual welfare concerns can enable earlier detection of potentially harmful factors compared to population-level assessments, such as health decline due to stress which may lead to population or species decline (Boys et al., 2022b; Clegg et al., 2021). Integrating individual animal welfare alongside conservation biology will ensure more effective protection of socially complex mammals by providing a better understanding of the pressures they face (Beausoleil et al., 2018; Clegg et al., 2021).

Common dolphins in New Zealand experience a range of pressures, including fisheries bycatch (Stockin et al., 2009; Stockin & Orams, 2009), vessel strike (Martinez & Stockin, 2013), tourism interactions (Stockin et al., 2008a; Stockin & Orams, 2009), and habitat pollution (Stockin et al., 2007; Stockin et al., 2021). In addition to these anthropogenic pressures, it is important to consider aggressive interactions as a potential adverse stressor for common dolphins, given the previously discussed costs associated with such interactions in a range of social species (Burgess et al., 2013; Georgiev et al., 2013; Grimes et al., 2022; Honess & Marin, 2006; Šabanović et al., 2020; Snyder-Mackler et al., 2020). However, studies examining aggression in dolphins are extremely limited, mostly restricted to captive environments and have not been previously assessed in *Delphinus*, either at individual or population levels.

1.1.2 Delphinid aggression

Delphinids display aggression through their posture, sound, and movements, including body slamming, ramming and biting (Samuels & Gifford, 1997; Scott et al., 2005). These behaviours are rarely observed firsthand in free-ranging cetaceans (Samuels & Gifford, 1997; Scott et al., 2005), as they demonstrate significant proportions of their behaviour subsurface (Hamilton et al., 2019; Marley et al., 2013). Understanding aggressive behaviour in delphinids is key to providing insights into behavioural ecology and informing conservation efforts. This is due to the implications of aggression on delphinid social structure and dynamics (Hamilton et al., 2019; Kleinschmidt, 2014; Scott et al., 2005), reproductive success (Brown et al., 2016; Evans & Stirling, 2001; Marley et al., 2013; Scott et al., 2005), resource allocation (Grimes et al., 2022; Hamilton et al., 2019; Lee et al., 2019; Serres et al., 2023), and stress and health (Hamilton et al., 2019; Waples & Gales, 2002).

Studies assessing captive delphinids can aid our understanding of aggression in free-ranging delphinid populations, as social associations of captive populations have been known to mirror those observed in the wild (Waples & Gales, 2002). In the study of captive common bottlenose dolphins, aggressive interactions were directly observed or inferred by the presence of additional rake marks (Waples & Gales, 2002). This revealed that aggression is influenced by various factors including social structure and space limitations (Waples & Gales, 2002). Additionally, Samuels and Gifford (1997) investigated aggression in captive common bottlenose dolphins, with specific comparison between sexes. They noted consistent male dominance over females, concluding that intra-specific aggression is not random (Samuels & Gifford, 1997). Such findings are supported by studies of free ranging Indo-Pacific bottlenose dolphins in Shark Bay, Australia (Lee et al., 2019; Scott et al., 2005).

Aggressive behaviours displayed by female common dolphins in captivity in New Zealand include bites, body slams, charges, tail slaps and displacement of other dolphins (Kyngdon et al., 2003). For common dolphins, a decrease in aggressive behaviour was observed during 'swim with dolphin' sessions, contradicting similar studies on male bottlenose dolphins which found an increase in aggressive behaviour during such sessions (Kyngdon et al., 2003). This highlights the significance of understanding social dynamics in relation to aggressive behaviour of delphinids, considering each species, and individual life history traits such as sex, age and maturity (Kyngdon et al., 2003).

Recognising species and life history differences, it must be noted that we cannot directly compare captive with free ranging delphinids, as those in captivity lack the social fluidity observed in free ranging populations (Samuels & Gifford, 1997; Waples & Gales, 2002). Likewise, limited space has been identified as a stressor for captive delphinids (Waples & Gales, 2002), but this factor is not typically experienced by free ranging individuals (Carter, 1982). Free ranging populations are further subject to pressures not experienced by captive delphinids, including predation and fisheries interactions (Crespo-Picazo et al., 2021; Murphy et al., 2013). An example of behavioural variation between captive and wild populations is evident in killer whales, where captive individuals exhibit higher levels of aggression towards both humans and conspecifics compared to their wild counterparts

(Marino et al., 2020). Self-harming behaviours such as refusal to eat, leaving the water to perch on tank ledges for extended times to escape aggression and head striking on tank walls have been described in captive killer whales, but are not noted in any free-ranging population (Marino et al., 2020). Consequently, meaningful comparison between captive and wild populations of delphinids must carefully consider the variation in environmental challenges faced (Marino et al., 2020; Samuels & Gifford, 1997). Therefore, while captive studies can assist our understanding of delphinid social behaviour, studies of wild populations are essential for developing an accurate, comprehensive understanding of social aggressive interactions.

1.2 Using scars (rake marks) as a quantitative measure of aggression

In cases where direct observation of aggressive behaviour in captivity or the wild is not feasible, this can be measured quantitatively by the degree of body scarring on individuals. This method has been implemented using scars on olive baboons (*Papio anubis*) (MacCormick et al., 2012) and dugongs (*Dugong dugon*) (Burgess et al., 2013), and rake mark scars on a range of delphinid species (Brown et al., 2016; Frantzis & Herzing, 2002; Hamilton et al., 2019; Lee et al., 2019; Marley et al., 2013; Reinhart et al., 2013). Rake marks herein refer to semi-permanent wounds or scars that appear as shallow, parallel lesions in the dermis or sub-dermis as a result of delphinids dragging their teeth across the skin of another animal (Hamilton et al., 2019; Hill et al., 2017; Lee et al., 2019; Marley et al., 2013; Scott et al., 2005; Waples & Gales, 2002). Such lesions have been observed on a range of delphinid species including bottlenose dolphins (Lee et al., 2019; Patińo-Pérez, 2022), humpback dolphins (*Sousa sahulensis*) (Brown et al., 2016), killer whales (Reinhart et al., 2013), Risso's dolphins (*Grampus griseus*) (Frantzis & Herzing, 2002), and common dolphins (Cords & Mann, 2014; Hamilton et al., 2019; Hupman et al., 2017; Lee et al., 2019; Orbach et al., 2015; Scott et al., 2005).

1.2.1 Insights from rake marks

As aggressive behaviours are rarely observed directly in wild delphinid populations, the assessment of rake marks allows insight into the occurrence and inferred context of aggressive interactions that might otherwise be missed (Hamilton et al., 2019; Orbach et al., 2015; Scott et al., 2005). Rake marks have been documented in the context of aggressive interactions due to conflict between animals of the same species (intra-specific competition) and animals of different species (inter-specific competition and predation) (Crespo-Picazo et al., 2021; Lee et al., 2019; Lockyer & Morris, 1990; Ross & Wilson, 1996; Tolley et al., 1995). The aggressor species is determinable by measuring the inter-rake distance i.e., the distance between parallel lesions within the rake marks, which aligns with species-specific dentition spacing (Crespo-Picazo et al., 2021; Frantzis & Herzing, 2002; Martin & Da Silva, 2006; Ross & Wilson, 1996). The degree of epidermal healing can be used to estimate how much time has passed since the aggressive interaction took place, based on the knowledge that rake marks heal over time. For example, for Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), it took approximately 400 days for epidermal healing to occur (Lee et al., 2019). Such information can provide an indication of the life stage and season at which the interaction occurred (Lee et al., 2019; Serres et al., 2023).

Life history traits, including size and age at attainment of sexual maturity, as well as lifespan and gestation period, directly impact a species' development, growth, reproduction, and survival (Boddy et al., 2020; Suraci et al., 2021; Wells et al., 2022). When paired with rake mark data, traits such as age, sex, sexual maturity and reproductive status can provide important context for aggressive interactions (Lee et al., 2019; Martin & Da Silva, 2006). For example, analysis of rake marks in the context of sex shows that rake marks are more likely to occur on males than females for a range of delphinid species, including killer whales (Grimes et al., 2022), and bottlenose dolphins (James et al., 2022; Lee et al., 2019; Marley et al., 2013; Scott et al., 2005; Tolley et al., 1995). Male delphinids are also likely to have a comparatively higher prevalence of rake marks than females, as showcased in Indo-Pacific humpback dolphins (*Sousa chinensis*) (Serres et al., 2023), bottlenose dolphins (Marley et al., 2013), Amazon river dolphins (*Inia geoffrensis*) (Martin & Da Silva, 2006) and killer whales (Grimes et al., 2022). This pattern potentially indicates that adult males display higher aggression levels compared to females (Scott et al., 2005). The increased rake mark occurrence and prevalence among males has been attributed to intra-sexual competition between males for dominance and mates, and sexual coercion of females during the breeding season (Hamilton et al., 2019; Marley et al., 2013; Scott et al., 2005; Serres et al., 2023).

Rake marks also vary with age across several species, including bottlenose dolphins (Lee et al., 2019; Scott et al., 2005), killer whales (Grimes et al., 2022), and Indo-Pacific humpback dolphins (Serres et al., 2023). This variability may indicate changes in aggression levels throughout their lifespan (Grimes et al., 2022). In Shark Bay, Australia, Scott et al. (2005) reported that Indo-Pacific bottlenose dolphin calves had less rake marks than juveniles and adults within the population. Conversely, Lee et al. (2019) reported that juveniles had more rake marks than calves and adults in the same Shark Bay population. In contrast, studies on Indo-Pacific humpback dolphins, killer whales, and captive common bottlenose dolphins report a decline in the number of rake marks as an individual increased in age and sexual maturity (Grimes et al., 2022; Kleinschmidt, 2014; Serres et al., 2023). As a result, adults were found to have significantly fewer rake marks than calves, juveniles, or subadults (Grimes et al., 2022; Kleinschmidt, 2014; Serres et al., 2023).

As sexual maturity occurs across a range of age and body lengths (Palmer et al., 2022; Palmer et al., 2023), variation in rake marks across different ages may relate to a shift in behaviour that correlates with a change in size, life stage, and the onset of sexual maturity (Ham et al., 2021; Lee et al., 2019; Scott et al., 2005; Serres et al., 2023). Such changes may require a shift from playful learning interactions to resource competition, the establishment of alliances, and interactions associated with breeding, including competition for mates and sexual coercion (Ham et al., 2021; Lee et al., 2019; Scott et al., 2005; Serres et al., 2023). While disparity exists on the prevalence of rake marks in calves, it is generally agreed that they likely receive these scars from socio-sexual, initially playful interactions that develop into low intensity conflict (Scott et al., 2005; Serres et al., 2023). Juveniles, more independent than calves, are likely involved in increased agonistic and socio-sexual interactions, along with competition for food during weaning, which would support an increase in rakes noted in juveniles (Ham et al., 2021; Lee et al., 2019; Serres et al., 2023).

Male-male competition, driven by the formation of alliances and the establishment of stable social networks, is another potential source of aggression during pubescence when attempting to establish dominance (Kleinschmidt, 2014; Lee et al., 2019; Scott et al., 2005; Serres et al., 2023). Aggressive interactions among ages associated with sexual maturity may be associated with inter-sexual coercion and competition for mates (Lee et al., 2019). We may further expect a reduction in rake marks as age increases because older adults may distance themselves to avoid aggressive interactions, as their status in the dominance hierarchy is already established (Lee et al., 2019; Serres et al., 2023). The range of hypotheses and the disparity in findings across species and studies highlights the need for continued research in this area.

There is no existing literature investigating rake marks as indicators of health in delphinids. Other epidermal lesions such as tattoo lesions and ulcers, are commonly associated with health deterioration, whereas squid marks are indicative of good health as they suggest recent feeding activity (Chan & Karczmarski, 2019; Hanninger et al., 2023a; Hanninger et al., 2023b; Van Bressem et al., 2009). In individuals with poor health, lesions may persist on the skin due to reduced immune response, possibly impacted by degradation of habitat quality through increased pollutants (Chan & Karczmarski, 2019), or stress (Gonzalez-Rivas et al., 2020; Kellar et al., 2015). Weakened immune response increases susceptibility to scarring, infection and disease (Chan & Karczmarski, 2019; Van Bressem et al., 2009) and prolongs the wound healing process (Williams & Barbul, 2003).

As rake marks are not cumulative, wound healing rate may influence the occurrence and prevalence of rake marks. In humans, sex steroid hormones, particularly estrogen, reduce healing time, and cutaneous wounds heal faster in females than males (Ashcroft, 2004; Fimmel & Zouboulis, 2005; Thomason et al., 2015). Female Indo-Pacific bottlenose dolphins may heal faster than males, possibly due to better immune responses (Lee et al., 2019; Scott et al., 2005). Additionally, wound healing rates in mammals, including humans, are slowed by poor body condition (Ghaly et al., 2021; Lux, 2022) and increased age (Ashcroft et al., 2002; Gilliver & Ashcroft, 2007; Wong & Chew, 2021). Therefore, for delphinids, variation in healing time should be considered as a potential factor contributing to observed variation in rake marks between different sexes, ages, body conditions, as well as stages of sexual maturity and reproduction.

1.2.2 Rake mark position

Studies have investigated the position and distribution of wounds and scars on various delphinid species, including Indo-Pacific humpback (Serres et al., 2023), bottlenose (Kleinschmidt, 2014; Scott et al., 2005), and common (Hupman et al., 2017) dolphins. Serres et al. (2023) found significant variation in the number of rake marks across body sectors, with more on the ‘flank’ (comprised of the mid-flank body section and the dorsal fin) compared to the ‘front’ and ‘peduncle’ sections. These results align with Scott et al. (2005) for bottlenose dolphins, although Scott noted a high prevalence of rake marks on the ‘posterior peduncle’, which was not observed by Serres et al. (2023). A study on free-ranging common dolphins in New Zealand used photo-identification to investigate the distribution of various lesions, including rake marks, which were included in the post prevalent lesion category, ‘indentations and impressions’ (Hupman et al., 2017). Results indicated that the majority of lesions appeared on the ‘anterior peduncle’, and over 80% of individuals demonstrated lesions on the dorsal fin (Hupman et al., 2017).

Understanding the position and distribution of rake marks can assist in discerning their origin and the nature of the interactions causing them, such as distinguishing aggression due to competition, sexual behaviour, or play (Hill et al., 2017). For instance, a higher density of scars around mid/posterior regions, as observed by Scott et al. (2005) and Serres et al. (2023), may indicate that aggressors often target or exert more force in those areas during aggressive behaviours involving biting or raking (Lanyon et al., 2021). It is possible that during playful or aggressive interactions, the recipient may orientate their dorsum or side towards the aggressor, either to evade the aggressor or to present the least vulnerable portion of their body as a form of protection (Serres et al., 2023). A prevalence of scars on the caudal region of body may suggest that the recipient was being pursued, indicating a chase potentially motivated by competition over resources or mates (Lanyon et al., 2021). Injuries around the head might also suggest that the recipient approached the aggressor or engaged in head-to-head clashes for dominance (Lanyon et al., 2021). Rakes on the peduncle section were found to be more common in younger captive bottlenose dolphins than older conspecifics, suggesting that younger dolphins are more frequently recipients attempting to escape the aggression, while older animals may more often be the aggressor (Kleinschmidt, 2014).

Research on captive and wild delphinids has demonstrated behavioural lateralisation, where certain behaviours are predominantly executed using a particular side of the body (Clark & Kuczaj II, 2016; Kaplan et al., 2019; Karenina et al., 2010; Lilley et al., 2022; Matrai et al., 2019). Although no studies specifically investigate lateralisation in relation to the position of rake marks, wild Indo-Pacific bottlenose dolphins have been found to keep conspecifics in view with their left eye, and preferentially rub their left side against others (Sakai et al., 2006). Similarly, wild beluga whale (*Delphinapterus leucas*) calves tend to position themselves on the right side of their mothers, keeping them in view with their left eye (Karenina et al., 2010). In contrast, free-ranging common bottlenose dolphins also show a right-side preference during foraging behaviours, such as making sharp left turns with their right side and right eye oriented downward (Kaplan et al., 2019). Examining behavioural lateralisation in delphinids, particularly in terms of rake mark position, may enable us to understand if certain sides of the body are more frequently targeted during aggressive encounters, potentially correlating with observed behavioural patterns.

In summary, the frequency, position and properties of rake marks, paired with associated life history data, presents quantifiable evidence of recent received aggressive interactions. Such data has the potential to provide new insights into reproductive strategies, social structures, and health of delphinids (Lee et al., 2019; Reinhart et al., 2013; Ross & Wilson, 1996; Scott et al., 2005; Waples & Gales, 2002) when examined in a standardised and quantifiable manner.

1.3 Thesis rationale and objectives

To date, the assessment of rake marks on common dolphins has been limited to field based studies that use opportunistic photo identification data to assess lesion prevalence (Hupman et al., 2017; Neumann, 2001a). Such studies are often restricted to observing rakes on the dorsum surface due to the partial submergence of the body under water. These studies, which usually focus specifically on the dorsal fin, typically lack the necessary insight into the ontogeny and demographic traits of each individual. For example, the inability to determine sex, age, sexual maturity and reproductive status in the field for most animals, limits our ability to contextualise rake scarring.

Laboratory based observation of rake marks postmortem, however, can enable critical knowledge gaps to be addressed. Specifically, the assessment of rake marks on cadavers allows accurate survey of the entire body surface for rake marks. This means a comprehensive analysis of scar positioning can be undertaken. Additionally, rake mark prevalence can be quantified in the context of critical biological factors: sex, derived anatomically or molecularly (Einfeldt et al., 2019; Neumann et al., 2002), age, determined via growth layer groups (Lockyer, 1995), physical/sexuality maturity, ascertained through skeletal and gonad examination (Roca-Monge et al., 2022; Walker, 1981), and reproductive stage, identified via histological assessment of gonads for evidence of spermatogenesis in males (Palmer et al., 2023; Westgate & Read, 2007) and ovulation, lactation and resting/senescence (Palmer et al., 2022) in females. Insights to position of rake marks on the cadaver and their potential correlation with such biological parameters will further broaden our understanding of the sociobiology of New Zealand common dolphins.

Here I examine the occurrence (presence/absence) and prevalence (rake density) of rake marks postmortem on New Zealand common dolphin cadavers in the context of ontogeny and scarring position to investigate causality. Specifically, this thesis aims to understand if rake density differs by: (a) sex, (b) age, (c) total body length (TBL), (d) sexual maturity, (e) female reproductive status (immature, pregnant and/or lactating, or resting), (f) body condition and (g) body sector.

1.4 Thesis structure

My thesis will follow a traditional thesis format as follows:

Chapter 1 – Introduction: Summarises existing literature on social aggression and rake scarring across species with focus on delphinids. The aim and significance of the study is highlighted.

Chapter 2 – Materials & Methods: Explains the full methodology used to investigate rake marks on common dolphins, including external examination, sample collection, data processing and statistical methods.

Chapter 3 – Results: Outlines the findings of this thesis, quantifying the occurrence and prevalence of rake marks on common dolphins.

Chapter 4 – Discussion: Presents the key findings of this thesis in the context of existing literature. Study limitations and future research recommendations are further discussed.

Chapter 2 - Materials & Methods

2.1 Postmortem database

Postmortem records of common dolphins examined at the Cetacean Pathology Unit, Massey University, between 2006 and 2024 were assessed, and a dataset was created for this study. Dolphins were included in the dataset if they had an intact body surface and high-quality photographs (assessed based on image clarity, focus and degree of contrast) of each body surface, and/or lesions and skin loss were recorded and annotated on necropsy datasheets (Figure A.2, Figure A.3). Inclusion in this study also required that datasheets provided the following biological metadata: sex (male or female), body morphometrics (cm), age (years), body condition (good or moderate), sexual maturity (immature or mature), reproductive stage (immature, pregnant and/or lactating, resting mature), decomposition score (fresh, mild, moderate). 102 dolphins met these criteria and were included in the study dataset.

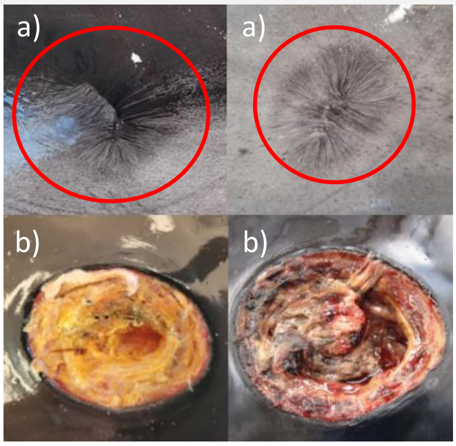
2.2 External examination

The external surface of each cadaver was grossly examined for the presence of natural skin lesions and photographed from dorsal, ventral, lateral, cranial and caudal orientations. Detailed photographs were taken of any detected lesions alongside a scale bar and grey scale marker. The lesion type (rake mark, cookie cutter scar, tattoo lesion, squid mark, linear scar, irregular scar, other lesion, Table 2.1) body sector (dorsal head, ventral head, dorsal cranial flank, ventral cranial flank, dorsal fin, dorsal caudal flank, ventral caudal flank, dorsal peduncle, ventral peduncle, pectoral fin, and fluke), length (cm), width (cm), inter-distance (mm) and healing stage (1 – new wound, 2 – healing wound with no granulation tissue, 3 – granulation tissue present, 4 – cellular and vascular blubber present on healed wound, 5 – no cellular and vascular blubber present, methods from Su et al. (2022)), where relevant, were recorded for each lesion. Any skin loss (induced by decomposition, cadaver transportation, injury or other factors that may have inhibited the detection of lesions should they be present) was noted as a percentage of body surface for each sector.

