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Studies of the Life History of School Sharks (*Galeorhinus galeus*)

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This thesis is dedicated to my Nanna and Poppa,

Ruth and Brian Crane.

Abstract

The school shark (*Galeorhinus galeus*) is a globally distributed, migratory species that was recently reclassified, globally, as Critically Endangered due to all but the New Zealand population having collapsed due to overfishing. Effective management and recovery of these populations is currently limited by a lack of accurate biological information, which is increasingly difficult to obtain due to the scarcity of school sharks throughout their range. By studying the last stable school shark population, located in New Zealand, the aim of this thesis is to provide accurate information on the biology of school sharks to better inform their management worldwide. Specifically, this thesis examines allometric relationships, inter-population variation in life-history stage transitions, intra-population variation in juvenile growth rates, extent of the transfer of elements from mother to pups, and the spatio-temporal connectivity of habitats important to life-history. To enable better standardisation of length data when combining datasets, the optimal model for converting between different length measurements of school sharks was first identified. After standardising length and life-history stage data, a novel Bayesian generative classifier model suggested that length at life-history stage transitions varied among several, globally distributed, school shark populations. A study of juvenile school shark growth across several regions in New Zealand (i.e., Kaipara Harbour, Tasman and Golden Bays, and the Canterbury Bight) revealed that somatic (increase in body length with age) and hepatosomatic (increase of energy stores in the liver with age) growth was consistent among regions, but body condition was generally greater in the Canterbury Bight compared to other two regions. Tracking the year-long, three-dimensional movements of large female school sharks tagged in the Kaipara Harbour with satellite tags showed these sharks dispersed to several potentially important reproductive and feeding habitats around New Zealand. Finally, nutrients and essential and non-essential elements maternally provided to developing young were likely sourced from those assimilated from the mother's diet during vitellogenesis. This thesis has national and international implications for school sharks and other elasmobranch species, as it provides information and techniques crucial to better understanding the biology of species that is needed to inform more effective management and recovery efforts.

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Ethics declaration

The capture and euthanasia, tagging, and/or release of sharks used in this thesis was approved under Massey University Animal Ethics Committee (MUAEC) Protocols 19/98 and 22/44. Copies of both protocols are available in Appendix 6.

Chapter 1: General introduction

Effective management of exploited marine populations requires information on the population's structure and dynamics (e.g., spatial extent, important habitats, sensitivity, and productivity) and potential threats (Grant et al., 2020; Hoffmann et al., 2010; Walker et al., 2008; Zimmermann & Enberg, 2020). Obtaining such information requires detailed knowledge on the fundamental biology of a population, such as life-history (e.g., age-at-maturity, length-at-birth, and growth in length) and movements, as well as how and when a population is exposed to threats, such as fishing and pollution (Braccini et al., 2016; Cortés et al., 2010; Kindsvater et al., 2018; Smith et al., 1998).

Elasmobranchs fill a variety of different roles in marine ecosystems and are of socio-economic importance to many human communities, yet many populations are in decline or have collapsed due to anthropogenic pressures such as over-exploitation, habitat degradation, and pollution (Dedman et al., 2024; Domi et al., 2005; Dulvy et al., 2024; Finucci et al., 2024). However, the knowledge needed to effectively manage and recover these populations is often limited or, in some cases, may be biased. Biases commonly arise from methodological limitations, including the use of datasets that are not representative of the study population (often those derived from captured individuals), inappropriate or lack of standardisation when combining data collected using different methods, and statistical models that are sensitive to non-representative data (Francis, 2006; Thorson & Simpfendorfer, 2009; Walker, 2007). In some cases, limited knowledge of a species' biology has led to assumptions about ecological processes without direct evidence of their occurrence. For example, correlations between physiological traits and reproductive events have sometimes been used to infer biological mechanisms, such as maternal liver reserves being the source of nutrients and contaminants in developing young, despite alternative explanations being possible (e.g., Frías-Espericueta et al., 2014; Rossouw, 1987). As a result, management strategies based on biased or limited information risk exacerbating population declines through misinformed decision-making (Beamish & McFarlane, 1995; Devine et al., 2012; Grant et al., 2020; Taylor et al., 2016). To address these challenges, it is essential to refine existing methodologies and expand our understanding of elasmobranch biology, ensuring that conservation and management efforts are based on accurate and reliable data.

The school shark (*Galeorhinus galeus*) is a globally distributed species found in coastal waters out to over the continental slope (McMillan et al., 2019; Thorburn et al., 2019; West & Stevens, 2001; Figure 1.1). Like other elasmobranchs, school sharks have spatio-temporally dynamic populations, where some individuals undertake large-scale migrations and show site-fidelity to habitats key to their life-history, such as gestation grounds (McMillan et al., 2021; Nosal et al., 2021; Walker et al., 2008). In the spring and summer, pregnant females move into one of several inshore areas within the population's geographic range to give birth (McMillan et al., 2018; Stevens & West, 1997). Pups remain in these areas for up to two years after birth, where they prioritise growth and learn how to effectively capture prey (McAllister et al., 2015; McMillan et al., 2021). Prey initially consists of a mixture of fish and benthic invertebrates and changes as they grow to predominantly fish and cephalopods (Lucifora et al., 2006; Torres et al., 2014). After the first few years, growth slows exponentially until 20-25 years and then becomes negligible (Dureuil & Worm, 2015; Ferreira & Vooren, 1991; Francis & Mulligan, 1998; Moulton et al., 1992). The slower growth causes school

sharks to mature at a late age and large length with females maturing around 15 years or 1350mm total length (TL), and males maturing around 12 years or 1250mm TL (Capapé et al., 2005; Dureuil & Worm, 2015; Francis & Mulligan, 1998; Walker, 2005). Unfortunately, the trophic position, low biological productivity, and spatio-temporal behaviours of school sharks make them susceptible to numerous threats, including overfishing, habitat degradation, and pollutant accumulation (Domi et al., 2005; Walker, 1998).

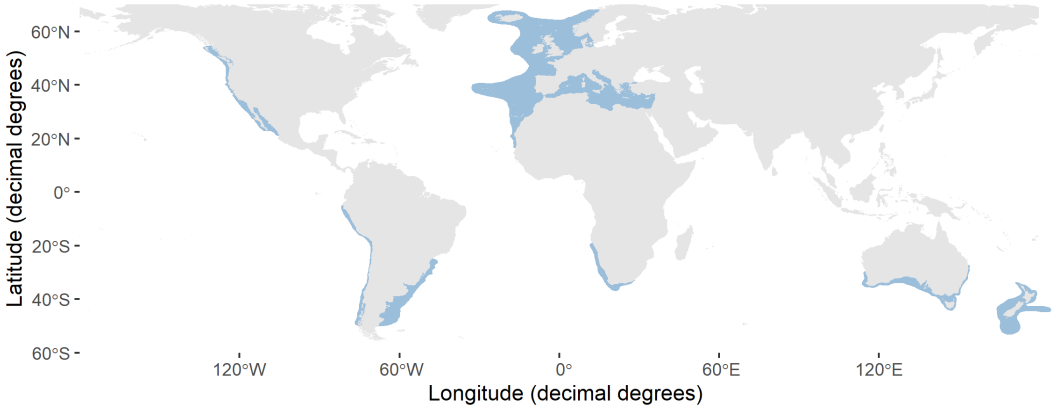


Figure 1.1: *The global geographic distribution of the school sharks (Galeorhinus galeus). The distribution is based on data from Afonso & Priester (n.d.); Charvet (n.d.); De Wysiecki et al. (2022); Kabasakal & Türetken (2021); Hurst et al. (1999); Ministry for Primary Industries (2024a); Ministry for Primary Industries (2024b); Personius et al. (2024); Thorburn et al. (2019); and Walker et al. (2020). n.d. refers to no date for the source.*

Although school sharks once supported many fisheries worldwide, all but the New Zealand school shark population have collapsed due to overfishing (Chiaramonte et al., 2016; Holts, 1988; Molfese et al., 2014; Pondella & Allen, 2008; Thomson et al., 2020; Walker, 1999; Winker et al., 2019). As a result, in 2020, school sharks were classified, globally, as Critically Endangered by the International Union for the Conservation of Nature (Walker et al., 2020) and listed in Appendix II of the Convention on the Conservation of Migratory Species of Wild Animals (2020). While research on the movements, growth, reproduction, and pollutant accumulation of school sharks exists (e.g., Francis & Mulligan, 1998; McMillan et al., 2019; Torres et al., 2014; Walker, 2005), this information is limited or potentially biased for many populations, possibly hindering effective management and recovery efforts. In particular, estimates of life-history parameters (e.g., length-at-birth, length-at-maturity, and growth rates) and inter-population variation of these parameters may be biased due to methodological inconsistencies. These inconsistencies include the use of inappropriate models for converting between measurement methods (Francis, 2006), statistical analyses that are sensitive to non-representative data (Cramer, 1999; Oommen et al., 2011; Thorson & Simpfendorfer, 2009), and comparison of published estimates that were obtained from datasets that vary in both representativeness of the study population and methods used to measure biological traits (e.g., Capapé et al., 2005; Peres & Vooren, 1991). Additionally, gaps persist in our understanding of school shark biology for many populations, including three-dimensional movements, length at life-history stage transitions (e.g., length-at-birth and length-at-maturity), degree of regional variation in juvenile growth rates, and mechanisms underlying the initial exposure to contaminants. For example, maternal transfer has been suggested as a possible