Fourteen body measurements, including total body length (TBL) were taken for each cadaver (Figure A.1, Table 2.5). Dorsal blubber thickness (mm) was also recorded. Body condition (good, moderate, poor, Table 2.2), used as a proxy of health, was assessed for each individual from a consistent angle, with the observer positioned cranial and marginally dorsal to the subject, which was positioned on its ventrum. Decomposition score (fresh, mild, moderate, severe decomposition, Table 2.3), was further determined for each cadaver following methods from Stockin et al. (2009).

While a range of skin lesions were observed and recorded (Table 2.1), the focus of this research and methods were applied to rake marks only.

Table 2.1 Lesions observed on common dolphin (*Delphinus delphis*) cadavers between 2006 and 2024 in New Zealand. Image credit: Cetacean Pathology Unit, Massey University. (Adapted from Hupman, 2016)

Category	Description	Image
Rake Marks	Shallow, parallel lesions in the dermis and/or sub dermis, with more than two parallel lines indicating tooth rakes (Auger-Méthé & Whitehead, 2007). Skin may be broken, or form thin white or grey lines, or faint indentations (Scott et al., 2005).	
Cookie Cutter Scars	Cookie cutter shark (*Istius* spp.) bites (Herr et al., 2023; Su et al., 2022). Healed scars (a) are white/grey in colour, forming an irregular oval shape (Grace et al., 2018; Su et al., 2022). In early to intermediate healing stages (b), cookie cutter scars are circular, with pink/red, or brown/yellow subdermal tissue exposed (Herr et al., 2023; Su et al., 2022).	
Tattoo Lesions	Pox-like cutaneous lesions, spotted or irregularly shaped splotches, grey to black, sometimes with a faint yellow tint. (Blacklaws et al., 2013; Van Bressem et al., 2009).	

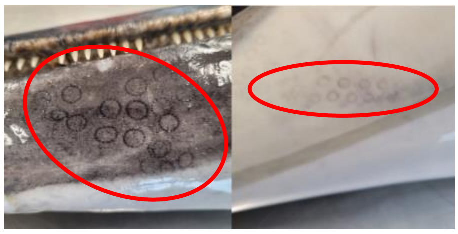
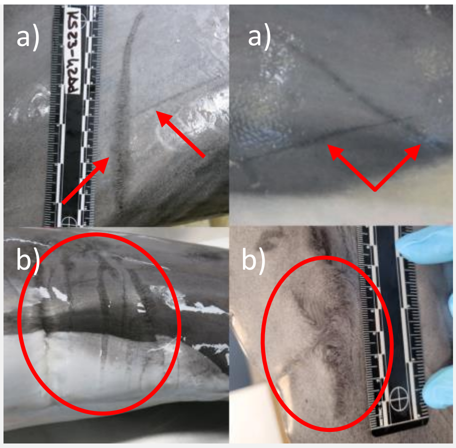
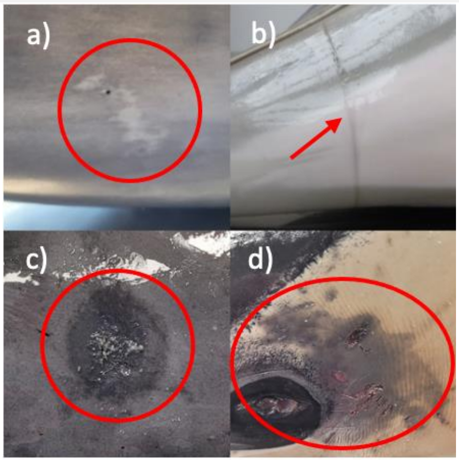
Squid Marks	Ring-shaped, superficial epidermal lesions from suckers and hooks on squid tentacles (Fernández et al., 2017). A single row of dimpled spots, with impressions of uniform depth (Auger-Méthé & Whitehead, 2007).	
Linear and Irregular Scars	Connective tissue with an outer layer of epithelial cells (Hupman et al., 2017). Either (a) linear, long and narrow or (b) irregular, asymmetrical, non-uniform.	
Other Lesions	(a) white lesions, (b) linear, net-like abrasions, (c) pox-like lesions, (d) discolouration/dark purple spots, as well as skin pitting and teeth punctures.	

Table 2.2 Characteristics of each body condition score.

Score	Definition
1. Good	Caudal and cranial dorsal flanks are rounded.
2. Moderate	Sloping of the caudal and cranial dorsal flanks.
3. Poor	Caudal and cranial dorsal flanks are hollow. The transverse process of the lumbar vertebrae is visible, a dorsal indentation caudal to the head can be observed.

Table 2.3 Characteristics of each decomposition score.

Score	Definition
1. Fresh	Dead for less than 48 hours, no signs of rigor mortis, clear cornea, eyes are firm (i.e. not flaccid).
2. Mild	Rigor mortis; early decomposition taking place, e.g., surface decay of eyes and skin; no decomposition smell; organs intact.
3. Moderate	Peeling of skin visible; decomposition signs visible, although moderate, e.g., a change in skin and organ colour or consistency may be seen; moderate decomposition odour present.
4. Severe decomposition	Collapsing carcass; skin sloughing; strong decomposition smell; soft blubber, with oil or gas pockets possibly present; muscle easily torn, possibly coming away from bones; thin and black blood; organs may be torn or difficult to detect; gas in gut.

2.3 Rake mark location and characteristics

Rake marks on cadavers were evaluated across 11 body sectors (Figure 2.2) from the dorsal, ventral, and lateral (left and right) orientations to examine the distribution of rake marks across the entire external surface. Data was not recorded for the lateral surfaces of the pectoral fins and flukes, and the dorsal surface of the dorsal fins, due to the limited surface area of these sector orientations. Due to sample size limitations, and to avoid overfitting of statistical models, body sectors were grouped into body sector groupings based on anatomical planes (dorsal, ventral, cranial, caudal, left and right) (Figure 2.3, Table 2.4). Any scar present across the boundary of two sectors was counted only once, in the sector where the majority (>50%) of the scar was located. Lesion characteristics were recorded for each rake mark, including the length of rake (cm) and the distance between the parallel lesions that make up a rake mark, the inter-rake distance (IRD in mm).

Photos and measurements were carefully reviewed to distinguish between conspecific and interspecies rake marks, and to exclude any postmortem lesions which may have been mistakenly recorded as rake marks during the initial postmortem examination. A scar was only categorised as a rake mark if multiple, parallel, and generally consistent indentations or lesions were present in a uniform pattern. Any scars that did not meet these criteria were likely the result of postmortem scarring from cadaver recovery and transport, and were therefore excluded from the analysis. This thesis considers rake marks to be indicative of conspecific interactions between common dolphins (*Delphinus delphis*), typically with an IRD ca 5 mm, based on known *Delphinus* dentition (Massey unpublished data, Figure 2.1). However, due to tooth loss and/or damage affecting the IRD, it is acknowledged that in some cases, variation may occur. Rake marks with an IRD exceeding 10 mm were likely a result of interspecies interactions, and were also excluded from the analysis.

Figure 2.1 Dentition of a common dolphin (*Delphinus delphis;* KS24-97Dd), assessed postmortem, showing ca 5mm gap between teeth, corresponding to the inter-rake distance. Image credit: Cetacean Pathology Unit, Massey University.

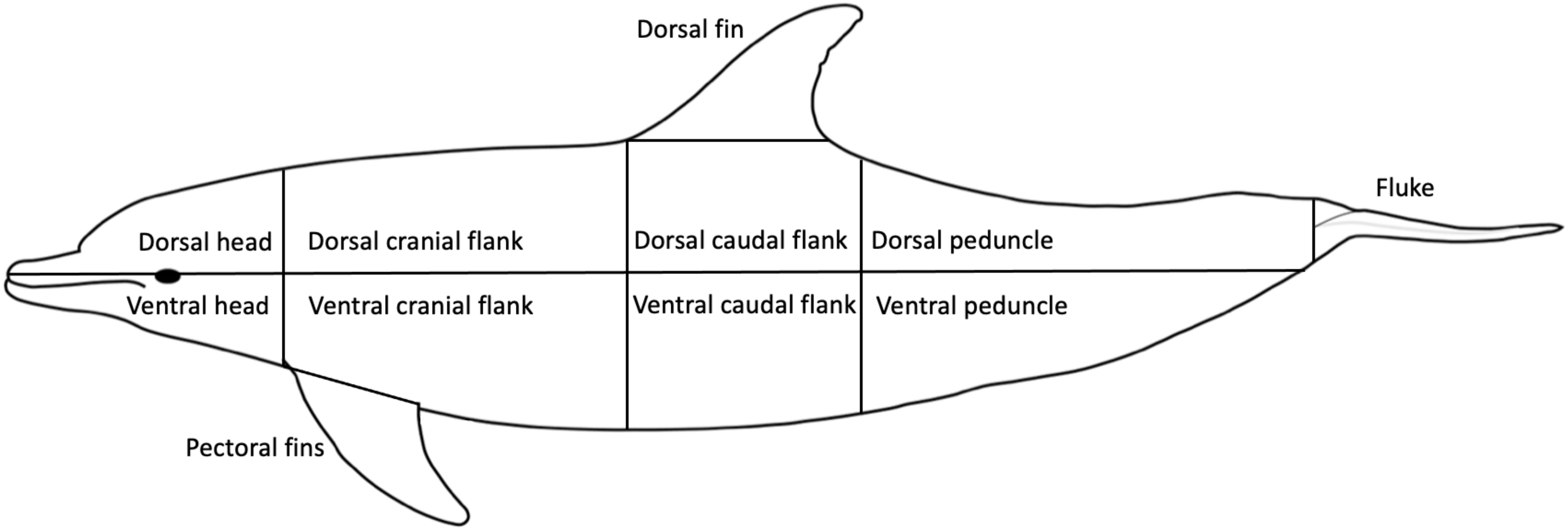


Figure 2.2 Body sectors used to record rake mark position on common dolphin (*Delphinus delphis*) cadavers (Modified from Hupman et al., 2017; Marley et al., 2013; Scott et al., 2005).

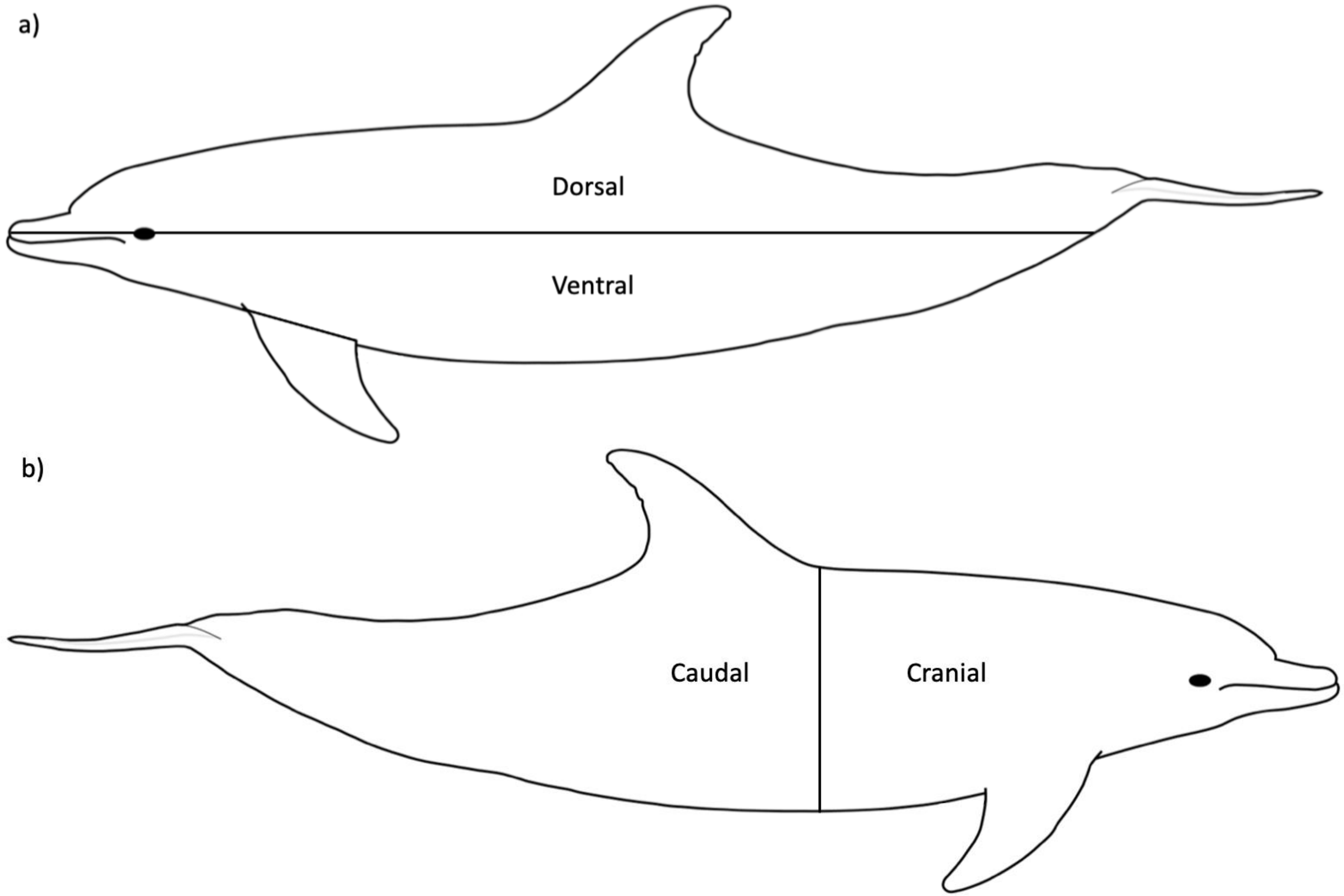


Figure 2.3 Body sector groupings dorsal and ventral (a), and cranial and caudal (b), on both the left (a) and right (b) anatomical planes of common dolphins (*Delphinus delphis*), used for rake mark analysis.

Table 2.4 Defining body sector groupings that categorise regions of the body based on anatomical planes, used for rake mark analysis.

Sector Grouping	Definition
Dorsal	Sectors dorsal to the eye, divided along the horizontal plane, extending from the cranial tip of the rostrum to the caudal tip of the flukes
Ventral	Sectors ventral to the eye, divided along the horizontal plane, extending from the cranial tip of the rostrum to the caudal tip of the flukes.
Cranial	Sectors cranial to the cranial origin of the dorsal fin along the transverse plane.
Caudal	Sectors caudal to the cranial origin of the dorsal fin along the transverse plane, includes the dorsal fin.
Left	Sectors to the left of the midline along the sagittal plane when the observer is posterior to the subject.
Right	Sectors to the right of the midline along the sagittal plane when the observer is posterior to the subject.

2.4 Sample collection

Sample collection followed standardized postmortem methods (Stockin et al., 2009). Reproductive organs were excised, measured, and sampled for histological assessment (Palmer et al., 2022; 2023). Teeth were extracted, fixed, decalcified and stained as per standard protocols (Lockyer, 1995; Murphy et al., 2014). Age, sex, sexual maturity, and reproductive status were determined for each individual.

2.4.1 Sex determination

Sex was determined anatomically based on genital slit positioning (Figure 2.4) and confirmed by gross and histological examination of the gonads postmortem (Stockin et al., 2009).

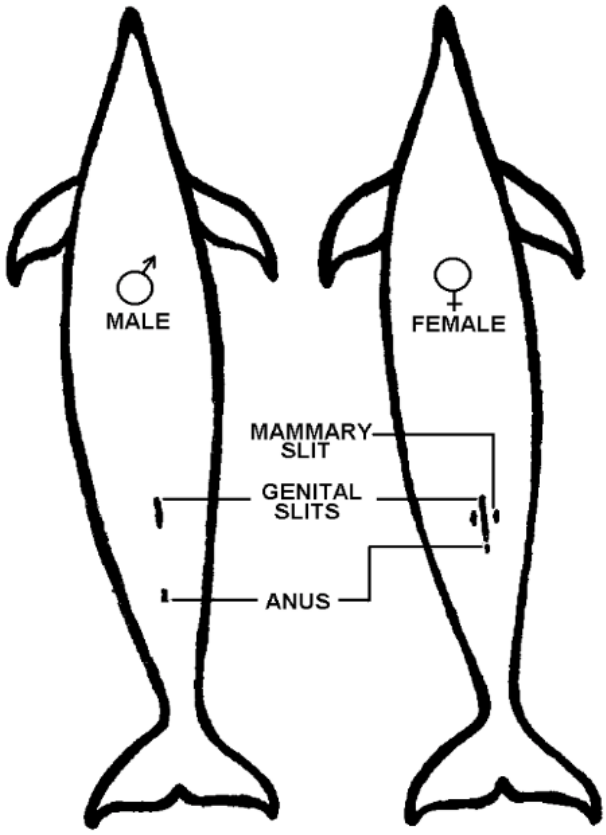


Figure 2.4 Anatomical differentiation between male and female delphinid genitalia. Image credit: Department of Conservation Te Papa Atawhai, New Zealand.

2.4.2 Age estimation

Five to ten of the straightest and least worn teeth were extracted from the middle of the lower jaw for processing (Palmer et al., 2022). Tooth processing methods were adapted from Lockyer (1995) and Murphy et al. (2014). Teeth were stored in 70% ethanol, fixed in formalin, and decalcified using 10% formic acid. After confirming decalcification, the teeth were sectioned along the longitudinal axis, stained with 0.2–0.5% Toluidine blue (pH 8.4), and mounted on microscope slides. Under a binocular microscope (10-40 x magnification), annual growth layer groups (GLGs) in the dentine, each representing one year of life, were counted to determine an estimate of the minimum age (Calzada et al., 1994; Gurevich et al., 1980). GLGs were counted blind (in the absence of TBL or reproduction data) by a minimum of two trained readers. Estimates were cross compared and where no agreement was reached, GLGs were counted by a third reader until an age estimate was agreed upon (Palmer et al., 2022).

2.4.3 Sexual maturity

Male and female gonads were examined grossly and histologically to determine sexual maturity (Murphy et al., 2005; Perrin & Donovan, 1984). Females were considered sexually mature if pregnant (foetus present in uterus and a *corpus luteum* is present on an ovary) or lactating (milk present in mammary glands) or *corpora albicantia* or *corpora lutea* were present on ovaries (or a combination of these) (Palmer et al., 2022; Perrin & Donovan, 1984). If none of these traits were observed, a female was deemed sexually immature (Palmer et al., 2022). A male was considered sexually immature if a large amount of interstitial tissue and small amount of spermatogonia (male germinal cells that represent the starting point of spermatogenesis) were detected in the seminiferous tubules (Murphy et al., 2005). Males with both spermatogonia and spermatocytes present, seminiferous tubules with increased diameter, and a reduced amount of interstitial tissue were deemed 'pubescent' (Murphy et al., 2005). Males were considered sexually mature if evidence of active spermatogenesis (i.e., spermatids and spermatozoa present) was observed (Murphy et al., 2005). In cases where histological data was not present, sexual maturity was estimated based on biological data which determined the age and body length of common dolphins at attainment of sexual maturity (Palmer et al., 2022; Palmer et al., 2023).

2.4.4 Reproductive status

Ovaries, uteri, and mammary glands were assessed in females to determine reproductive status (Murphy et al., 2009). Reproductive status was categorized into the following stages; (1) Immature, a sexually immature female as defined above, (2) Pregnant and/or lactating, where a female is either a) Pregnant, with a foetus observed in the uterus and a *corpus luteum* present on an ovary, b) Lactating, where milk is present in the mammary glands, or c) Pregnant and lactating, if there is a foetus in the uterus, a *corpus luteum* is present on an ovary, and milk is noted in both mammary glands, and (3) Resting mature, a sexually mature female as defined above, in which no pregnancy or lactation is detected (Perrin & Donovan, 1984).

2.5 Data analysis

2.5.1 Rake mark prevalence

To account for skin loss, decomposition, and any other aberrations that may mask the appearance of rake marks, and to allow for a fair comparison of the degree of raking between body sectors with different surface areas, a weighted method was applied to assess rake prevalence. To do this, the rake density i.e., the number of rake marks per dm^2, (10 cm by 10 cm) of skin visible in any given sector, was calculated.

2.5.2 Calculation of body sector area

Fourteen categories of morphometric data (Table 2.5) were recorded during postmortem to calculate the area (dm^2) of each body sector for each animal. Three additional measurements were derived from morphometric data collated postmortem: (15) cranial origin of pectoral fin to cranial origin of dorsal fin, (16) caudal tip of dorsal fin to fluke origin, and (17) eye to mandible along the transverse plane (Figure A.1).

Table 2.5 Body morphometrics recorded for common dolphin (*Delphinus delphis*) cadavers assessed postmortem from 2006 to 2024 in New Zealand.

1. Total body length	cm	2. Snout to origin flipper	cm
3. Snout to origin dorsal fin	cm	4. Snout to tip dorsal fin	cm
5. Eye to blowhole	cm	6. Dorsal fin height	cm
7. Dorsal fin lat. base	cm	8. Fluke width	cm
9. Fluke length	cm	10. Int pec length	cm
11. Ext pec length	cm	12. Pec width	cm
13. Girth at pec	cm	14. Girth at navel	cm

The cranial and caudal flank body sector areas were calculated using the area of a rectangle formula as follows:

$$Area\ of\ a\ rectangle = L \times W$$

where L is the length measurement of the rectangle and W represents the width measurement.

The head and peduncle body sector areas were calculated using the area of a triangle formula as follows:

$$Area\ of\ a\ triangle = \frac{1}{2}\,(b \times h)$$

where b measures the base of the triangle, and h represents the triangle height.

The body sector areas for dorsal fin, flukes and pectoral fins were calculated using Adobe Photoshop, due to their irregular shape. In Photoshop, sector images were traced to select the number of pixels that comprised each appendage. The corresponding morphometric measurements (either dorsal fin height, fluke width, or internal pectoral length) were then applied to calculate the ratio of selected pixels to centimetres. This ratio was used to calculate the area of the selected pixels, and therefore the area of each sector.

2.5.3 Estimation of body sector area

A resampling technique was used to estimate the area of irregular shaped sectors (pec fin, dorsal fin and flukes) for individuals where photographs were not available for Photoshop area calculations. The 'square area', the area of each sector if it were square shaped (dorsal fin base^2, fluke width^2, internal pec length^2), was calculated for each individual. For individuals with Photoshop area measurements, the 'percentage of square area', the percentage of the square area that was taken up by the Photoshop area, was calculated, as well as the standard deviation to monitor variability of the dataset.

$$Percentage\ of\ square\ area = \frac{Photoshop\ area}{Square\ area} \times 100$$

The sector area was resampled 100 times from a normal distribution around the mean and standard deviation of the percentage of square area. The median of these values was calculated as an estimate of the sector area. This controlled for variation in size and shape of sectors across individuals and accounted for outliers in the data.

Based on randomization test results, this analysis was conducted separately for pectoral fins and flukes of immature and mature individuals to account for the expected effect of maturity status on area estimation. Immature and mature individuals were not separated for dorsal fin estimates as randomization testing showed no significant impact of maturity status on the area estimation of this sector.

2.5.4 Validation of area estimates

A leave one out cross validation (LOOCV) was performed to determine the reliability of the sector area estimates. To do this, I subset the data to include only animals with Photoshop measurements of area and calculated the mean and standard deviation of the percentage of square area. LOOCV was used to estimate the area of each sector for each animal, using 1000 resampling iterations. For each iteration, an individual was excluded from the dataset (test individual). The mean and standard deviation of percentage of square area was calculated for the remaining individuals (training set). The excluded test individual's percentage of square area was estimated by 1) resampling from a normal distribution based on the mean and standard deviation calculated for the remaining individuals, and 2) taking the median of the resampled values. To determine the reliability of these new area estimates, I calculated a 95% confidence interval of the resampled values and estimated the percentage of area calculations for the test individual that fell within the respective confidence intervals of the estimate.

2.5.5 Calculating rake density

Due to skin loss, the 'area of skin visible' was calculated for each sector, sector grouping, and the entire body. This was done by subtracting the percentage of skin loss from the corresponding body area. The rake density (rm/dm^2) was then calculated for each sector, sector grouping and the entire body using the following formula.

$$Rake\ density = \frac{Rake\ count}{Area\ of\ skin\ visible}$$

2.6 Statistical analysis

2.6.1 Descriptive statistics

Descriptive statistics (mean, standard deviation, minimum and maximum) of rake density were calculated for each category within sex (male and female), sexual maturity (immature and mature), female reproductive status (immature, pregnant and/or lactating, and resting mature), and body condition (good or moderate). For age and total body length (TBL), scatterplots were created to show the relationship of each variable with rake density. Descriptive statistics of rake density were also calculated for each body sector and sector grouping. Additionally, descriptive statistics were calculated for cookie cutter scars, tattoo lesions, linear scars, irregular scars, and other lesions (as defined in Table 2.1). Squid marks were assessed as present or absent on each individual.

2.6.2 Multivariate analysis

Zero-inflated models are particularly useful for analysing semi-continuous, heteroscedastic data with a high proportion of zeros and a positive skew of non-zero values, which commonly occur in biomedical and ecological research (Lee et al., 2010; Liu et al., 2019; Martin et al., 2005), including rake density data used in this thesis. Therefore, zero-inflated models were used in R version 4.3.3 (R Core Team, 2024) for multivariate analysis of the effect of predictor variables (age, sex, sexual maturity, female reproductive status, body condition, and TBL) on the response variable, rake density. Such models consist of two parts: (i) the conditional model, a gamma regression model of the positive values of the response variable (rake density > 0), examining the effect of predictors on rake mark prevalence (measured by rake density value), and (ii) the zero-inflation model, a binary outcome model that determines the probability of a zero outcome (rake density = 0) or not (rake density > 0), assessing the effect of predictors on rake mark occurrence (D'Este et al., 2020; de Freitas Costa et al., 2021). Zero-inflation models estimate the probability of a zero occurring, where a negative estimate indicates a higher chance of occurrence, while a negative estimate for the conditional model indicates a lower rake density level (Brooks et al., 2017).

To analyse the effect of a suite of predictor variables (sex, sexual maturity, TBL, age, female reproductive status, and body condition) on the frequency and occurrence of the response variable, rake density of the entire body, zero-inflated generalised linear models (ZIGLMs) were used.

Zero-inflated generalised linear mixed-effect models (ZIGLMMs) were used to analyse the effect of a suite of predictor variables (sector grouping categories (dorsal, ventral, cranial, caudal, left, right), body condition, sex, sexual maturity, TBL, and age) on the frequency and occurrence of rake density within specific body sector groupings (dorsal vs ventral, cranial vs caudal, left vs right). This approach allowed the inclusion of individual identification (ID), the code used to identify each dolphin, as a random factor to account for repeated measures on the same animal (i.e., left and right sector grouping).

For each analysis and its corresponding response variable, models were built for all possible combinations of predictor variables using a log linked zero-inflated gamma error distribution. Model fit was evaluated using AICc and wAICc values. For each model that was deemed the best fit, interaction effects between predictor variables were assessed and maintained in cases where they improved model fit. Final models were checked for normality of random effects, heteroscedasticity, multicollinearity, and uniformity of residuals. In cases where heteroscedasticity was detected, a square root transformation of the response variable was performed to stabilise variance. However, the comparison of final model results showed that the transformation did not affect the results, so the original non-transformed models were retained.

Chapter 3 - Results

3.1 Sample summary

The entire dataset of common dolphins (*Delphinus delphis*) (n = 102) were included in the descriptive analysis of rake density (rm/dm^2) for both the entire body and body sector analysis. Rake marks were observed on 79.4% of animals (n = 81), including 45 females (n = 17 immature and n = 28 mature) and 36 males (n = 19 immature and n = 17 mature). An additional 21 animals did not display any rake marks (n = 11 females and n = 10 males). A total of 89 individuals (n = 75 with rake marks and n = 14 without rake marks) were included in the multivariate analysis of rake density, due to the removal of individuals missing age data (n = 13).

3.2 Rake mark occurrence and prevalence

Rake density ranged from 0 to 1.06 (mean = 0.17; SD = 0.20). The best fit model for the analysis of rake density of the entire body retained sex and total body length (TBL, in cm) as predictor variables (Table A.1).

3.2.1 Sex

Rake density in females ranged from 0 to 1.06 (n = 56, mean = 0.20; SD = 0.23), while males ranged 0 to 0.60 (n = 46, mean = 0.13; SD = 0.15). Sex was the most important predictor of rake density (Table 3.1). The conditional model showed that females had higher rake density than males, with a large effect size and a small confidence interval supporting this result (Table 3.1 – A). The zero-inflated model indicated that females may be more likely to have a rake density of zero than males (Table 3.1 – B). However, despite the large effect size, the standard error and confidence interval for this result were high ($p > 0.05$).

Table 3.1 Best fit zero-inflated generalised linear model (ZIGLM) of rake mark occurrence and frequency (rake density, rm/dm^2) across the entire body in common dolphins (*Delphinus delphis*) assessed postmortem. Prevalence of rakes is modeled by the conditional model (A), while occurrence of rakes is modeled by the zero-inflation model (B). This best fit model includes sex (female or male) and total body length (TBL, in cm) as predictors. Also displayed are estimated coefficients for predictor variables (Est), their standard errors (SE), and probabilities of the occurrence of the outcome by chance (Pr).

Model	**Variable**	**Est**	**SE**	**Pr**
Rake density ~ Sex + TBL				
(A) Conditional model:				
	(Intercept)	-6.64	0.72	$<2.0 \times 10^{-16}$
	Sex_Male	-0.52	0.18	3.0×10^{-3}
	TBL	0.03	3.8×10^{-3}	2.3×10^{-13}
(B) Zero-inflation model:				
	(Intercept)	10.25	2.71	1.5×10^{-4}
	Sex_Male	-0.83	0.91	0.36
	TBL	-0.08	0.02	4.0×10^{-5}

3.2.2 Age and total body length (TBL)

Of the aged animals, age ranged from 0 to 33 years (mean = 8.48, SD = 7.07, n = 89). Visual inspection indicated that rake density increased with age (Figure 3.1). However, age was not retained as a predictor variable in the top ranked model, indicating no evident relationship between age and rake density, or the probability of a zero-value for rake density (Table A.1).

TBL ranged from 85.5 to 234 cm (mean = 169.23, SD = 38.74, n = 102) for the entire dataset. Visual inspection indicated that larger individuals had a higher rake density than smaller individuals (Figure 3.2). The conditional model also showed that rake density was higher in larger individuals than smaller individuals, although this effect was small (Table 3.1 – A). The zero-inflated model showed that smaller individuals are more likely to have a zero-value for rake density than larger individuals, however, the effect size was moderate, and the confidence interval was small (Table 3.1 – B).

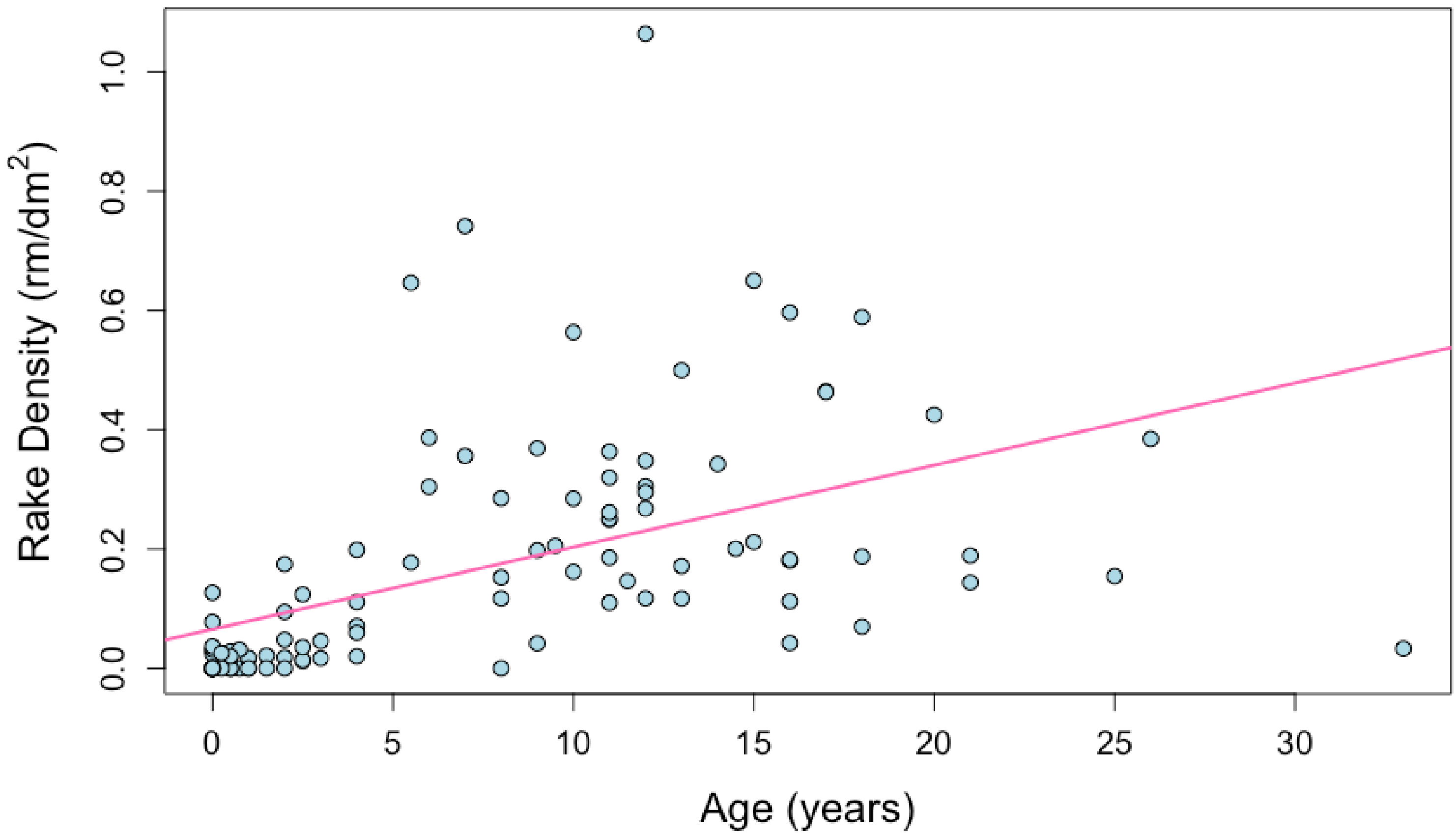


Figure 3.1 The relationship between rake density (rm/dm^2) and age (years) in common dolphins (*Delphinus delphis*) assessed postmortem between 2006 and 2024 in New Zealand. Each blue dot represents an individual dolphin's age and corresponding rake density. The pink linear regression line indicates the general trend, showing how rake density changes with age.

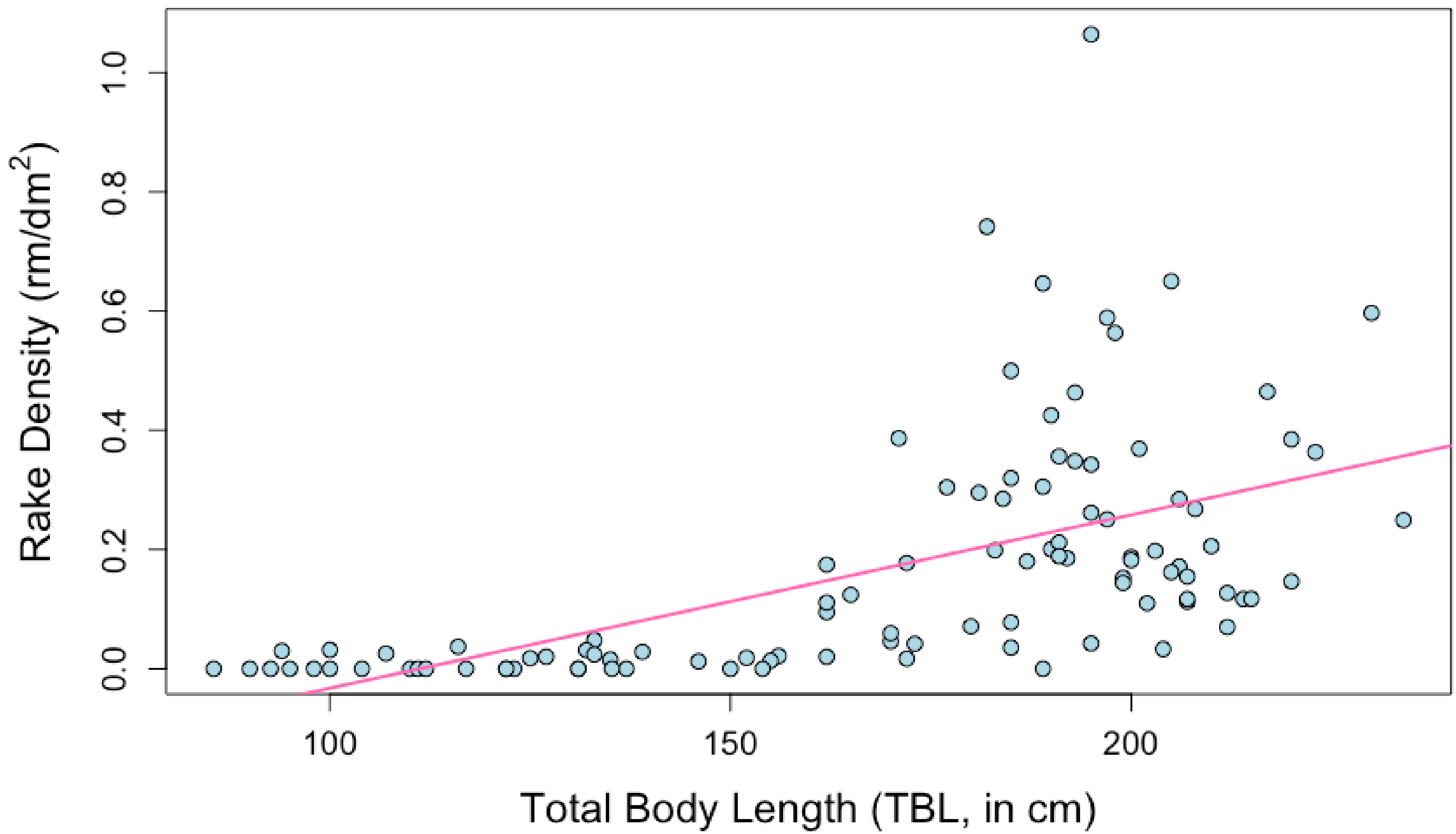


Figure 3.2 The relationship between rake density (rm/dm^2) and total body length (TBL, in cm) in common dolphins (*Delphinus delphis*) assessed postmortem between 2006 and 2024 in New Zealand. Each blue dot represents an individual dolphin's TBL and corresponding rake density. The pink linear regression line indicates the general trend, showing how rake density changes with TBL.

3.2.3 Sexual maturity

Sexually mature and immature individuals ranged in rake density from 0 to 0.74 (mean = 0.08; SD = 0.15, n = 46) and 0 to 1.06 (mean = 0.28; SD = 0.20, n = 56), respectively. For females, rake density ranged from 0 to 0.74 (mean = 0.09; SD = 0.18, n = 27) and 0 to 1.06 (mean = 0.31; SD = 0.22, n = 29) for sexually immature and mature individuals, respectively. Sexually mature and immature males ranged from 0.03 to 0.60 (mean = 0.22; SD = 0.15, n = 17) and 0 to 0.39 (mean = 0.08; SD = 0.12, n = 29), respectively. Models including sexual maturity as a predictor variable did not provide the best fit for the data, suggesting no clear difference in rake density, or the likelihood of a zero-value for rake density between immature and mature common dolphins (Table A.1). Therefore, no further multivariate analysis investigated a potential difference in the effect of sexual maturity on rake marks between males and females.

3.2.4 Body condition

Rake density ranged from 0 to 0.74 (mean = 0.17; SD = 0.19, n = 66) for individuals with good body condition, and 0 to 1.06 (mean = 0.17; SD = 0.22, n = 36) for those with good and moderate body condition. Models that included body condition as a predictor variable were not the best fit for the data, implying no apparent relationship between body condition and rake density, or the probability of rake density being zero (Table A.1).

3.2.5 Female reproductive status

Rake density ranged from 0 to 0.74 (mean = 0.09; SD = 0.18, n = 27) for females with an immature reproductive status, 0 to 0.65 (mean = 0.28; SD = 0.17, n = 23) for those that were pregnant and/or lactating, and 0.04 to 1.06 (mean = 0.41; SD = 0.35, n = 6) for resting mature females.

The best fit model analysing the effect of reproductive status on female rake density retained TBL alongside reproductive status as predictor variables (Table A.2). The conditional model found that resting mature females had the highest rake density, followed by immature, then pregnant and/or lactating females. While the effect for resting mature females was large, the effect for pregnant and/or lactating females was moderate, and the confidence interval was high for both results ($p > 0.05$, Table 3.2 – A). The model also indicated that rake density was higher in larger compared to smaller individuals, although the effect was of this result was small (Table 3.2 – A). The zero-inflation model demonstrated that pregnant and/or lactating females had the highest probability of zero for rake density followed by immature, then resting mature females. Despite the large effect for resting mature females, and moderate effect for pregnant and/or lactating females, the corresponding confidence interval was high ($p > 0.05$, Table 3.2 – B). The probability of rake density being zero was also higher in smaller than larger individuals. However, this effect was small (Table 3.2 – B).

Table 3.2 Best fit zero-inflated generalised linear model (ZIGLM) of rake mark occurrence and frequency (rake density, (rm/dm^2) across the entire body in common dolphins (*Delphinus delphis*) assessed postmortem. Prevalence of rakes is modelled by the conditional model (A), while occurrence of rakes is modeled by the zero-inflation model (B). This model uses a subset of the full dataset that only includes females, and the top-ranked model includes total body length (TBL, in cm) and female reproductive status (immature, pregnant and/or lactating, and resting mature) as predictors. Also displayed are estimated coefficients for predictor variables (Est), their standard errors (SE), and probabilities of the occurrence of the outcome by chance (Pr).