pathway for the initial exposure to contaminants in developing school sharks (e.g., Walker, 1976), but mechanistic ("direct") evidence of this process is lacking. The collapse of many school shark populations has hindered efforts to refine life-history parameter estimates or investigate key aspects of their biology necessary for effective management, as this species has become increasingly scarce throughout much of its range. Fortunately, New Zealand hosts the last stable population and viable fishery of school sharks (Tremblay-Boyer, 2021), providing a unique opportunity to study the species biology to inform management and recovery strategies worldwide. However, there are growing concerns that the New Zealand population has declined in recent years (Tremblay-Boyer, 2021), highlighting the urgent need to acquire accurate biological data to support management and recovery efforts.

In this thesis, I sought to generate fundamental knowledge on the biology of school sharks and develop the tools necessary to better inform the management of the New Zealand population and recovery of school shark populations worldwide. To achieve this, I aimed to address key gaps in our understanding of the life-history, growth, movements, and initial contaminant exposure of school sharks, with a focus on the New Zealand population. More specifically, a multidisciplinary approach was used to:

1) Identify appropriate models for converting between different length measurement variants of school sharks.
2) Assess variation in life-history stage transitions among school shark populations around the world.
3) Investigate regional variation in somatic (increase in body length with age) and hepatosomatic (increase of energy stores in the liver with age) growth of juvenile school sharks in New Zealand.
4) Examine the three-dimensional movements of large female school sharks between the Kaipara Harbour and other areas around New Zealand.
5) Evaluate the extent to which school sharks transfer essential and non-essential elements to their pups.

This thesis is organised into seven chapters: a general introduction chapter, five data chapters, and a general discussion chapter. The data chapters are written as standalone chapters for future submission as journal articles. Hence, each data chapter has its own abstract, introduction, discussion, limitations, and recommendations. Below, I summarise the focus and content of the subsequent chapters.

Chapter 2 evaluates statistical models for converting between different length measurement variants of school sharks. Linear and log-linear Bayesian models, with and without a term for modelling explicit heteroscedasticity, were compared via out-of-sample predictive performance to determine the optimal model.

Chapter 3 combines datasets of length and life-history stage of school sharks from several populations around the world to investigate global variation in life-history stage transitions. Models from Chapter 2, together with new techniques to standardise life-history stage classifications and a novel Bayesian generative classifier model, were applied to mitigate common methodological limitations of life-history studies.

Chapter 4 examines the variation in the somatic and hepatosomatic growth of juvenile school sharks between several regions of likely significance to school sharks in New Zealand. Hierarchical Bayesian growth models, which account for variation in the length- and condition-at-birth as well as birth date, were applied to assess the variation in growth between regions.

Chapter 5 explores the movement of school sharks between the Kaipara Harbour and other habitats of likely significance to the New Zealand school shark population. Pop-up archival satellite tags and data from citizen science initiatives were used to describe the three-dimensional movement of mature female school sharks that dispersed from the Kaipara Harbour. This work led to the identification of habitats of likely significance that are used by female school sharks that dispersed from the Kaipara Harbour.

Chapter 6 evaluates the extent to which school sharks transfer essential and non-essential elements to their pups. Nutrient provision and concentrations of several essential and non-essential elements in maternal and embryonic tissues were analysed to infer mechanisms responsible for the initial exposure of these elements to developing school sharks.

Chapter 7 is the general discussion chapter, which summarises the key findings of each data chapter and discusses their implications for the management and recovery of school shark populations worldwide.