Model	**Variable**	**Est**	**SE**	**Pr**
Rake density ~ Reproductive status + TBL				
(A) Conditional model:				
	(Intercept)	-8.03	1.11	$4.0 \times 10^{-}$
	Repro_Preg/lact	-0.09	0.32	0.78
	Repro_Resting	0.39	0.40	0.32
	TBL	0.04	6.6×10^{-3}	1.0×10^{-7}
(B) Zero-inflation model:				
	(Intercept)	10.05	4.00	0.01
	Repro_Preg/lact	1.87	2.15	0.38
	Repro_Resting	-	2.3×10^{4}	1.00
	TBL	-0.08	3.0×10^{-2}	9.5×10^{-3}

3.3 Rake mark distribution and position

Among the body sectors, the right dorsal peduncle demonstrated the highest mean and maximum rake density, while the dorsal caudal flank on the dorsum had the lowest (Table 3.3). The body sector grouping with the highest mean and maximum rake density was the caudal sector grouping, whereas cranial had the lowest (Table 3.4).

Table 3.3 Summary statistics of rake density (rm/dm^2) for each body sector in stranded common dolphins (*Delphinus delphis*) assessed postmortem between 2006 and 2024 in New Zealand. Refer to figure 2.2 for sector location. Note: SD = standard deviation, min = minimum, max = maximum.

Sector	Mean	SD	Min	Max
Dorsum				
Dorsal caudal flank	0.00	0.01	0.00	0.09
Dorsal cranial flank	0.03	0.09	0.00	0.75
Dorsal head	0.05	0.10	0.00	0.45
Dorsal peduncle	0.03	0.09	0.00	0.64
Fluke	0.01	0.09	0.00	0.85
Left lateral				
Dorsal caudal flank	0.07	0.19	0.00	0.97
Dorsal cranial flank	0.25	0.48	0.00	3.81
Dorsal head	0.12	0.31	0.00	2.17
Dorsal fin	0.05	0.17	0.00	1.13
Dorsal pectoral fin	0.08	0.37	0.00	2.69
Dorsal peduncle	0.51	0.79	0.00	5.03
Ventral caudal flank	0.04	0.10	0.00	0.60
Ventral cranial flank	0.06	0.12	0.00	0.57
Ventral head	0.04	0.10	0.00	0.61
Ventral pectoral fin	0.04	0.27	0.00	2.07
Ventral peduncle	0.20	0.35	0.00	2.60
Right lateral				
Dorsal caudal flank	0.12	0.31	0.00	2.22
Dorsal cranial flank	0.24	0.58	0.00	4.76
Dorsal head	0.13	0.30	0.00	2.17
Dorsal fin	0.03	0.13	0.00	0.79
Dorsal pectoral fin	0.07	0.33	0.00	2.69
Dorsal peduncle	0.60	1.05	0.00	7.55

Ventral caudal flank	0.06	0.14	0.00	0.95
Ventral cranial flank	0.06	0.17	0.00	1.37
Ventral head	0.02	0.07	0.00	0.41
Ventral pectoral fin	0.05	0.24	0.00	1.54
Ventral peduncle	0.16	0.23	0.00	1.05
Ventrum				
Ventral fluke	0.01	0.08	0.00	0.51
Ventral caudal flank	0.08	0.23	0.00	1.77
Ventral cranial flank	0.10	0.29	0.00	2.22
Ventral head	0.03	0.10	0.00	0.83
Ventral peduncle	0.09	0.22	0.00	0.99

Table 3.4 Summary statistics of rake density (rm/dm^2) for each body sector grouping in stranded common dolphins (*Delphinus delphis*) assessed postmortem between 2006 and 2024 in New Zealand. Refer to (Figure 2.3) for sector grouping location. Note: SD = standard deviation, min = minimum, max = maximum.

Sector Grouping	Mean	SD	Min	Max
Dorsal	0.17	0.19	0.00	1.03
Ventral	0.17	0.21	0.00	1.11
Caudal	0.19	0.22	0.00	1.12
Cranial	0.13	0.18	0.00	0.75
Left	0.14	0.17	0.00	1.01
Right	0.14	0.18	0.00	0.78

3.3.1 Dorsal vs. ventral

For the dorsum and ventrum, the best fit model included body sector grouping, sex and TBL as the predictor variables, with an interaction effect between sector grouping and sex (Table A.3). The conditional model showed that while rake density was higher for females than males in both the dorsum and ventrum, females had a higher rake density on the dorsum compared to the ventrum, whereas males had higher rake density on the ventrum compared to the dorsum (Table 3.5 – A, Figure **3.3**). Although despite the large effect, the corresponding confidence interval was high ($p > 0.05$, Table 3.5 – A). Rake density also increased marginally as TBL increased, but the effect was small (Table 3.5 – A). The zero-inflated model indicated that the probability of rake density being zero may be higher on the dorsum than the ventrum for both females and males (Table 3.5 – B, Figure **3.4**). However, similar to the conditional model, the confidence interval was high despite the large effect ($p > 0.05$). In addition, the likelihood of rake density being zero decreased as TBL increased, with a moderate effect and small confidence interval (Table 3.5 – B).

Table 3.5 Best fit zero-inflated generalised linear mixed model (ZIGLMM) of rake mark occurrence and frequency (rake density, rm/dm^2) across body sector groupings in stranded common dolphins (*Delphinus delphis*) assessed postmortem. Prevalence of rakes is modeled by the conditional model (A), while occurrence of rakes is modelled by the zero-inflation model (B). These models include individual ID as a random factor and incorporate sex (female or male), total body length (TBL, in cm), and sector grouping (dorsal or ventral) as predictors, investigating interactions between them. Also displayed are estimated coefficients for predictor variables (est), their standard errors (SE), and probabilities of the occurrence of the outcome by chance (Pr).

Model	Variable	Est	SE	Pr
Dorsal vs Ventral:				
Rake density ~ TBL + Sex * Sector grouping + (1 | ID)				
(A) Conditional model:				
	(Intercept)	-5.56	0.60	$<2.0\times10^{-16}$
	TBL	0.02	3.2×10^{-3}	1.9×10^{-11}
	Sex_Male	-0.53	0.18	2.4×10^{-3}
	Sector_Ventral	-0.07	0.10	0.50
	SexM:SectorVentral	0.26	0.15	0.08
(B) Zero-inflation model:				
	(Intercept)	12.1	3.50	5.7×10^{-4}
	TBL	-0.08	0.02	3.9×10^{-4}
	Sex_Male	-1.30	1.00	0.19
	Sector_Ventral	0.28	0.76	0.71
	SexM:SectorVentral	2.19	1.33	0.10

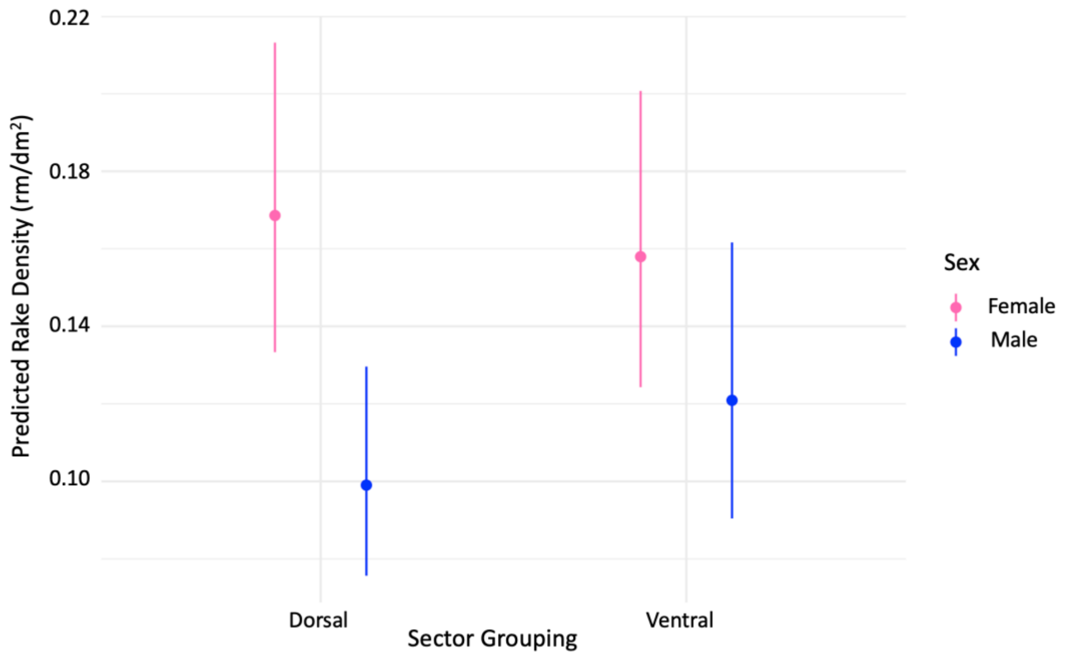


Figure 3.3 Interaction effects of predictor variables sector grouping (dorsal and ventral) and sex (male and female) on rake density (rm/dm^2) for the conditional model of the dorsal vs ventral zero-inflated generalised linear mixed model (ZIGLMM) of common dolphins (*Delphinus delphis*) assessed postmortem.

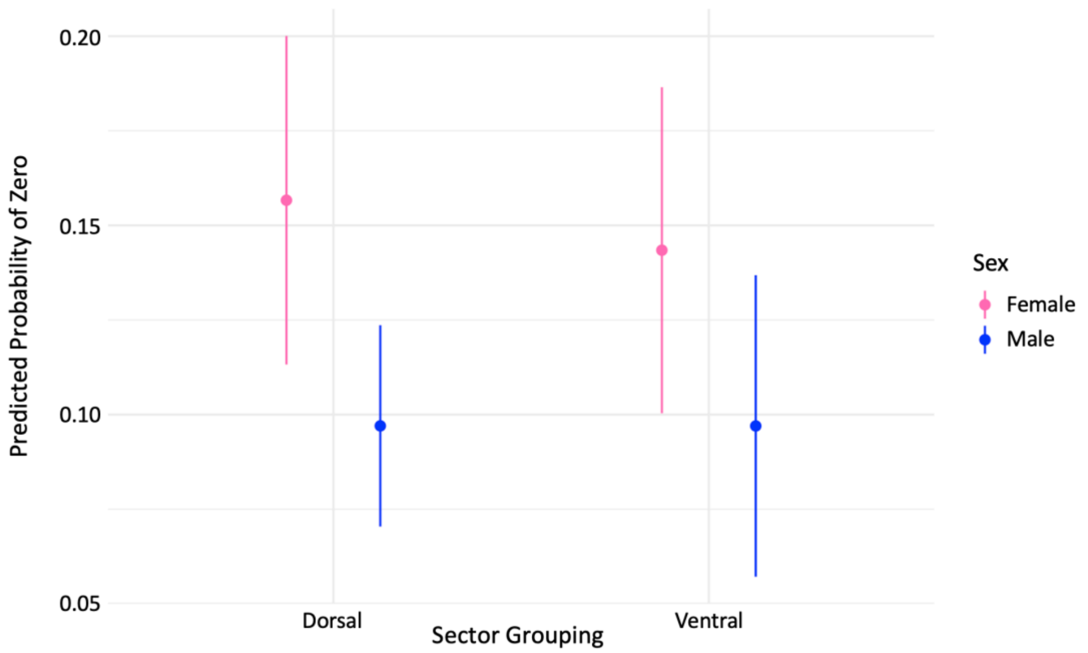


Figure 3.4 Interaction effects of predictor variables sector grouping (dorsal and ventral) and sex (male and female) on rake density (rm/dm^2) for the zero-inflated model of the dorsal vs ventral zero-inflated generalised linear mixed model (ZIGLMM) of common dolphins (*Delphinus delphis*) assessed postmortem.

3.3.2 Cranial vs. caudal

For cranial and caudal, the best-fit model retained sector grouping, sex and TBL as the predictor variables, with an interaction effect between sector grouping and TBL (Table A.4). The conditional model showed that larger common dolphins had a higher caudal rake density than cranial, while smaller individuals had a slightly higher cranial rake density than caudal, however the effect of this predictor was small (Table 3.6 – A, Figure **3.5**). It also indicated that female common dolphins had a higher rake density than males, although this effect was also small (Table 3.6 – A). The zero-inflated model showed that the likelihood of rake density being zero was also higher for females than males, with a moderate effect size (Table 3.6 – B). Larger individuals had a higher probability of zero caudal rake density compared to cranial, whereas smaller dolphins had a higher probability of zero cranial rake density in the cranial compared to caudal, although again this effect size was small (Table 3.6 – B, Figure 3.6).

Table 3.6 Best fit zero-inflated generalised linear mixed model (ZIGLMM) of rake mark occurrence and frequency (rake density, rm/dm^2) across body sector groupings in common dolphins (*Delphinus delphis*) assessed postmortem. Prevalence of rakes is modeled by the conditional model (A), while occurrence of rakes is modelled by the zero-inflation model (B). These models include individual ID as a random factor and incorporates sex (female or male), total body length (TBL, in cm), and sector grouping (cranial or caudal) as predictors, investigating interactions between them. Also displayed are estimated coefficients for predictor variables (est), their standard errors (SE), and probabilities of the occurrence of the outcome by chance (Pr).

Model	Variable	Est	SE	Pr
Cranial vs Caudal:				
Rake density ~ Sex + TBL * Sector grouping + (1 | ID)				
(A) Conditional model:				
	(Intercept)	-7.20	0.80	<2.0x10^{-16}
	Sex_Male	-0.40	0.18	0.02
	TBL	0.03	4.2x10^{-3}	6.4x10^{-13}
	Sector_Cranial	3.86	0.96	5.9x10^{-5}
	TBL:SectorCranial	-0.02	5.0x10^{-3}	1.5x10^{-5}

(B) Zero-inflation model:

	(Intercept)	10.53	2.40	$1.1x10^{-5}$
	Sex_Male	-0.08	0.50	0.88
	TBL	-0.07	0.02	$1.9x10^{-6}$
	Sector_Cranial	-2.97	2.92	0.31
	TBL:SectorCranial	0.02	0.02	0.22

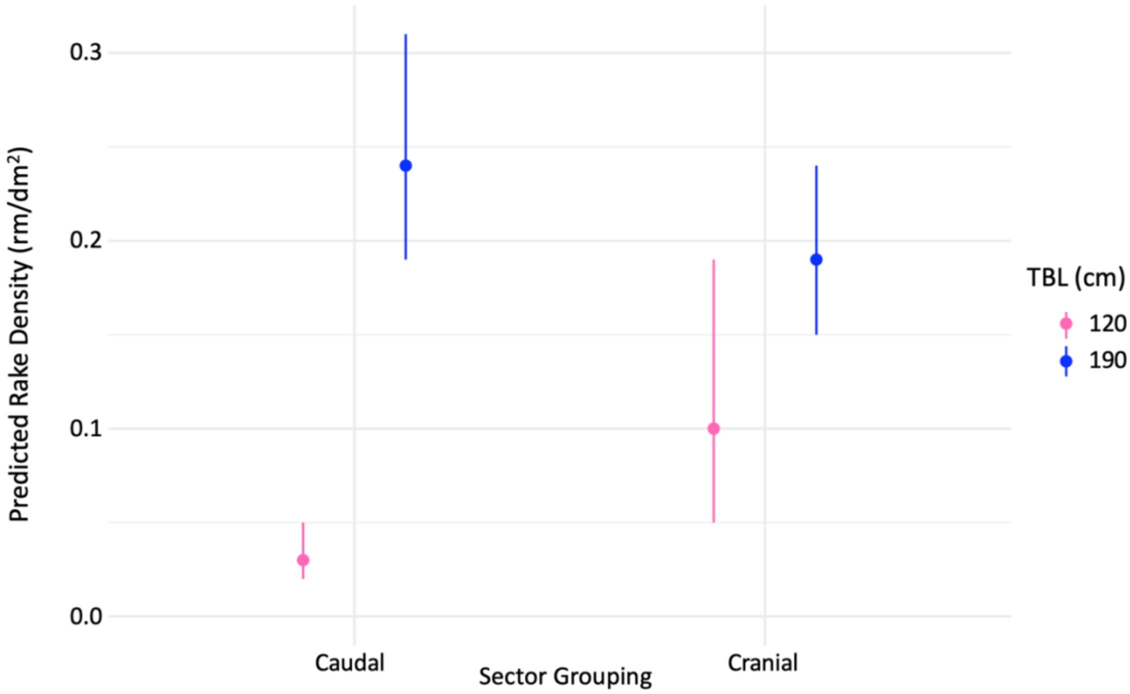


Figure 3.5 Interaction effects of predictor variables sector grouping (cranial and caudal) and total body length (TBL, 120 and 190 cm, chosen for display purposes) on rake density (rm/dm^2) for the conditional model of the cranial vs caudal zero-inflated generalised linear mixed model (ZIGLMM) of common dolphins (*Delphinus delphis*) assessed postmortem.

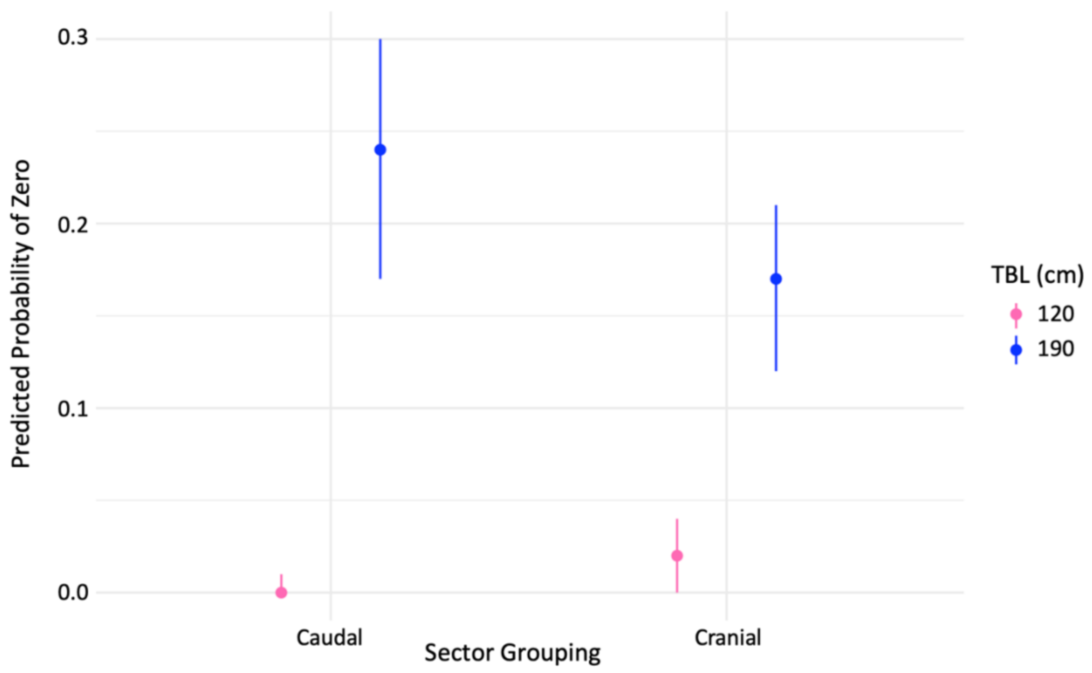


Figure 3.6 Interaction effects of predictor variables sector grouping (cranial and caudal) and total body length (TBL, 120 and 190 cm, chosen for display purposes) on rake density (rm/dm^2) for the zero-inflated model of the cranial vs caudal zero-inflated generalised linear mixed model (ZIGLMM) of common dolphins (*Delphinus delphis*) assessed postmortem.

3.3.3 Left vs. right

For the left and right lateral surfaces, the best-fitting model retained body sector grouping, sex and TBL as the predictor variables, with an interaction effect between sector grouping and TBL (Table A.5). The conditional model showed that female common dolphins had a higher rake density than males, with a moderate effect size (Table 3.7 – A). Larger individuals had a higher rake density for the right compared to the left surface, whereas smaller individuals had a higher rake density for the left compared to the right, although the effect of this result was small (Table 3.7 – A, Figure 3.7). The zero-inflated model indicated that larger common dolphins had a higher probability of zero inflated rake density for the right surface compared to the left, whereas smaller individuals had a higher probability of zero inflated rake density for the left compared to the right, but again, the effect was small (Table 3.7 – B, Figure 3.8). Females had a greater probability of zero rake density than males, although despite the moderate effect size, the confidence interval was high ($p > 0.05$, Table 3.7 – B).

Table 3.7 Best fit zero-inflated generalised linear mixed model (ZIGLMM) of rake mark occurrence and frequency (rake density, rm/dm^2) across body sector groupings in common dolphins (*Delphinus delphis*) assessed postmortem. Prevalence of rakes is modeled by the conditional model (A), while occurrence of rakes is modelled by the zero-inflation model (B). These models include individual ID as a random factor and incorporate sex (female or male), total body length (TBL, in cm), and sector grouping (left or right) as predictors, investigating interactions between them. Also displayed are estimated coefficients for predictor variables (est), their standard errors (SE), and probabilities of the occurrence of the outcome by chance (Pr).

Model	Variable	Est	SE	Pr
Left vs Right: Rake density ~ Sex + Sector grouping * TBL + (1 | ID)				
(A) Conditional model:				
	(Intercept)	-4.01	0.68	3.6×10^{-9}
	Sex_Male	-0.41	0.16	0.01
	Sector_Right	-2.21	0.77	4.0×10^{-3}
	TBL	0.01	3.6×10^{-3}	3.0×10^{-4}
	SectorRight:TBL	0.01	4.0×10^{-3}	6.6×10^{-3}
(B) Zero-inflation model:				
	(Intercept)	6.71	1.62	3.6×10^{-5}
	Sex_Male	-0.21	0.48	0.66
	Sector_Right	5.34	3.11	0.09
	TBL	-0.04	9.4×10^{-3}	3.3×10^{-6}
	SectorRight:TBL	-0.04	0.02	0.05

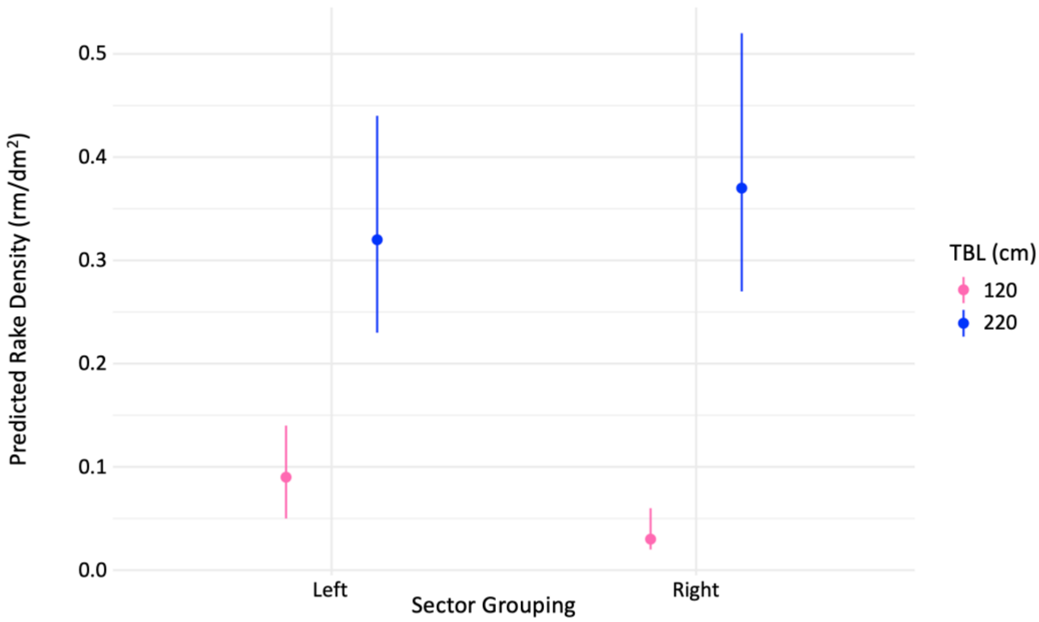


Figure 3.7 Interaction effects of predictor variables sector grouping (left and right) and total body length (TBL, 120 and 220 cm, chosen for display purposes) on rake density (rm/dm^2) for the conditional model of the left vs right zero-inflated generalised linear mixed model (ZIGLMM) of common dolphins (*Delphinus delphis*) assessed postmortem.

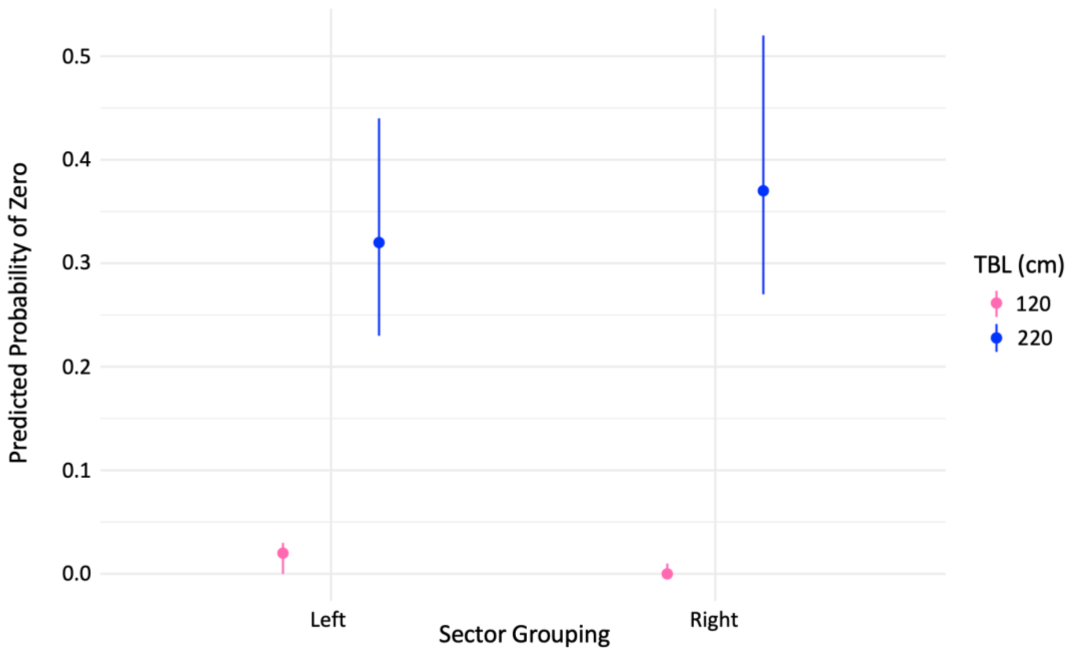


Figure 3.8 Interaction effects of predictor variables: sector grouping (left and right) and total body length (TBL, 120 and 220cm, chosen for display purposes), on rake density (rm/dm^2), for the zero-inflated model of the left vs right zero-inflated generalised linear mixed model (ZIGLMM) of stranded common dolphins (*Delphinus delphis*) assessed postmortem.

3.4 Descriptive statistics for non-rake lesions

Descriptive statistics (mean, standard deviation, minimum and maximum) were calculated for cookie cutter scars, tattoo lesions, linear scars, irregular scars and other lesions (as defined in Table 2.1), for the entire dataset (Table A.6), as well as independently for females (Table A.7), and males (Table A.8). Additionally, 34 individuals displayed small circular putative squid lesions, including 24 females and 10 males.

Chapter 4 - Discussion

Existing literature examines rake marks as indicators of social aggression in delphinids (Crespo-Picazo et al., 2021; Grimes et al., 2022; Gross et al., 2020; Hamilton et al., 2019; Lee et al., 2019; Marley et al., 2013; Orbach et al., 2015; Patiño-Pérez, 2022; Reinhart et al., 2013; Scott et al., 2005; Serres et al., 2023; Waples & Gales, 2002). Therefore, the majority of the discussion of rake marks in this thesis is placed within the context of aggressive interactions between aihe (common dolphin, *Delphinus delphis*) in New Zealand.

Aggressive behaviour associated with social living includes competition for status (Creel et al., 2013; Dantzer et al., 2017a; Dantzer et al., 2017b; Drea & Davies, 2022; Hobson et al., 2021; Honess & Marin, 2006; Šabanović et al., 2020), resources (Milewski et al., 2022; Waples & Gales, 2002), and mates (Beaulieu et al., 2014; Lemonnier et al., 2022). Such aggression can be energetically, physically and physiologically costly, and interfere with beneficial social relationships (Georgiev et al., 2013; Grimes et al., 2022; Snyder-Mackler et al., 2020). Adverse health effects associated with stress from aggression include accelerated aging (Milewski et al., 2022; Wright et al., 2007), increased susceptibility to and symptoms of disease (Aich et al., 2009; Paital et al., 2016; Wright et al., 2007), as well as impairment of reproduction, wound healing and development (Christian et al., 2007; Dantzer et al., 2017b; Moberg & Mench, 2000; Waples & Gales, 2002; Wright et al., 2007). Consideration of these aggressive interactions is important from both an animal welfare (Beausoleil et al., 2018; Boys et al., 2023; Boys et al., 2022a, 2022b; Clegg et al., 2017) and a conservation biology perspective (Kaisin et al., 2021; Kophamel et al., 2022; Schweinfurth, 2020).

Direct observation of aggressive behaviour in wild animals can be challenging. However, quantitative measures of body scarring can be used as a proxy of aggressive behaviour received by an individual. This method has been applied to the examination of wounds on olive baboons (*Papio anubis*) (MacCormick et al., 2012), scars on dugongs (*Dugong dugon*) (Burgess et al., 2013) and rake mark scars on a range of delphinid species (Brown et al., 2016; Frantzis & Herzing, 2002; Hamilton et al., 2019; Lee et al., 2019; Marley et al., 2013; Orbach et al., 2015; Reinhart et al., 2013; Scott et al., 2005). Aggressive behaviour can influence delphinid social structure and dynamics (Hamilton et al., 2019; Kleinschmidt, 2014; Scott et al., 2005), reproductive success (Brown et al., 2016; Evans & Stirling, 2001; Marley et al., 2013; Scott et al., 2005), resource allocation (Grimes et al., 2022; Hamilton et al., 2019; Lee et al., 2019; Serres et al., 2023), as well as stress and health (Hamilton et al., 2019; Waples & Gales, 2002). Therefore, an understanding of such behaviour provides insights into behavioural ecology and informs conservation efforts.

Rake marks have been documented in the context of aggressive interactions due to intra- and inter-specific competition, and predation (Crespo-Picazo et al., 2021; Lee et al., 2019; Lockyer & Morris, 1990; Ross & Wilson, 1996; Tolley et al., 1995). In this thesis, I attribute rake marks to conspecific interactions based on measurements of inter-rake distance (IRD ca 5mm), acknowledging potential variation in this measurement depending on the state of dentition. Therefore, this thesis primarily investigates rake density (rm/dm^2), considering the occurrence (the likelihood of rake density being greater than zero), prevalence (rake density value) and position of rake marks on common dolphins in the context of age, sex, total body length (TBL), body condition, sexual maturity, and reproductive stage, to gain insight into aggressive interactions between conspecifics.

4.1 Occurrence and prevalence of rake marks

4.1.1 Sex

A contradicting difference in rake mark occurrence and prevalence with sex was observed. Males demonstrated a higher rake occurrence, though lower rake prevalence than females (Table 3.1). An unpublished thesis that assessed *Delphinus* post mortem in Ireland also found that females were significantly more raked than males (Murphy, 1999). My results also align with previous research which reported that males are more likely to have rake marks than females in killer whales (*Orcinus orca*) (Grimes et al., 2022), and bottlenose dolphins (*Tursiops* spp.) (James et al., 2022; Lee et al., 2019; Scott et al., 2005; Tolley et al., 1995). Other studies found that male delphinids have a higher rake mark prevalence than females (Grimes et al., 2022; Marley et al., 2013; Martin & Da Silva, 2006; Serres et al., 2023), which is contrary to results presented here. It is possible that male common dolphins engage in more frequent, but lower intensity conflicts, leading to a higher occurrence of rakes, at a lower prevalence than females. Females might engage in less frequent, but more severe aggressive interactions than males. This could possibly be attributed to the consistency of female dominance relationships compared to instability among males (Grimes et al., 2022; Samuels & Gifford, 1997), resulting in more frequent aggressive challenges for dominance between males (Wright et al., 2019). Females may also engage in more severe contests when protecting themselves or their calves from male harassment (Weir et al., 2008), and/or when receiving sexually coercive behaviour from males (Hamilton et al., 2019; Marley et al., 2013).

An alternative explanation might relate to variation in healing rates hypothesized between males and females (Hamilton et al., 2019; Lee et al., 2019; Marley et al., 2013; Scott et al., 2005; Serres et al., 2023). In humans (*Homo sapiens*), cutaneous wounds heal faster in females than males (Ashcroft, 2004; Fimmel & Zouboulis, 2005; Thomason et al., 2015). A similar pattern has also been observed in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (Lee et al., 2019). The lower occurrence of rake marks in female common dolphins could be due to a better immune response or less frequent exposure to severe aggression compared to males, resulting in faster average healing rates (Lee et al., 2019; Scott et al., 2005). However, the increased prevalence of rake marks on females suggests that when females do experience severe aggression, the inflicted rake marks may take longer to heal (Lee et al., 2019). This prolonged healing time could account for the higher prevalence of rake marks observed in females, despite the overall lower occurrence among females.

4.1.2 Age and TBL

No relationship between age and rake mark prevalence or occurrence was evident (Table A.1). However, variation in social interactions across different ages has been detected in a range of species, including olive baboons (Silk et al., 2020), alpine ibexs (*Capra ibex*) (Brambilla et al., 2022), and beluga whales (*Delphinapterus leucas*) (Ham et al., 2021). Likewise, age has been associated with variation in rake marks in bottlenose dolphins (Lee et al., 2019; Scott et al., 2005), killer whales (Grimes et al., 2022), and Indo-Pacific humpback dolphins (*Sousa chinensis*) (Serres et al., 2023), likely due to behavioural shifts that occur throughout an individual's lifespan. While it is plausible that each age class could be involved in similar levels of conflict, an alternative possibility is that age differences in common dolphin aggressive behaviour might occur, but the detection of such relationship may be masked by age effects on rake mark healing (Ashcroft et al., 2002; Gilliver & Ashcroft, 2007; Wong & Chew, 2021).

In humans, wound healing rates are known to vary with age (Ashcroft et al., 2002; Gilliver & Ashcroft, 2007; Wong & Chew, 2021). This might be because older individuals are more vulnerable to malnutrition, as a range of health factors may reduce appetite and physical ability, leading to poor body condition and reduced immune function (Ghaly et al., 2021; Gilliver & Ashcroft, 2007). Conversely, younger, healthier individuals might be more likely to heal faster and more efficiently (Ghaly et al., 2021; Gilliver & Ashcroft, 2007; Wong & Chew, 2021). It is possible that as common dolphins age, healing efficiency may be reduced, resulting in longer healing times and increased detection of rake marks. Should this be the case, variable healing time could mask the detection of an age relationship with social aggression using rake marks.

In contrast to age, rake mark occurrence and prevalence did increase marginally with total body length (TBL) (Table 3.1). This concurs with Murphy (1999), who also found that the number of rake marks on common dolphins increased with TBL. This may simply reflect the increasing probability of being raked as body surface area increases with TBL. However, a plausible alternative hypothesis is that larger common dolphins might engage in more frequent, and potentially more severe, aggressive interactions than smaller individuals. This role of body size in aggressive interactions is evident across a range of terrestrial mammals, including mountain gorillas (*Gorilla beringei beringei*) (Wright et al., 2019), bighorn sheep (*Ovis canadensis*) (Favre et al., 2008), and eastern grey kangaroos (*Macropus giganteus*) (Montana et al., 2022). Body size influences success in aggressive encounters, and often correlates with dominance rank and reproductive success (Wright et al., 2019).

There is limited literature investigating TBL in the context of rake marks in delphinids, although body size correlates with reproductive success in killer whales, possibly due to the benefit of size in aggressive contests (Wright et al., 2023). In addition, the large testes-to-body size ratio in male common dolphins favours sperm competition, rather than direct physical contests, indicating that post-anal hump size may act as a signal of dominance (MacLeod, 2010; Murphy et al., 2005; Murphy & Rogan, 2006; Palmer et al., 2023). Therefore, larger individuals might have more rake marks as they engage in more frequent aggressive contests, possibly to determine and/or sustain their dominance rank. However, given age was not deemed important within the model, this may imply that the increased surface area available to be raked in larger compared with smaller individuals is a more likely explanation for the relationship observed with TBL.

4.1.3 Body condition

Body condition demonstrated no effect on either rake mark occurrence or prevalence (Table A.1). Body condition was measured as a proxy of health, via nutritional index (Brosset et al., 2023; Hart et al., 2013; Joblon et al., 2014; Risco et al., 2018). In some species, healthier individuals with better body condition likely have enhanced fighting ability due to increased energy, strength, agility, and reflexes (Liu et al., 2020). This may enable them to assert dominance more effectively, potentially influencing the occurrence and outcome of contests (Liu et al., 2020). However, my results suggest that body condition might not impact the frequency or severity of aggressive interactions in common dolphins.

Poor health impacts physiological systems of the body, potentially inhibiting or slowing wound healing (Ghaly et al., 2021; Lux, 2022). Good health, supported by optimal nutritional status, provides the necessary conditions for collagen synthesis required for wound healing (Ghaly et al., 2021; Lux, 2022). Poor health reduces immune function, increasing the likelihood of infection and susceptibility to wounds, causing a delay in healing (Ghaly et al., 2021; Lux, 2022). Therefore, healing efficiency could be reduced in common dolphins experiencing poor health. If so, rake marks may persist for a longer period of time on common dolphins with poor body condition, making them more likely to be detected. This might complicate the use of rake marks as a measure of received aggression in animals of variable body condition, because a relationship between health and scarring itself may be masking a potential relationship with body condition and social aggression.

4.1.4 Sexual maturity and reproductive status

There was no clear relationship between sexual maturity and rake mark occurrence or prevalence (Table A.1). This contradicts existing hypotheses that suggest aggression among delphinids may be related to sexual coercion of females as well as male competition for dominance and reproduction (Lee et al., 2019; Marley et al., 2013; Scott et al., 2005; Serres et al., 2023). Such behaviours are observed in a broad range of mammals (Cassini, 2021), including chimpanzees (*Pan troglodytes*) (Enigk et al., 2021), mandrils (*Mandrillus sphinx*) (Smit et al., 2022), and bottlenose dolphins (Lee et al., 2019; Marley et al., 2013; Scott et al., 2005), and are thought to shape interactions of social species across different stages of sexual maturity. The lack of relationship detected in common dolphins may indicate that all stages of sexual maturity are exposed to a similar level of social aggression, leading to a constant likelihood of rake marks.

However, female rake mark occurrence and prevalence did vary with reproductive status (Table 3.2). Resting mature females demonstrated the highest rake mark occurrence and prevalence, followed by immature, then pregnant and/or lactating females. This suggests that resting mature females may receive the highest amount of aggression, possibly because they are available for reproduction, and subject to a higher rate of sexual coercion from males (Marley et al., 2013; Scott et al., 2005). This hypothesis is supported by Scott et al. (2005), who observed that cycling bottlenose dolphin females were more likely to have new rake marks than non-cycling females, likely due to increased male sexual coercion. Pregnant and/or lactating females had the lowest rake mark occurrence and prevalence, suggesting that they might engage in the least amount of aggressive interactions. This may be attributed to their unavailability for mating, resulting in reduced aggression from males (Karniski et al., 2018; Orbach et al., 2015; Scott et al., 2005), or due to increased avoidance behaviour during calf rearing (Stanton et al., 2011; Weir et al., 2008).

Reproductive status impacts wound healing in some species of wild primates, although existing literature appears contrary to the results presented in this thesis (Archie, 2013; Archie et al., 2014). In wild baboons (*Papio* spp.), lactating females heal from wounds more slowly than those that are pregnant or ovarian cycling (Archie et al., 2014). This is thought to be due to the high energy expenditure associated with reproduction, which leads to a resource allocation trade-off with immune function, slowing the rate of wound healing (Archie, 2013; Archie et al., 2014). This hypothesis contradicts the findings of this thesis, as pregnant and/or lactating common dolphins had the lowest rake mark occurrence and prevalence, suggesting either a lower level of aggression or, alternatively, faster healing rates in these individuals. Notably, this thesis does not separate lactating females from those that are pregnant, or pregnant and lactating. Thus, as observed in wild baboons, wound healing may vary between females within the pregnant and/or lactating subgroup (Archie et al., 2014). However, based on the results of this thesis, it would appear that the variation in rake marks observed with reproductive status in common dolphins is more likely associated with social interactions rather than wound healing.

4.2 Reproduction

Sexual behaviour, such as sexual coercion in the form of forced mating or harassment, is linked to and can influence aggressive interactions of wild animals (Cassini, 2021; Clutton-Brock & Parker, 1995; Muller & Wrangham, 2009). Such behaviours are thought to contribute to the occurrence and prevalence of rake marks on a range of delphinid species (Lee et al., 2019; Scott et al., 2005; Serres et al., 2023). In some delphinid species, aggressive behaviours, likely related to sexual coercion and motivated by mating success, vary across age classes, with distinct patterns of interaction and rake marks being observed (Lee et al., 2019; Scott et al., 2005; Serres et al., 2023). Scott et al. (2005) found bottlenose dolphin calves to be the only age class without a sex difference in rake marks. This may be because they do not engage in aggressive interactions associated with direct reproduction. However, they are thought to display play and socio-sexual behaviours, possibly to gain experience for future interactions, including mating acts (Harvey et al., 2017; Lee et al., 2019; Scott et al., 2005).

Juvenile dolphins, although sexually immature, engage in increased aggressive contests for dominance, which may present beneficial preferential access to mates and resources (Scott et al., 2005). Juveniles also engage in socio-sexual acts as a form of practice for mating (Scott et al., 2005).

Adult males of many species employ aggressive tactics to coerce females into mating (Grimes et al., 2022). For example, in some primate species, males engage in repeated harassment of females to increase mating success (Baniel et al., 2017; Van Schaik et al., 2004). Similarly, male bottlenose dolphins use physical force to control and mate with females (Orbach, 2019; Wallen et al., 2016). In some cases, they form alliances with other males to coordinate efforts in sexually coercing females (Hamilton et al., 2019; Marley et al., 2013). Therefore, aggression from juvenile and adult males due to sexual coercion is expected to be a key contributor towards the rake marks observed on adult female common dolphins.