Chapter 2: Navigating Morphometric Minefields: Importance of accounting for heteroscedasticity in length-length conversions

2.1: Abstract

Length measurements play a crucial role in the assessment of elasmobranch populations as they are linked to various biological parameters and analyses, such as attainment of sexual maturity. Given that length can be measured in various ways, techniques for standardising measurements are often required for studies that use data from different sources. Many studies that convert length measurements from one variant to another pay little attention to the patterns of residuals, trusting that log-transforming the data adequately accounts for heteroscedasticity. In addition, studies often assume that, in the absence of data from fresh (or live) individuals, models built from defrosted specimens can adequately convert between fresh length measurements, without directly testing this assumption. Using a Bayesian modelling approach, this study compared the out-of-sample predictive performance of linear and log-linear models, with and without a model term that explicitly modelled heteroscedasticity as a function of the predictor variable, for converting between several length measurement variants for school sharks (*Galeorhinus galeus*). The log-linear model with a term for heteroscedasticity performed best, as the model was flexible to non-linear data and able to account for heteroscedasticity in the linear and log-scales. Furthermore, models built using length variants measured from defrosted animals can be used to convert between length variants measured from fresh animals. It is recommended that models used to convert between length variants include a term that explicitly models heteroscedasticity to sufficiently account for any heteroscedasticity when it arises.

2.2: Introduction

Sustainable management of elasmobranch populations requires accurate knowledge of biological information, such as life history characteristics (Heithaus et al., 2022; Simpfendorfer & Dulvy, 2017; Stevens et al., 2000). For widely distributed species, it can be valuable to compile life-history data from various sources, allowing the pooling of information and comparison of life-history parameters among geographically dispersed populations. However, a problem is often encountered when compiling data from different research groups because they often have different ways of measuring the same trait (De Wysiecki & Braccini, 2017; Francis, 2006; Natanson et al., 2022). For example, lengths may be recorded as fork length or total length, total length may be recorded with the tail in a stretched or a natural position, and sexual maturity may be determined according to the ability to produce gametes or when the copulation organs mature (Francis, 2006; Walker, 2005; Chapter 3).

Having different variants of measured traits can hamper efforts to combine datasets and conduct comparisons across populations because the different variants are often confounded with time

and/or geographic location. When this is the case, it is useful to have a dataset in which multiple trait variants are measured on the same individuals. With such a dataset, it is possible to build statistical models that can convert one variant to another, thus ameliorating the problem of having different variants and enabling cross-population analyses of combined datasets (Bartes & Braccini, 2023; Francis, 2006).

Allometry is the theory of how different morphological traits relate to one another, and, as such, allometric regression models are well suited to the task of converting among different measurement variants (Downs & Cheng, 2013; Manaster & Manaster, 1975; Siers, 2021; Xiao et al., 2011).

The basic allometric equation can be written as

$$Y = \alpha X^{\beta}$$

where *Y* is the target trait measurement, and *X* is the predictor trait measurement. When the trait measurements are log-transformed, the allometric equation can be expressed as,

$$\log(Y) = \log(\alpha) + \beta\log(X)$$

where $log(\alpha)$ and β are intercept and slope parameters, respectively, of a simple linear regression.

The approach of using simple linear regression models on log-transformed trait variables (hereafter, the "log-linear model") dates back to the early 20th century (Clark, 1928; Green & Green, 1932), though some authors have warned against uncritical application of this approach for relating biological traits to one another (Nijhout & German, 2012; Packard, 2023; Smith, 1980; Thompson, 1945). Relationships between biological traits can be linear or non-linear, and deviations from the relationship (i.e., the errors) are almost always heteroscedastic, in that the deviations are generally greater on average for larger fitted values (Francis, 2006; Gingerich, 2000). The utility of the log-linear model is that it can fit linear and curvi-linear relationships while allowing for some degree of heteroscedasticity.

It has recently become more straightforward to fit more sophisticated models with components that explicitly model heteroscedastic errors as a relationship between the error standard deviation and the predictor (Packard, 2017, 2020, 2023; Xu et al., 2017), for example, using the R packages glmmTMB (Brooks et al., 2017) or brms (Bürkner, 2017). Moreover, there have been significant advances in methods of comparing out-of-sample predictive performance in the context of Bayesian models (Magnusson et al., 2020; Vehtari et al., 2017). Yet, few studies have investigated whether the log-linear model is a better fit than the linear model with heteroscedasticity, or whether the log-linear model adequately accounts for heteroscedasticity in the context of trait-variant conversion models.