Aggressive sexual coercion and male-male competition for mates may be reduced depending on the reproductive status of females (Karniski et al., 2018; Orbach et al., 2015; Scott et al., 2005). This might lead to females having a lower overall occurrence of rake marks than males. Unlike males, females have a maternal responsibility to rear their calves, which could lead females to withdraw from potentially risky conflict throughout their gestation and lactation period, as observed in bottlenose dolphins (Stanton et al., 2011). Similar avoidance takes place in dusky dolphins (*Lagenorhynchus obscurus*), as mother and calf pairs moved to inhabit shallow waters in association with potential harassment from males (Weir et al., 2008). This avoidance may reduce the aggression these females receive, and therefore the rake marks observed. It is also possible that when females are not available to mate, either because they are sexually immature, pregnant, have a dependent calf, or are too old to reproduce, they might receive less aggression because males may be more likely to direct their sexual coercion efforts towards females that are available to reproduce (Karniski et al., 2018; Orbach et al., 2015; Scott et al., 2005). This was observed in bottlenose dolphins, where females that became pregnant within six months were more likely to have new rake marks (Scott et al., 2005). These factors may further explain why pregnant and/or lactating common dolphin females demonstrated the lowest prevalence and occurrence of rake marks, comparatively with immature and resting mature females.

It is also possible that resting mature females may lose reproductive value as they age, potentially resulting in fewer mating attempts and therefore, less rakes in older females (Karniski et al., 2018; Lee et al., 2019). As such, male preference for sexually available females might result in reduced aggressive interaction received by females that are pregnant or have dependent calves, possibly impacting the observation of females on average having a lower rake mark occurrence than males. However, there are situations where adult females could be required to engage in aggressive interactions (Mann, 2019; Orbach et al., 2015). Females that are available for reproduction may need to defend themselves from aggressive harassment from males during sexual coercion (Karniski et al., 2018; Scott et al., 2005; Serres et al., 2023). This is supported by resting mature females having the highest rake mark occurrence and prevalence, compared with immature and pregnant and/or lactating females. In these situations, interactions might be more intense, resulting in a higher prevalence of rakes from more severe aggressive encounters. This could potentially explain why female common dolphins are less likely to have rakes than males, but when they do, they have a higher prevalence than males.

Under extreme circumstances, mothers may need to protect their calves from male nonparental infanticide, where males kill offspring to bring females back into estrus, increasing their mating opportunities (Boyko & Marshall, 2009; Lukas & Huchard, 2014; Patterson et al., 1998). While there is no direct evidence of this behaviour in common dolphins, infanticide has been observed in bottlenose dolphins (Patterson et al., 1998; Ramos et al., 2022; Robinson, 2014), killer whales (Towers et al., 2018), and Indo-Pacific humpback dolphins (Zheng et al., 2016). The intensity of intrasexual male competition suggests that infanticide could potentially be a reproductive strategy employed by male common dolphins. It is also important to note that not all aggressive encounters involve biting. Some severe aggressive attacks involve body slamming and ramming behaviours (Samuels & Gifford, 1997; Scott et al., 2005). Such encounters are more likely to result in internal trauma such as fractures or haemorrhages, rather than external rake marks, and accordingly may go undetected (Orbach et al., 2015; Ross & Wilson, 1996).

Maternal protection could also lead to variation in rake mark occurrence and prevalence with age in common dolphins. For many mammals, including delphinids, young offspring benefit from the protection of their mothers, while older, more independent individuals may be more vulnerable (Lévy & Fleming, 2005; Mann, 2019; Sepúlveda & Harcourt, 2021). This would potentially result in increased aggression and more prevalent rakes in juveniles compared with calves. As mentioned previously, I did not detect a relationship between age and rake density, possibly because age-related variation in aggressive behaviour might result in consistent levels of aggressive interactions in each age class. However, a range of factors, including age and health, may influence the longevity and healing time of rake marks, potentially masking the detection of a relationship between age and rake density in common dolphins (Ghaly et al., 2021; Thomason et al., 2015; Wong & Chew, 2021).

Rake density may be influenced by various factors related to reproduction in common dolphins, including sex and reproductive status. Additionally, these factors should be considered in the context of social status.

4.3 Social status

Dominance hierarchies are structured social systems where individuals are ranked relative to one another, influencing their access to resources and mating opportunities (Fulenwider et al., 2022; Milewski et al., 2022; Silk et al., 2019; Tibbetts et al., 2022). These relationships are often established and maintained by a combination of social norms and individual characteristics, including sex, body size, age, and body condition, usually involving either direct aggressive behaviours, or indirect signals of aggressive ability (Arnott & Elwood, 2009; Cheng, 2020; Fulenwider et al., 2022; Liu et al., 2020; Milewski et al., 2022; Tibbetts et al., 2022; Wright et al., 2019). Consequently, individual social status within the dominance hierarchy influences aggressive interactions across a range of taxa, including humans (Cheng, 2020; Von Rueden et al., 2008), non-human primates (Bray et al., 2021; Kavanagh et al., 2021; Wright et al., 2019), canines (Cordoni & Palagi, 2016; Silk et al., 2019), and delphinids (Grimes et al., 2022; Pinto de Sá Alves et al., 2013; Samuels & Gifford, 1997; Scott et al., 2005; Serres et al., 2019). The long-term maintenance of such hierarchies is beneficial as individuals conserve time and energy, and experience less injury by avoiding unnecessarily costly and potentially lethal contests (Arnott & Elwood, 2009; Liu et al., 2020; Silk et al., 2019; Tibbetts et al., 2022).

Delphinid calves typically engage in playful or pseudo fights that are thought to contribute to social development and learning, although these interactions may escalate, resulting in conflict induced rake marks (Grimes et al., 2022; Scott et al., 2005; Serres et al., 2023). As they develop, juveniles likely engage in male-male aggressive competition for dominance and mating rights, in doing so leading to physical altercations resulting in rake marks (Lee et al., 2019; Scott et al., 2005; Serres et al., 2023). Males are vulnerable during this period, and subject to high aggression rates, as they have yet to establish partners to protect them from more dominant individuals (Grimes et al., 2022; Lee et al., 2019).

In many delphinid species, a decrease in rake marks is observed around the age of sexual maturity, likely explained by the establishment and increased stability of dominance hierarchies upon adulthood, as noted in bottlenose dolphins (Lee et al., 2019; Scott et al., 2005), Indo-Pacific humpback dolphins (Serres et al., 2023), and killer whales (Grimes et al., 2022). As no relationship between age and rake density was observed in common dolphins, it is possible that aggression levels are consistent across each age class of common dolphins. This may indicate that the factors contributing to rake marks in calves, juveniles and adults offset each other, resulting in no detectable relationship.

Based on observations of aggressive conspecific behaviour, male delphinids appear more aggressive and dominant over females (Samuels & Gifford, 1997; Scott et al., 2005). For example, male bottlenose dolphins compete for dominance and priority access to mates through direct physical contests (Connor & Vollmer, 2009; Harvey et al., 2017; Scott et al., 2005). In contrast, female bottlenose dolphins have been described as highly tolerant and very rarely aggressive compared to their male counterparts, although they are sometimes aggressive towards their dependent calves (Scott et al., 2005).

Female dominance hierarchies are often more stable than males (Grimes et al., 2022; Samuels & Gifford, 1997). This may result in a lower frequency of conflicts and less rake marks among females, as aggressive contests to achieve or maintain dominance likely occur less often (Wright et al., 2019). However, the stability of female dominance hierarchies may mean that on rare occasions when their social status is challenged, the resulting contests may be more intense than male interactions, possibly leading to a higher prevalence of rake marks among females. This variation in social stability between males and females could explain why females are less likely to have rakes, but when they do, they have more than males. However, female avoidance behaviour, and rare, intense protection of themselves and their calves, as previously discussed, offer more likely explanations for the observed pattern of rake marks. This is because common dolphin female groups are often centred around the mutual responsibility of calf rearing, rather than asserting dominance (Castro et al., 2024).

In contrast, male dominance relationships often fluctuate between periods of apparent stability and competition (Grimes et al., 2022; Samuels & Gifford, 1997). In some species, this instability is thought to lead to a high frequency of aggressive contests among males, as they compete to challenge dominants or defend their social status from subordinates (Wright et al., 2019). Some populations of bottlenose dolphins form long-term adult male alliances, where males work together to sexually coerce females (Hamilton et al., 2019; Marley et al., 2013). In populations where males do not form alliances, aggression between males may be more common due to fierce competition for mates (Marley et al., 2013). No evidence of male alliances has been observed in common dolphins, although it should be noted there have been few ethological studies on *Delphinus* (Dwyer et al., 2020; Mason et al., 2021; Mason et al., 2016; Neumann, 2001a; Neumann & Orams, 2005; Stockin et al., 2008a; Stockin et al., 2008b). Conversely, the high occurrence of rake marks observed in male common dolphins may be attributed to frequent intrasexual aggressive competition between individuals for dominance and preferential mate access (Scott et al., 2005; Serres et al., 2023).

However, male common dolphins have a large testes-to-body size ratio (MacLeod, 2010; Plön & Bernard, 2007). This morphology reflects the promiscuous mating system of common dolphins, associated with strong male investment into sperm competition (Murphy et al., 2005). Species with a relatively small testes to body size ratio, such as bottlenose dolphins, are likely to engage in frequent male contests for mating opportunities (Scott et al., 2005;

Serres et al., 2023). In contrast, common dolphins may not need to physically fight other males to sire a calf, as their mating success is more likely determined by testes size, because sperm and testes development is energetically costly (Kenagy & Trombulak, 1986). Therefore, the difference in rake mark occurrence and prevalence between male and female common dolphins is more likely attributed to female avoidance and sexual coercion, as previously discussed, rather than intrasexual male competition for mates.

A marginal increase in rake mark occurrence and prevalence was observed with an increase in TBL in common dolphins. Body size, among other physical characteristics, can act as a signal of social status in wild animals, influencing their aggressive interactions (Wright et al., 2019). In some delphinid species, the accumulation of rake marks themselves may act as a signal of rank, to inform potential competitors and mates of increased individual fitness (MacLeod, 1998; Wright et al., 2023). However, this is unlikely the case for common dolphins, as rake marks are expected to completely heal and disappear over time, as observed in bottlenose dolphins, where healing typically occurs within 400 days (Grimes et al., 2022; Lee et al., 2019). This suggests that, rather than serving as lasting signals of dominance, rake marks in common dolphins are more likely indicators of recent social interactions.

A more likely indicator of dominance status in common dolphins is post-anal hump size in adult males (Murphy et al., 2005; Murphy & Rogan, 2006; Neumann et al., 2002). Post-anal hump size may act as a signal of quality to potential mates and competitors in common dolphins, due to its correlation with testis size and advantage in sperm competition (Murphy et al., 2005; Palmer et al., 2023). Therefore, individuals with a large post-anal hump may be targeted by smaller individuals looking to improve their rank in the dominance hierarchy, resulting in increased rake marks on larger individuals.

Body size also plays an important role in fighting ability, and often dictates the likelihood and outcome of aggressive interactions, correlating with dominance rank and reproductive success in a broad range of taxa (Arnott & Elwood, 2009), including virile crayfish (*Faxonius virilis)*, Asian particolored bats (*Vespertilio sinensis*) (Liu et al., 2020), and mountain gorillas (Wright et al., 2019). Therefore, larger, and potentially more dominant common dolphin males may be more prone to engage in frequent aggressive interactions due to their physical advantage during conflict. They might be required to defend their dominance rank from frequent challenges from subordinates slightly smaller than them. In addition, females possibly prefer to mate with larger males, which may increase the intrasexual competition between larger males. This could result in a greater occurrence and prevalence of rake marks in larger individuals. Smaller individuals might engage in less frequent or intense aggressive interactions as they are less likely to have attained an age or maturity status where aggressive sexual coercion of females take place. This potentially explains the lower rake mark occurrence and prevalence observed in smaller common dolphins. Additionally, smaller subordinate individuals may have less rake marks than larger individuals as they are at more risk during aggressive encounters, possibly leading them to favour avoidance behaviours to withdraw from harmful aggressive interactions with dominants (Lee et al., 2019; Serres et al., 2023; Wright et al., 2023; Wright et al., 2019).

However, as the mating strategy of common dolphins favours sperm competition rather than direct aggressive contests between males for mates, testes-to-body size ratio or post-anal hump size is more likely to impact dominance status, rather than fighting ability. Therefore, the relationship between TBL and rake mark prevalence and occurrence might more likely be explained by the post-anal hump size as a signal of sperm quality and/or dominance in larger common dolphins. Although, given the lack of relationship observed between age and rake density, another possible, albeit simple, explanation for the relationship between rake density and TBL is that larger dolphins have a greater body surface area available to receive rake marks during social encounters, therefore may be more likely to have rake marks than smaller individuals.

Body condition, in some cases used as a proxy for health, is another factor that might influence dominance relationships in some species (Liu et al., 2020). Specifically, healthier individuals in better body condition are likely to have more energy, strength, agility, and faster reflexes, enhancing their fighting ability, enabling them to assert dominance more effectively (Liu et al., 2020). However, I found no evidence of a relationship between body condition and rake mark occurrence or prevalence, suggesting that health may not be a key factor influencing rake marks, and therefore aggressive interactions between common dolphins.

As previously discussed, poor body condition is associated with reduced immune function in some animals, which slows wound healing and increases the likelihood of infection and susceptibility to wounds (Ghaly et al., 2021; Lux, 2022). Therefore, it could be hypothesised that common dolphins with poor health (inferred by body condition) might have reduced healing efficiency. If so, this could possibly increase the likelihood of the detection of rake marks, as they would persist longer and accumulate on the skin. This would potentially mask an existing relationship between body condition and social aggression.

It is also possible that body condition may be an insufficient indicator of health, as not all health conditions have an immediate or visible impact on an individual's nutritional status (Hart et al., 2013). Thus, while health might indeed impact rake density in common dolphins, this relationship may not be apparent through body condition alone. Instead, poor health may be expressed through the presence of epidermal (Van Bressem et al., 2009; Wilson et al., 1999) and internal lesions (Seguel et al., 2020), and/or variation in blubber thickness (Noren & Wells, 2009) and quality (Castrillon et al., 2017; Hinton, 2023). This suggests that a comprehensive assessment of health in common dolphins may require a combination of indicators, beyond body condition alone, to fully understand its impact on rake density.

4.4 Rake mark position

The distribution and position of lesions on the body has been investigated across a range of delphinid species, including Indo-Pacific humpback (Serres et al., 2023), bottlenose (Kleinschmidt, 2014; Scott et al., 2005), and common (Hupman et al., 2017) dolphins. Significant variation in rake marks across body sectors has been observed, although results vary across studies and species (Scott et al., 2005; Serres et al., 2023). Scott et al. (2005) reported more rake marks on the 'posterior peduncle' of bottlenose dolphins, whereas a high prevalence was noted on the 'flank' of Indo-Pacific humpback dolphins (Serres et al., 2023). Murphy (1999) observed that the 'torso' (corresponding to the dorsal and ventral caudal flanks in this thesis, Figure 2.2) was the most frequently raked body region on common dolphins in Ireland. In New Zealand common dolphins, the majority of lesions (including but not exclusively limited to rake marks) identified from photo-identification, appeared on the ‘anterior peduncle’ region, with over 80% of individuals showing lesions on the dorsal fin (Hupman et al., 2017).

4.4.1 Dorsal vs. ventral

Studies of scar distribution across the body can assist in inferring the nature and context of their origins (Hill et al., 2017). A high prevalence of rake marks in a given region may indicate that aggressors often target or exert more force in those areas during aggressive biting or tooth raking behaviours (Lanyon et al., 2021; Serres et al., 2023). Both male and female common dolphins had a higher rake mark occurrence on the ventral compared to the dorsal sector grouping (Table 3.5 – B, Figure 3.4), potentially suggesting that the ventrum is targeted by aggressors during attacks (Lanyon et al., 2021; Serres et al., 2023). However, female common dolphins had higher prevalence of rake marks on the dorsum compared with the ventrum (Table 3.5 – A, Figure 3.3). This may suggest that during playful or aggressive interactions, the recipient might orient their dorsum towards the aggressor, either to evade the aggressor or to present the least vulnerable portion of their body to the attacker as a form of defence (Serres et al., 2023). Therefore, females might turn their dorsum towards their aggressors during forceful mating attempts from males. The presentation of and contact with the ventrum sometimes occurs during sexual and socio-sexual behaviour of cetaceans (Ham et al., 2023; Hill et al., 2015). This could be a plausible explanation for why males had a higher prevalence of rake marks on the ventrum than the dorsum (Table 3.5 – A, Figure 3.3), as males likely engage in frequent sexual coercion of females (Hamilton et al., 2019; Marley et al., 2013). This may result in males presenting their ventrum during these interactions, which might then be vulnerable to receive a high amount of rake marks (Ham et al., 2023; Hill et al., 2015).

4.4.2 Cranial vs. caudal

Larger common dolphins are more likely to have cranial as opposed to caudal rake marks, although any evidence of raking caudally tends to have a comparatively higher rake prevalence (Table 3.6, Figure 3.5, Figure 3.6). Trauma across the melon and wider skull might suggest that scar recipients approached the aggressor cranially or engaged in head-to-head clashes for dominance (Lanyon et al., 2021). Rake marks around mid/caudal regions may indicate that the recipients might have been pursued in a chase or attempted to flee from the interaction (Lanyon et al., 2021). Such chases have been observed predominantly in offshore bachelor pods of common dolphins in New Zealand (Neumann & Orams, 2005), and in contrast, are rarely noted in coastal mother-offspring groups (Schaffar, 2004; Stockin, 2008). Larger dolphins might initiate or engage in frequent, low intensity head-to-head clashes, resulting in the higher occurrence of cranial rake marks. However, in more severe and rare aggressive interactions that result in a higher prevalence of rake marks, they may attempt to avoid or flee from aggressors, resulting in caudal scarring as the aggressor chases the recipient. Alternatively, recipients might present tail slapping behaviour towards their aggressor in retaliation or as a protective measure (Connor et al., 2000; Neumann & Orams, 2005). This could explain why the caudal region demonstrated a higher rake density comparative to the cranial area.

Smaller dolphins demonstrated a higher occurrence of caudal rake marks than cranial (Table 3.6 – B, Figure 3.6), potentially indicating that they are more likely to avoid or be required to protect themselves from aggressive interactions. This seems intuitive since smaller individuals more likely represent subordinates within the social hierarchy (Lanyon et al., 2021). However, the high prevalence of rake marks observed cranially (Table 3.6 – A, Figure 3.5) may suggest that smaller individuals might sometimes engage in less frequent but more severe head-to-head aggressive interactions, potentially as subordinates compete in an effort to improve their social rank (Lanyon et al., 2021).

4.4.3 Lateralisation

The position of rake scarring might further represent preliminary evidence of behavioural lateralisation in delphinids, who have demonstrated preferential use of a particular side of their body in a range of captive and wild studies (Clark & Kuczaj II, 2016; Kaplan et al., 2019; Karenina et al., 2010; Lilley et al., 2022; Matrai et al., 2019). Behavioural lateralisation occurs due to variation between brain hemispheres (Karenina et al., 2010; Lilley et al., 2022; Rogers & Andrew, 2002). Murphy (1999) detected lateral variation in the location of rake marks, with the right side showing a more broad rake mark distribution than the left, although no overall difference in rake prevalence between sides was observed. In New Zealand common dolphins, lateralisation may be evidenced by the differing occurrence and prevalence of rake marks between the left and right sides of the body. In the present study, the relationship between scar lateralisation varied with TBL, suggesting a possible correlation with behaviours that vary with body growth. For larger common dolphins, rake mark occurrence was higher on the left side, while rake prevalence was greater on the right. In contrast, smaller dolphins showed marginally higher rake mark occurrence on the right and higher prevalence on the left (Table 3.7, Figure 3.7, Figure 3.8). These patterns could potentially relate to known lateralisation behaviours, such as predominant rubbing of their left side against others (Sakai et al., 2006), calves remaining on their mothers' right side (Karenina et al., 2010) and preferred right-side foraging (Kaplan et al., 2019).

It is possible that the observed shift in high rake mark prevalence from the left in smaller dolphins to the right in larger dolphins may be age-related. Pectoral fin dominance shifts with age in a range of cetaceans, including bottlenose dolphins (Winship et al., 2017), and humpback whales (*Megaptera novaeangliae*) (Canning et al., 2011). Results presented here that suggest mother-calf associations may potentially influence lateralisation in smaller common dolphins, as noted in wild beluga whales (Karenina et al., 2010). Aggression from mothers directed at their calves has been observed in bottlenose and common dolphins (Schaffar, 2004; Scott et al., 2005). Common dolphin mothers are known to herd and chase their calves away from boats, in some cases including bite attempts, which may result in rake marks (Schaffar, 2004). Smaller common dolphins have a higher rake mark prevalence on the left, which might indicate that mothers prefer to keep their calves on their right side, or calves possibly prefer to keep their mothers in view in their left eye. This may result in calves receiving more rakes from their mothers on their left side. The shift in prevalence to the right side of the body in larger animals could be a result of increased independence from their mothers, potentially reducing the likelihood of rake marks on an individual's left side.