For sharks, length conversion models are typically used to convert between measurements from fresh (or live) individuals, as these measurements best represent the length of animals observed in situ. However, collecting sufficient data from live individuals to build length conversion models can be difficult due to various constraints in the field, such as depredation and limiting air exposure

(Francis, 2006; Natanson et al., 2022). Although multiple measurements of length can be more easily obtained from dead individuals, specimens may need to be frozen prior to processing, leading to shrinkage of measurements by up to 5% (Francis, 1997; Francis & Francis, 1992). Theoretically, the relationship among different length variants should be conserved between fresh and defrosted individuals, meaning models derived from measurements of defrosted specimens could be used to convert between fresh length variants. Yet, few studies have tested this assumption directly, leaving uncertainty about the reliability of models built from defrosted specimens to convert between fresh length measurements.

Here, a modern Bayesian modelling approach was utilised to investigate the out-of-sample predictive performance of four different models for converting between different variants of length measurements taken from school sharks (*Galeorhinus galeus*). The four models considered were simple linear regressions on the untransformed (linear) and on the natural log-transformed (log-linear) variables and, in each case, with and without an explicit term for heteroscedasticity (where the log of the error standard deviation was modelled as a linear function of the log of the predictor variable). Models with and without different parameter values for males vs females were also compared. Summarising the results of 17 different pairs of length variants, this study investigated whether (1) the relationships were linear or curvi-linear, (2) the models required a component that explicitly models heteroscedasticity, even when the log-linear form of the model was fit, and (3) sex specific parameters were required. Finally, the selected models were used to (4) examine whether models fit to length variants of defrosted animals generalised to converting length variants of fresh animals when data was lacking.

2.3: Methods

2.3.1: Morphological data

The morphological data used in this study were collected from school sharks captured in New Zealand's exclusive economic zone between February 2020 and October 2023. Data from 286 animals were analysed. These were captured by various methods, including angling, longlining, set netting, and trawling. When a school shark was captured, variants of the total, fork, and precaudal lengths were measured using measuring boards or measuring tapes (Figure 2.1). In instances where the specimens were collected rather than returned alive, multiple measurements were taken during post-mortems on fresh or defrosted specimens, including full and partial body lengths (Figure 2.1; Appendix 1.1). In some cases, not all the length variants could be taken due to the condition of the animal. Measurements were taken with an individual lying flat on the ventral surface of its abdomen (except for preoral length, which was measured with the shark on the lateral surface of its abdomen) and recorded to the nearest mm, if possible, otherwise to the nearest 5mm.

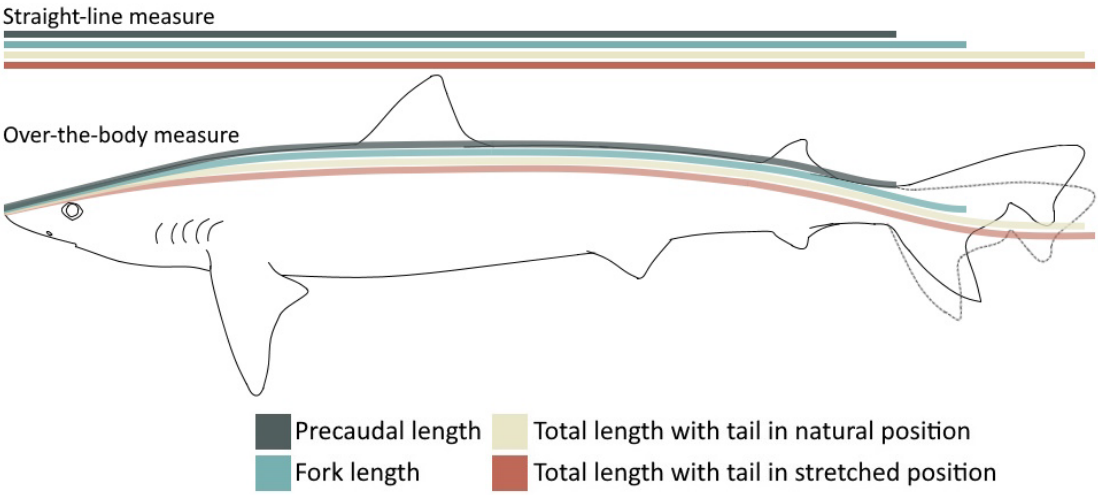


Figure 2.1: *Most common body morphometrics that can be used to derive total body length for sharks. The grey outlined tail illustrates when the tail is in a stretched position. Definitions of the length variants are available in Table A1.1.1.*

In addition to the main dataset collected in New Zealand, this study used supplementary data from school sharks caught in Australia (Braccini unpublished data). The Australian data were not used for fitting any models; they were used as an independent test set. Specifically, they were used to assess whether conversion models fit to data measured from defrosted sharks could be used to convert fresh variants (aim 4 in section '*2.2: Introduction*'). These data were collected from school sharks, captured by gillnets in Australian waters between 1993 and 1995 (Braccini unpublished data), with all measurements taken from fresh specimens.