4.5 Abiotic parameters

As previously outlined, rake marks have been widely studied as indicators of social aggression in delphinids (Crespo-Picazo et al., 2021; Grimes et al., 2022; Gross et al., 2020; Hamilton et al., 2019; Lee et al., 2019; Marley et al., 2013; Orbach et al., 2015; Patiño-Pérez, 2022; Reinhart et al., 2013; Scott et al., 2005; Serres et al., 2023; Waples & Gales, 2002). Accordingly, this thesis primarily examines rake marks within the context of aggressive interactions among common dolphins in New Zealand, and considers the effect of biotic factors on wound healing and potentially rake mark longevity (Ghaly et al., 2021; Hamilton et al., 2019; Lee et al., 2019; Lux, 2022). However, the potential effect of abiotic factors, such as salinity and sea surface temperature, on rake marks should be considered.

While it is unlikely that abiotic factors would impact social behaviours associated with rake marks, such factors may affect the rate of wound healing, and thus the longevity of rake marks on examined dolphins (Croft et al., 2020; Guinn et al., 2024; Duignan et al., 2020; Hurst & Orbach, 2022; McClain et al., 2020). This might have implications for the findings of this thesis, as rake mark longevity likely impacts the probability of the detection of rake marks as evidence of social interactions.

Hypo-salinity and low water temperature correlate with a higher prevalence of epidermal lesions (Croft et al., 2020; Duignan et al., 2020; Fazioli & Mintzer, 2020; Guinn et al., 2024; Wilson et al., 1999) and slower wound healing in delphinids (Bloom & Jager, 1994; Fazioli & Mintzer, 2020; Hurst & Orbach, 2022). Changes in epidermal properties associated with exposure to low salinity may contribute to this effect (Ewing et al., 2017; McClain et al., 2020). An increase in the absorption of water in hypo-saline environments is known to lead to the development of freshwater skin lesions (Duignan et al., 2020; Ewing et al., 2017; Fazioli & Mintzer, 2020). Low water temperature increases the expression of tattoo lesions, which can disappear following an increase in water temperature, possibly due to improved viral defences (Croft et al., 2020; Hart et al., 2012; Wilson et al., 1999).

The high occurrence of lesions observed in correlation with low salinity and sea surface temperature may be associated with increased vulnerability to infection or disease (Croft et al., 2020; Fazioli & Mintzer, 2020; Guinn et al., 2024; Hart et al., 2012; Wilson et al., 2000). Therefore, lesions may serve as an indicator of reduced immune function, which is associated with a slower rate of healing (Ghaly et al., 2021; Lux, 2022), possibly attributed to stressful changes in environmental conditions (Ewing et al., 2017; Fazioli & Mintzer, 2020; Guinn et al., 2024; Van Bressem et al., 2009; Wilson et al., 2000). Changes in salinity and sea surface temperature may lead to variation in rake marks due to impaired skin properties, which may slow wound healing, increasing rake longevity. Alternatively, environmental changes might directly impact individual health, in turn altering healing rates and rake mark longevity.

Variation in rake mark longevity may influence not only the prevalence of rake marks at one time, but also influence the accumulation and likelihood of detection of rake marks across wider temporal scales. Therefore, these abiotic factors should be considered as uncontrolled factors potentially influencing rake marks on common dolphins, alongside any inference of social aggression.

4.6 Summary

This thesis assessed the occurrence and prevalence of rake marks on common dolphins examined postmortem in the context of age, sex, TBL, sexual maturity, female reproductive status, body condition and scarring position. Males demonstrated a higher occurrence of rake marks than females, while females had a higher prevalence of rake marks than males. This is possibly due to frequent male-male competition for mates and dominance. Females may engage in less frequent, but likely more severe, aggressive interactions due their maternal responsibilities involving rearing and protection of calves, defence of sexual coercion from males, and potentially more stable social status.

Sexual coercion also likely explains the high rake mark occurrence and prevalence observed in resting mature females, as they are available for mating and may be targeted by males. In contrast, pregnant and/or lactating females, being unavailable for mating, demonstrated the lowest rake mark prevalence and occurrence, possibly because they were less likely to be targeted by males for sexual coercion, or due to increased avoidance during calf rearing.

Both rake mark occurrence and prevalence increased marginally with TBL. This may be attributed to the increased surface area available for raking in dolphins with a larger TBL. However, it could also indicate that larger common dolphins experience more frequent and severe aggressive interactions, possibly related to dominance status. This dominance may be due to the advantage of body size in fighting ability. However, male morphology suggests that testes-to-body size ratio is potentially a more accurate measure of dominance and reproductive success in common dolphins, due to the advantages for sperm competition.

No relationship between rake marks and sexual maturity, body condition, or age was detected. This might mean that aggressive behaviours that lead to rake marks may occur at a similar frequency or intensity throughout an individual's lifetime, regardless of body condition or sexual maturity. However, the longevity of scarring may be influenced by various biotic and abiotic factors, including age, sex, body condition, reproductive status, salinity and temperature. Such factors may affect individual susceptibility to rake marks and wound healing time, in turn impacting their detection. It is possible that these factors may mask the detection of potential relationships between rake density and biological parameters in this study.

Investigating the position and distribution of rake marks across each cadaver provided initial inference into the origin of such lesions. For instance, a difference in rake mark prevalence between the dorsum and ventrum suggests that females may display defensive behaviours where they present their dorsum to their aggressor, whereas males may present their ventrum during reproductive and sociosexual behaviour. In addition, both a cranial versus caudal difference and a lateralised difference in rake mark prevalence and occurrence was noted. Both relationships appeared to be influenced by TBL, which may indicate variation in social interactions with size. For example, variation in rake mark prevalence between the cranial and caudal regions may be related to changes in severity of aggression or conflict strategies (i.e., cranial confrontation or caudal chase) with size, potentially in relation to dominance status. A shift in rake mark lateralisation with size may indicate the potential influence of mother-calf associations on scarring patterns.

The results of this thesis provide initial insights into the occurrence and prevalence of rake marks, in the context of biological parameters, in common dolphins in New Zealand. This broadens our understanding of their sociobiology through the association of rake marks with sex, TBL, and reproductive status. Additionally, this study offers preliminary insights into the position and distribution of rake marks across the body. This builds on field based studies which are often limited to the observation of the dorsum, in some cases lacking biological context such as sex, age, TBL, sexual maturity, reproductive status and body condition. My findings offer the first inference into the effect of ontogeny and demographic traits on the prevalence and occurrence of rake marks on common dolphins in New Zealand, as well as the inferred context and nature of the interactions resulting in such lesions.

4.7 Study limitations

The range of factors potentially impacting rake marks on common dolphins highlights the complexity of ecological and social dynamics, underscoring the need for further research to fully understand their interactions. While this study presents useful first insights into rake scarring on a poorly studied species, it is not without caveats discussed here. Firstly, the use of rake marks to infer social aggression is limited. While rake marks are a useful tool to investigate social aggression, I recognise that some aspects of social aggression may not result in rake marks. Therefore, rake marks alone may underestimate social aggression because some severe, potentially lethal conflicts result in internal trauma and/or fractures, which were not accounted for in this study (Orbach et al., 2015; Ross & Wilson, 1996). Additionally, while male aggressive encounters for mates are thought to be the primary cause of rake marks in adults, play and socio-sexual interactions may also result in rake marks, making it difficult to differentiate between these causes (Serres et al., 2023). Examining additional wounds, such as dorsal fin notches, would provide further insights into the nature of these interactions (Serres et al., 2023).

The use of body condition alone as a proxy of health also comes with limitations. Body condition can provide a general indication of the nutritional status of an individual but may not always capture specific health issues (Hart et al., 2013). Future studies should consider a broader range of health indicators alongside body condition to reduce the likelihood of potential misinterpretations of health. In addition, the assessment of body condition can be subjective, and may vary between observers or studies. To mitigate this, I used consistent definitions for each body condition classification, and assessed body condition for each individual from a consistent angle, with the observer positioned cranial and marginally dorsal to the subject, which was positioned on its ventrum.

The caveats of obtaining data postmortem from stranded dolphins further presents a range of constraints. For example, skin loss and/or damage due to decomposition, cadaver transportation, and/or injury (e.g., bruising, lacerations) may inhibit the detection of lesions when present. While this was addressed by assessing skin surface area to calculate rake density as a measure of rake marks proportionate to visible skin, it may not account for undetected or faint rake marks that might have been obscured or altered during decomposition or transport. In addition, strandings data may over-represent individuals predisposed to poor health due to sickness or injury, increasing their likelihood of mortality and stranding.

The vast majority of rake marks included in this dataset fall within the IRD range that aligns with the dentition spacing of *Delphinus*, which is typically around 5mm. However, in some cases, missing and/or damaged teeth may result in rake marks with an inconsistent distance between individual scars in one set of rakes, introducing potential bias in measurements of IRD. Consequently, this study includes IRD measurements up to 10mm to account for this variation, while excluding any rake marks with an IRD exceeding this threshold. This variation may give rise to the inclusion of rake marks that occurred as a result of social interactions with bottlenose dolphins. Therefore, while the majority of the rake marks in this thesis are likely indicative of conspecific social interactions, a small proportion may also be attributed to interspecific interactions.

Opportunistic sampling introduces bias in the range of data collected. For instance, the sex ratio in the dataset is biased towards females (56 females to 46 males). There is also a bias towards younger individuals. With some ages unknown, the age data had a smaller sample size (n = 89) compared to other factors (n = 102). The number of resting mature females included in the dataset was also limited (n = 6). In addition, there were no individuals of poor body condition included in this study.

Due to limited sample sizes, immature and pubescent sexual maturity subgroups were pooled into one group, classified as immature. Consequently, these results cannot distinguish whether there is considerable variation in rake mark occurrence or prevalence during the key developmental stage of pubescence. Similarly, reproductive status subgroups (pregnant, lactating, and pregnant and lactating) were pooled into one group, pregnant and/or lactating. Additionally, the determination of sexual maturity was limited by the quality of gonadal samples collected postmortem, as tissue quality can vary depending on the level of decomposition and whether the samples are assessed fresh or frozen. Continued expansion of this dataset will allow for a broader range of subgroups and improved sample sizes for these categories.

The circumstances leading to strandings are highly variable and often unknown, making it challenging to control for environmental variables. As previously discussed, this study did not identify a relationship between rake density and age, sexual maturity or body condition. It is possible that these variables may still influence rake density, but their effects could be undetected, due to variation in salinity (Fazioli & Mintzer, 2020; Hurst & Orbach, 2022; Wilson et al., 1999), and sea surface temperature (Croft et al., 2020; Guinn et al., 2024; Hart et al., 2012; Wilson et al., 1999) that might influence rake mark healing and longevity. This study includes common dolphins which have stranded across a broad latitudinal range (34 to 47^{o} S), spanning the entire coast of New Zealand. This presents the possibility of exposure to considerable variation in salinity and sea surface temperature due to habitat partitioning. For example, nursery groups are typically located in inshore waters such as the Hauraki Gulf (Dwyer et al., 2020; Stockin et al., 2008b), whereas bachelor pods more often inhabit oceanic waters (Neumann et al., 2002). *Delphinus* assessed in this thesis stranded between 2006 to 2024, spanning over 18 years of potential environmental change. Such changes may include a reduction in salinity due to increased rainfall, and an increase in sea surface temperature over time. Accordingly, spatiotemporal environmental changes in salinity and temperature may contribute to variation in health, wound healing, and the detection of rake marks on common dolphins. While the effect of these environmental factors on rake marks on common dolphins in New Zealand is not currently known, they should be considered as uncontrolled factors potentially influencing rake mark occurrence and prevalence, alongside any inference of social aggression.

4.8 Future research

The protection of common dolphins (*aihe*) holds great cultural significance, as marine mammals in New Zealand are considered taonga (treasured possessions), that hold great value in tikanga Māori. However, few ethological studies have been conducted on *Delphinus*, and even less is known about their sociobiology. While rake marks provide one perspective into sociobiology, this study highlights the need for further investigation into several key areas to better understand the occurrence and implications of such lesions in common dolphins.

Firstly, as not all aggressive interactions result in external wounds, assessment and inclusion of internal trauma in future studies may offer a more comprehensive insight into aggressive interactions. Additionally, studying dorsal fin notches as indicators of more extreme aggression or bites could help differentiate between rake marks caused by play versus those resulting from aggression. Incorporating these additional markers of aggression into future research would enhance our understanding of social interactions among common dolphins.

Additionally, to address the sample size limitations previously mentioned, future studies should expand this dataset, thereby reducing variation and outliers. This would broaden the range of subgroups, providing deeper insights into whether rake marks vary at the critical stage of pubescence, as well as between resting mature and pregnant and/or lactating females, or with body condition. This distinction is important as it could reveal significant differences in social interactions during these pivotal stages of reproduction, development, and potential health status.

To address limitations associated with the use of body condition as a health indicator, future studies should consider a broader range of health indicators. These might include histopathological assessment of blubber, as well as internal and external lesions, and evaluations of parasite and contaminant loads. Integrating these wider health factors may offer a more accurate health measure, and reduce the likelihood of misinterpretations of health. This is essential for understanding the influence of health on social aggression, rake mark healing, and the longevity of such marks, all of which impact the detection of these interactions.

Finally, this study included dolphins covering a broad sampling range of latitudes, temperatures, and salinity levels throughout New Zealand. Future research should account for these variables, potentially by focusing on a specific region with consistent environmental conditions, such as the Hauraki Gulf, or by comparing dolphins from different regions and environmental conditions. This is critical because understanding how environmental factors affect rake mark healing and visibility can provide more accurate insights into social interactions and aggression in dolphins. By isolating and comparing these variables, future studies will be able to better discern whether differences in rake mark patterns are due to behavioural or environmental factors.

Through addressing these areas, future research can build on the findings of this study, offering a more comprehensive understanding of the factors influencing rake marks and the social interactions of common dolphins.

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Appendices

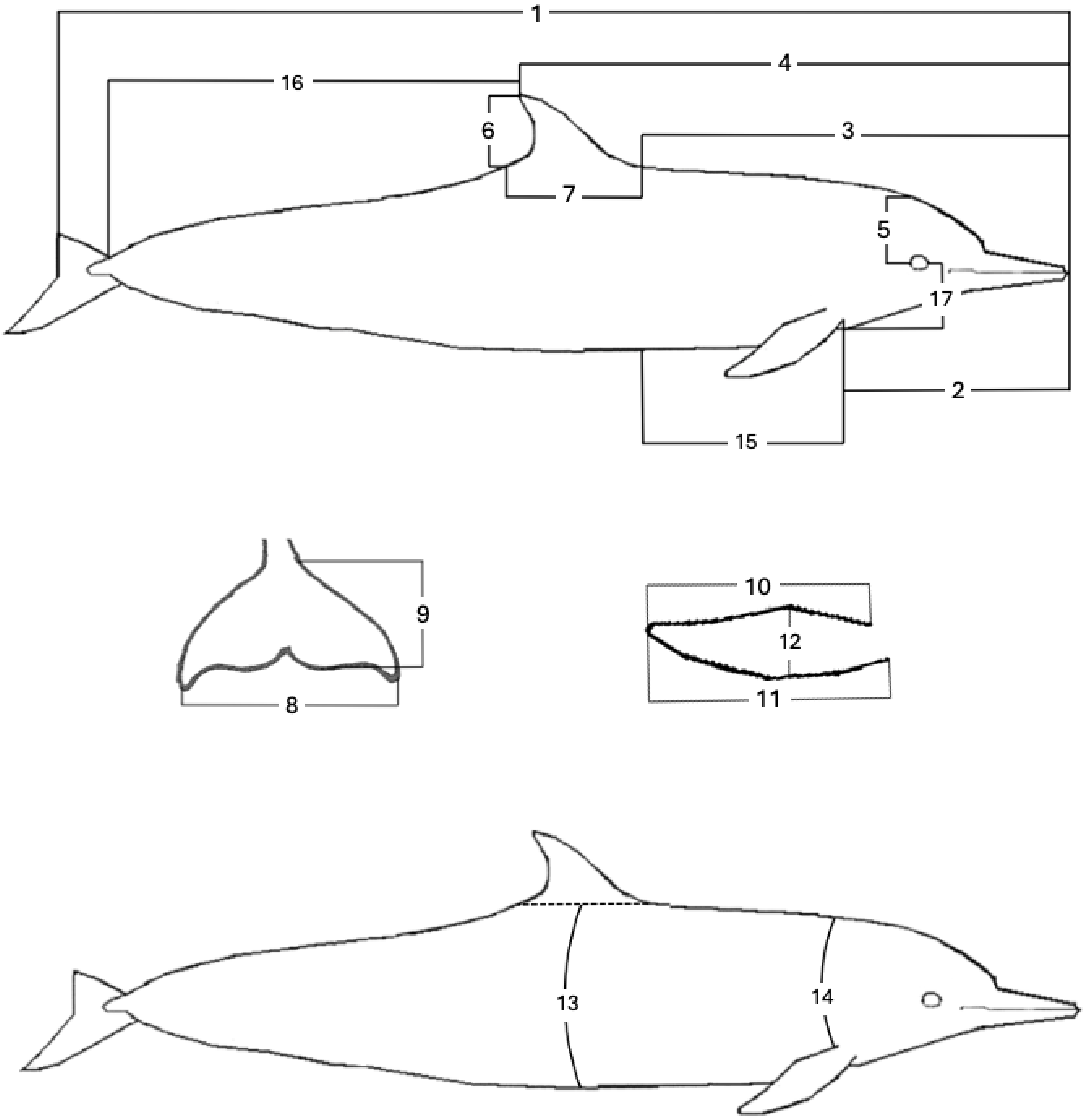

Figure A.1 Key showing the morphometric measurements recorded for stranded common dolphin (*Delphinus delphis*) cadavers during postmortem examination.

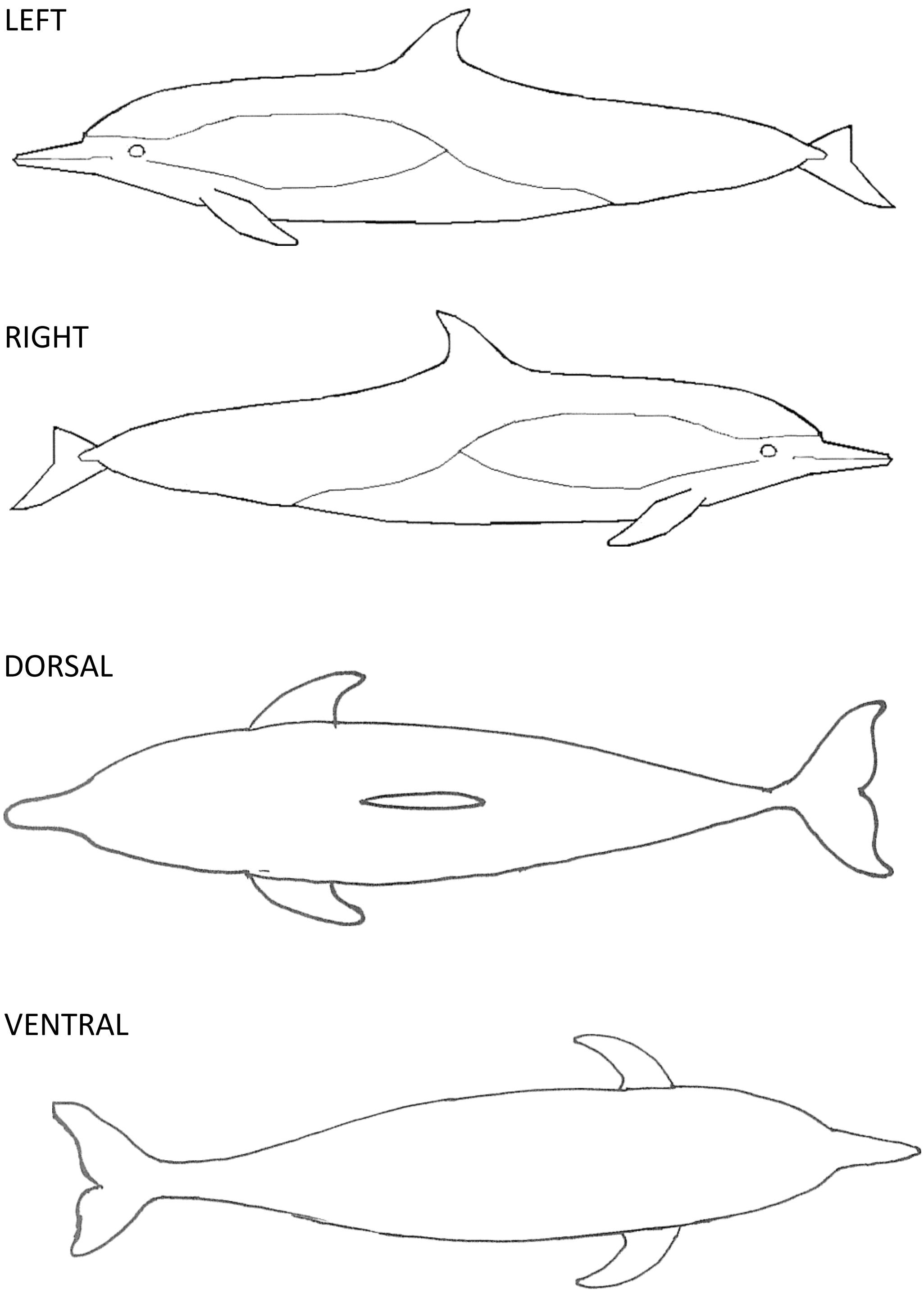

Figure A.2 Necropsy datasheets used to record lesion occurrence and distribution on the left, right, dorsal and ventral surfaces of common dolphin (*Delphinus delphis)* cadavers during postmortem examination between 2006 and 2024 in New Zealand. Detected lesions were drawn and numbered on the datasheets in the corresponding body surface and location that they were observed on the cadaver.

# on drawing	Mark type	Dolphin side	Total length	Width	Inter-distance

Figure A.3 Data recording sheet used to annotate the drawings of lesions recorded on the necropsy datasheets. Recorded on the table were the types of lesions detected, the body surface each lesion was observed on, and the lesion characteristics, including the length (cm), width (cm) and the distance between the parallel lesions that make up a rake mark, the inter-rake distance (IRD in mm) on common dolphin (*Delphinus delphis)* cadavers during postmortem examination.

Table A.1 Performance values for zero-inflated generalised linear models (ZIGLMs) analysing the rake density of the entire body surface in common dolphins (*Delphinus delphis*) assessed postmortem. These models incorporate sex (male or female), maturity (sexual maturity; immature or mature), age (years), TBL (total body length, cm), and BC (body condition; good or moderate) to estimate the rake density (rm/dm^2) of each individual. Note: k = number of parameters, LogLik = minimized negative log-likelihood, AICc = corrected Akaike Information Criterion for small sample sizes, wAICc = Akaike weight adjusted to sum up to 1, ER = evidence ratio, calculated in comparison to the best-performing model.

Model	k	ER	AICc	wAICc	LogLik
Rake density (entire body)					
~ Sex + TBL	7	-	-61.34	0.41	38.38
~ Sex + TBL + Maturity	9	0.66	-60.52	0.27	40.43
~ Age + Sex + TBL + Maturity	11	0.18	-57.89	0.07	41.71
~ TBL	5	0.17	-57.83	0.07	34.28
~ Sex + TBL + BC	9	0.11	-56.86	0.04	38.60
~ Age + Sex + TBL	9	0.10	-56.65	0.04	38.49
~ TBL + Maturity + BC + Sex	11	0.08	-56.26	0.03	40.89
~ TBL + Maturity	7	0.06	-55.70	0.02	35.56
~ TBL + BC	7	0.02	-53.83	0.01	34.62
~ Age + TBL + Maturity + BC + Sex	13	0.02	-53.75	0.01	42.37
~ Age + TBL	7	0.02	-53.20	0.01	34.31
~ Age + TBL + Maturity	9	0.02	-53.10	0.01	36.72
~ TBL + Maturity + BC	9	0.01	-52.07	0.00	36.20
~ Age + Sex + TBL + BC	11	0.01	-51.91	0.00	38.72
~ Age + BC + TBL + Maturity	11	$2.9x10^{-3}$	-49.68	0.00	37.60
~ Age + TBL + BC	9	$2.1x10^{-3}$	-48.99	0.00	34.66
~ Age + Maturity	7	$4.6x10^{-6}$	-36.76	0.00	26.09
~ Age + Sex + Maturity	9	$2.4x10^{-6}$	-35.45	0.00	27.89
~ Age + BC + Maturity	9	$9.9x10^{-7}$	-33.68	0.00	27.01
~ Age + Sex + BC + Maturity	11	$3.7x10^{-7}$	-31.69	0.00	28.61
~ Age + Sex	7	$2.6x10^{-7}$	-31.03	0.00	23.22
~ Age + Sex + BC	9	$2.7x10^{-8}$	-26.46	0.00	23.40
~ Maturity	5	$9.6x10^{-12}$	-10.61	0.00	10.67

~ Sex + Maturity	7	$2.9x10^{-12}$	-8.22	0.00	11.82
~ Maturity + BC	7	$1.4x10^{-12}$	-6.72	0.00	11.07
~ Sex + Maturity + BC	9	$3.6x10^{-13}$	-4.05	0.00	12.19
~ Sex	5	$2.8x10^{-16}$	10.26	0.00	0.24
~ BC	5	$1.0x10^{-16}$	12.28	0.00	-0.77
~ Sex + BC	7	$4.3x10^{-17}$	14.01	0.00	0.70

Table A.2 Performance values for zero-inflated generalised linear models (ZIGLMs) analysing rake density of females for the entire body surface in common dolphins (*Delphinus delphis*) assessed postmortem. These models incorporate reproductive status (immature, pregnant and/or lactating, and resting mature), age (years), TBL (total body length, cm), and BC (body condition; good or moderate) to estimate the rake density (rm/dm^2) of each individual. Note: k = number of parameters, LogLik = minimized negative log-likelihood, AICc = corrected Akaike Information Criterion for small sample sizes, wAICc = Akaike weight adjusted to sum up to 1, ER = evidence ratio, calculated in comparison to the best-performing model.

Model	**k**	**ER**	**AICc**	**wAICc**	**LogLik**
Female rake density (entire body)					
~ Reproductive_status + TBL	9	-	-4.99	0.72	13.80
~ Reproductive_status + TBL + BC	11	4.54	-1.96	0.16	15.55
~ Reproductive_status + TBL + Age	11	7.22	-1.04	0.10	15.09
~ Reproductive_status + TBL + BC + Age	13	34.97	2.12	0.02	17.14
~ Reproductive_status + Age	10	$1.9x10^3$	10.05	0.00	7.87
~ Reproductive_status + BC + Age	11	$3.1x10^3$	11.07	0.00	9.03
~ Reproductive_status	7	$1.5x10^5$	18.78	0.00	-1.03
~ Reproductive_status + BC	9	$3.4x10^5$	20.47	0.00	1.07

Table A.3 Performance values for zero-inflated generalised linear mixed models (ZIGLMMs) analysing dorsal versus ventral sector groupings in common dolphins (*Delphinus delphis*) assessed postmortem. These models incorporate sex (male or female), sector (sector grouping; dorsal or ventral), maturity (sexual maturity; immature or mature), age (years), TBL (total body length, cm), BC (body condition; good or moderate), and ID (individual identity) to estimate the rake density (rm/dm^2) of each individual. Note: k = number of parameters, LogLik = minimized negative log-likelihood, AICc = corrected Akaike Information Criterion for small sample sizes, wAICc = Akaike weight adjusted to sum up to 1, ER = evidence ratio, calculated in comparison to the best-performing model.

Model	k	ER	AICc	wAICc	LogLik
Rake density (dorsal vs ventral)					
~ Sex * Sector + TBL + (1 | ID)	13	-	-77.42	0.43	52.85
~ Sex + TBL + Sector + (1 | ID)	11	0.60	-76.39	0.26	50.01
~ Sector + TBL + (1 | ID)	9	0.36	-75.38	0.16	47.24
~ Sex + Age + TBL + Sector + (1 | ID)	13	0.09	-72.62	0.04	50.45
~ Sex + Maturity + TBL + Sector + (1 | ID)	13	0.06	-71.86	0.03	50.07
~ Age + TBL + Sector + (1 | ID)	11	0.06	-71.82	0.03	47.72
~ Maturity + TBL + Sector + (1 | ID)	11	0.05	-71.58	0.02	47.60
~ Sex + BC + TBL + Sector + (1 | ID)	15	0.05	-71.26	0.02	52.15
~ BC + TBL + Sector + (1 | ID)	13	0.02	-69.89	0.01	49.08
~ Sex + Age + Maturity + TBL + Sector + (1 | ID)	15	$8.8x10^{-3}$	-67.95	0.00	50.49
~ Maturity + Age + TBL + Sector + (1 | ID)	13	$8.1x10^{-3}$	-67.78	0.00	48.03
~ Sex + Age + BC + TBL + Sector + (1 | ID)	17	$7.2x10^{-3}$	-67.55	0.00	52.74
~ Sex + Maturity + TBL + BC + Sector + (1 | ID)	17	$5.2x10^{-3}$	-66.90	0.00	52.41
~ Age + TBL + BC + Sector + (1 | ID)	15	$3.9x10^{-3}$	-66.33	0.00	49.68
~ BC + Maturity + TBL + Sector + (1 | ID)	15	$3.7x10^{-3}$	-66.22	0.00	49.63
~ Sex + Age + Maturity + BC + TBL + Sector + (1 | ID)	19	$5.9x10^{-4}$	-62.54	0.00	52.74
~ BC + Age + Maturity + TBL + Sector + (1 | ID)	17	$4.6x10^{-4}$	-62.04	0.00	49.98
~ Maturity + Age + BC + Sector + (1 | ID)	14	$1.7x10^{-5}$	-55.47	0.00	43.06
~ Age + Maturity + Sector + (1 | ID)	11	$5.4x10^{-11}$	-30.14	0.00	26.88
~ Age + Sector + (1 | ID)	9	$3.3x10^{-11}$	-29.17	0.00	24.13
~ Age + Sex + Sector + (1 | ID)	11	$1.1x10^{-11}$	-27.01	0.00	25.32
~ Sex + Age + Maturity + Sector + (1 | ID)	13	$1.0x10^{-11}$	-26.80	0.00	27.54

~ Sector + Maturity + (1 | id),	9	$5.2x10^{-12}$	-25.45	0.00	22.27
~ Sex + Maturity + Sector + (1 | ID),	11	$9.4x10^{-13}$	-22.02	0.00	22.83
~ Age + BC + Sector + (1 | ID)	13	$8.4x10^{-13}$	-21.80	0.00	25.04
~ Sex + Age + Maturity + BC + Sector + (1 | ID)	17	$3.2x10^{-13}$	-19.86	0.00	28.89
~ Sex + Age + BC + Sector + (1 | ID)	15	$2.8x10^{-13}$	-19.63	0.00	26.33
~ BC + Maturity + Sector + (1 | ID)	13	$1.2x10^{-13}$	-17.95	0.00	23.11
~ Sex + Maturity + BC + Sector + (1 | ID)	15	$2.2x10^{-14}$	-14.53	0.00	23.79
~ Sector + (1 | ID)	7	$1.3x10^{-20}$	14.16	0.00	0.26
~ Sector + Sex + (1 | ID)	9	$2.9x10^{-21}$	17.16	0.00	0.97
~ BC + Sector + (1 | ID)	11	$2.4x10^{-22}$	22.14	0.00	0.74
~ BC + Sex + Sector + (1 | ID)	13	$5.2x10^{-23}$	25.19	0.00	1.54

Table A.4 Performance values for zero-inflated generalised linear mixed models (ZIGLMMs) analysing cranial versus caudal sector groupings in common dolphins (*Delphinus delphis*) assessed postmortem. These models incorporate sex (male or female), sector (sector grouping; cranial or caudal), maturity (sexual maturity; immature or mature), age (years), TBL (total body length, cm), BC (body condition; good or moderate), and ID (individual identity) to estimate the rake density (rm/dm^2) of each individual. Note: k = number of parameters, LogLik = minimized negative log-likelihood, AICc = corrected Akaike Information Criterion for small sample sizes, wAICc = Akaike weight adjusted to sum up to 1, ER = evidence ratio, calculated in comparison to the best-performing model.

Model	**k**	**ER**	**AICc**	**wAICc**	**LogLik**
Rake density (cranial vs caudal)					
~ Sex + TBL * Sector + (1 | ID)	13	-	-44.29	1.00	36.28
~ Sex + TBL + Sector + (1 | ID)	11	$1.3x10^{-4}$	-30.98	0.00	27.30
~ Sector + TBL + (1 | ID)	9	$6.2x10^{-6}$	-29.49	0.00	24.29
~ Sex + Age + TBL + Sector + (1 | ID)	13	$5.0x10^{-4}$	-29.08	0.00	28.68
~ Age + TBL + Sector + (1 | ID)	11	$2.0x10^{-5}$	-27.27	0.00	25.45
~ Sex + Age + Maturity + TBL + Sector + (1 | ID)	15	$2.0x10^{-3}$	-27.04	0.00	30.04
~ Sex + Maturity + TBL + Sector + (1 | ID)	13	$1.5x10^{-4}$	-26.64	0.00	27.46

~ Maturity + Age + TBL + Sector + (1 | ID)	13	1.1×10^{-4}	-26.08	0.00	27.18
~ Maturity + TBL + Sector + (1 | ID)	11	6.8×10^{-6}	-25.15	0.00	24.39
~ Sex + BC + TBL + Sector + (1 | ID)	15	6.0×10^{-4}	-24.68	0.00	28.86
~ BC + TBL + Sector + (1 | ID)	13	2.2×10^{-5}	-22.88	0.00	25.58
~ Sex + Age + BC + TBL + Sector + (1 | ID)	17	1.7×10^{-5}	-21.91	0.00	29.92
~ Sex + Age + Maturity + BC + TBL + Sector + (1 | ID)	19	1.2×10^{-2}	-20.78	0.00	31.86
~ Sex + Maturity + TBL + BC + Sector + (1 | ID)	17	7.4×10^{-4}	-20.21	0.00	29.07
~ Age + TBL + BC + Sector + (1 | ID)	15	5.4×10^{-5}	-19.88	0.00	26.46
~ BC + age + Maturity + TBL + Sector + (1 | ID)	17	5.8×10^{-4}	-19.73	0.00	28.83
~ BC + Maturity + TBL + Sector + (1 | ID)	15	2.9×10^{-5}	-18.62	0.00	25.83
~ Age + Maturity + Sector + (1 | ID)	11	1.9×10^{-8}	-13.36	0.00	18.49
~ Maturity + Age + BC + Sector + (1 | ID)	14	3.5×10^{-7}	-12.18	0.00	21.41
~ Sex + Age + Maturity + Sector + (1 | ID)	13	3.9×10^{-8}	-10.14	0.00	19.21
~ Age + Sector + (1 | ID)	9	1.2×10^{-10}	-7.80	0.00	13.45
~ Age + Sex + Sector + (1 | ID)	11	5.6×10^{-10}	-6.32	0.00	14.98
~ Sex + Age + Maturity + BC + Sector + (1 | ID)	17	2.3×10^{-7}	-4.06	0.00	20.99
~ Age + BC + Sector + (1 | ID)	13	2.2×10^{-10}	0.17	0.00	14.05
~ Sex + Age + BC + Sector + (1 | ID)	15	1.2×10^{-9}	1.59	0.00	15.72
~ Sector + Maturity + (1 | ID)	9	2.2×10^{-15}	14.01	0.00	2.55
~ Sex + Maturity + Sector + (1 | ID)	11	4.7×10^{-15}	17.04	0.00	3.29
~ BC + Maturity + Sector + (1 | ID)	13	4.7×10^{-15}	21.68	0.00	3.30
~ Sex + Maturity + BC + Sector + (1 | ID)	15	1.2×10^{-14}	24.60	0.00	4.22
~ Sector + (1 | ID)	7	7.4×10^{-25}	53.25	0.00	-19.29
~ Sector + Sex + (1 | ID)	9	2.3×10^{-24}	55.39	0.00	-18.15
~ BC + Sector + (1 | ID)	11	1.1×10^{-24}	61.44	0.00	-18.90

Table A.5 Performance values for zero-inflated generalised linear mixed models (ZIGLMMs) analysing left versus right sector groupings in common dolphins (*Delphinus delphis*) assessed postmortem. These models incorporate sex (male or female), sector (sector grouping; left or right), maturity (sexual maturity; immature or mature), age (years), TBL (total body length, cm), BC (body condition; good or moderate), and ID (individual identity) to estimate the rake density (rm/dm^2) of each individual. Note: k = number of parameters, LogLik = minimized negative log-likelihood, AICc = corrected Akaike Information Criterion for small sample sizes, wAICc = Akaike weight adjusted to sum up to 1, ER = evidence ratio, calculated in comparison to the best-performing model.

Model	k	ER	AICc	wAICc	LogLik
Rake density (left vs right)					
~ Sex + Sector * TBL + (1 | ID)	13	-	-86.50	0.94	57.39
~ Sex + TBL + Sector + (1 | ID)	11	$3.2x10^{-3}$	-79.64	0.03	51.64
~ Sector + TBL + (1 | ID)	9	$1.5x10^{-4}$	-78.03	0.01	48.56
~ Sex + Maturity + TBL + Sector + (1 | ID)	13	$4.1x10^{-3}$	-75.48	0.00	51.88
~ Sex + Age + TBL + Sector + (1 | ID)	13	$3.6x10^{-3}$	-75.24	0.00	51.76
~ Maturity + TBL + Sector + (1 | ID)	11	$1.8x10^{-4}$	-73.88	0.00	48.76
~ Sex + BC + TBL + Sector + (1 | ID)	15	0.02	-73.72	0.00	53.38
~ Age + TBL + Sector + (1 | ID)	11	$1.6x10^{-4}$	-73.59	0.00	48.61
~ BC + TBL + Sector + (1 | ID)	13	$5.2x10^{-4}$	-71.35	0.00	49.81
~ Sex + Age + Maturity + TBL + Sector + (1 | ID)	15	$4.2x10^{-3}$	-70.77	0.00	51.91
~ Sex + Maturity + TBL + BC + Sector + (1 | ID)	17	0.03	-69.58	0.00	53.75
~ Maturity + Age + TBL + Sector + (1 | ID)	13	$2.0x10^{-4}$	-69.50	0.00	48.89
~ Sex + Age + BC + TBL + Sector + (1 | ID)	17	0.02	-69.13	0.00	53.53
~ BC + Maturity + TBL + Sector + (1 | ID)	15	$8.2x10^{-4}$	-67.53	0.00	50.29
~ Age + TBL + BC + Sector + (1 | ID)	15	$5.6x10^{-4}$	-66.75	0.00	49.90
~ Sex + Age + Maturity + BC + TBL + Sector + (1 | ID)	19	0.03	-64.68	0.00	53.81
~ BC + Age + Maturity + TBL + Sector + (1 | ID)	17	$9.9x10^{-4}$	-63.01	0.00	50.47
~ Maturity + Age + BC + Sector + (1 | ID)	14	$2.8x10^{-6}$	-58.56	0.00	44.60
~ Age + Maturity + Sector + (1 | ID)	11	$1.3x10^{-11}$	-41.07	0.00	32.35
~ Age + Sector + (1 | ID)	9	$1.4x10^{-12}$	-41.03	0.00	30.07
~ Age + Sex + Sector + (1 | ID)	11	$6.7x10^{-12}$	-39.68	0.00	31.65

~ Sex + Age + Maturity + Sector + (1 | ID)	13	$3.5x10^{-11}$	-38.32	0.00	33.30
~ Age + BC + Sector + (1 | ID)	13	$3.2\ x10^{-12}$	-33.58	0.00	30.93
~ Sector + Maturity + (1 | ID)	9	$2.1x10^{-14}$	-32.67	0.00	25.88
~ Sex + Age + BC + Sector + (1 | ID)	15	$2.2x10^{-11}$	-32.67	0.00	32.85
~ Sex + Age + Maturity + BC + Sector + (1 | ID)	17	$1.8x10^{-10}$	-32.00	0.00	34.96
~ Sex + Maturity + Sector + (1 | ID)	11	$5.2x10^{-14}$	-29.98	0.00	26.81
~ BC + Maturity + Sector + (1 | ID)	13	$6.3x10^{-14}$	-25.69	0.00	26.98
~ Sex + Maturity + BC + Sector + (1 | ID)	15	$2.1x10^{-13}$	-23.36	0.00	28.20
~ Sector + (1 | ID)	7	$1.4x10^{-24}$	9.79	0.00	2.44
~ Sector + Sex + (1 | ID)	9	$3.8x10^{-24}$	12.19	0.00	3.45
~ BC + Sector + (1 | ID)	11	$5.6\ x10^{-24}$	15.93	0.00	3.85
~ BC + Sex + Sector + (1 | ID)	13	$2.0x10^{-23}$	18.08	0.00	5.10

Table A.6 Summary statistics for the count of non-rake mark lesion types (cookie cutter scars, tattoo lesions, linear scars, irregular scars and other lesions) on stranded common dolphins (*Delphinus delphis*) assessed postmortem between 2006 and 2024 in New Zealand. Note: SD = standard deviation, min = minimum, max = maximum.

Category	Mean	SD	Min	Max
Cookie cutter scar	1.86	5.02	0.00	28.00
Tattoo lesion	0.25	0.88	0.00	5.00
Linear scar	4.40	7.92	0.00	44.00
Irregular scar	0.56	1.56	0.00	9.00
Other lesions	1.01	2.00	0.00	10.00

Table A.7 Summary statistics for the count of non-rake mark lesion types (cookie cutter scars, tattoo lesions, linear scars, irregular scars and other lesions) on **female** stranded common dolphins (*Delphinus delphis*) assessed postmortem between 2006 and 2024 in New Zealand. Note: SD = standard deviation, min = minimum, max = maximum.

Category	Mean	SD	Min	Max
Cookie cutter scar	2.57	6.29	0.00	28.00
Tattoo lesion	0.43	1.14	0.00	5.00
Linear scar	4.86	9.03	0.00	44.00
Irregular scar	0.77	1.89	0.00	9.00
Other lesions	1.38	2.27	0.00	10.00

Table A.8 Summary statistics for the count of non-rake mark lesion types (cookie cutter scars, tattoo lesions, linear scars, irregular scars and other lesions) on **male** stranded common dolphins (*Delphinus delphis*) assessed postmortem between 2006 and 2024 in New Zealand. Note: SD = standard deviation, min = minimum, max = maximum.

Category	Mean	SD	Min	Max
Cookie cutter scar	1.00	2.62	0.00	10.00
Tattoo lesion	0.04	0.21	0.00	1.00
Linear scar	3.85	6.37	0.00	30.00
Irregular scar	0.30	1.01	0.00	6.00
Other lesions	0.57	1.53	0.00	8.00