2.3.2: Statistical models

All analyses were undertaken using R and R Studio (Posit team, 2024; R Core Team, 2024). Models were constructed and compared using the brms and rstan packages (Bürkner, 2017; Stan Development Team, 2024).

The four models described in Table 2.1 were tested and compared on a total of 17 conversions. These conversions consisted of converting nine length variants (six full and three partial body lengths) to the two most used length variants for school sharks; that is, total length measured in a straight line with the tail in the natural vs stretched (tail in line with body axis) position (Figure 2.1; Table 2.2).

Table 2.1: *Different forms of the linear model with and without explicit terms for heteroscedasticity. $y_i$is the desired length variant, and $x_i$is the length variant being converted. For models without a term for explicit heteroscedasticity, σ denotes the standard deviation of y_i, assumed to be constant across all observations. For models with a term for explicit heteroscedasticity, σ_i denotes the standard deviation of y_i, which varies as a function of x_i. For the linear models, μ_i and σ (or σ_i) denote the mean and standard deviation of y_i on the arithmetic scale, respectively. For the log-linear models, μ_i and σ (or σ_i) denote the mean and standard deviation of y_i on the log-scale i.e., $log\ (y_i)$. β_0 and $\beta_1$denote the intercept and slope parameters for the mean, and ζ_0 and ζ_1 denote the intercept and slope parameters for the standard deviation.*

Model name	Model description	Mathematical notation
Linear	Linear model with homoscedastic errors	$y_i \sim \text{Normal}(\mu_i, \sigma)$ $\mu_i = \beta_0 + \beta_1 x_i$
Linear sigma	Linear model with explicit heteroscedasticity	$y_i \sim \text{Normal}(\mu_i, \sigma_i)$ $\mu_i = \beta_0 + \beta_1 x_i$ $\log(\sigma_i) = \zeta_0 + \zeta_1 \log(x_i)$
Log-linear	Log-linear (natural log-normal) model without explicit heteroscedasticity	$y_i \sim \text{Log-Normal}(\mu_i, \sigma)$ $\log(\mu_i) = \beta_0 + \beta_1 \log(x_i)$
Log-linear sigma	Log-linear (natural log-normal) model with explicit heteroscedasticity	$y_i \sim \text{Log-Normal}(\mu_i, \sigma_i)$ $\log(\mu_i) = \beta_0 + \beta_1 \log(x_i)$ $\log(\sigma_i) = \zeta_0 + \zeta_1 \log(x_i)$

In addition, variants of these models that included different parameters for each sex were also fit. An example of the log-linear model with explicit heteroscedastic errors with sex-specific parameters is:

$$\begin{aligned} y_i &\sim \text{Log-Normal}(\mu_i, \sigma_i) \\ \log(\mu_i) &= \beta_{0,Sex[i]} + \beta_{1,Sex[i]} \log(x_i) \\ \log(\sigma_i) &= \zeta_0 + \zeta_1 \log(x_i) \end{aligned}$$

To provide conversion models for measurements from fresh individuals (rather than frozen and defrosted) when data is lacking, length conversion models built from defrosted sharks were evaluated for their ability to accurately convert the same length variants measured from fresh animals.

For each model, weakly informative priors were used.

2.3.2.1: Model comparison and testing

The Expected Log Predictive Density (ELPD) was used to compare the four models and establish whether models needed to account for sex when converting between length variants. ELPD is a measure of predictive accuracy for out-of-sample data, which is estimated using Pareto-Smoothed Importance Sampling (Vehtari et al., 2017). Differences in ELPD < 4 and/or the standard deviation of the difference was greater than the difference in ELPD indicated there was no evidence in the

difference of the predictive ability of a model (McLatchie & Vehtari, 2024; Sivula et al., 2020). When there was no evidence of a difference in predictive ability between the models, the simplest model was selected. Testing of the selected model on new data and visualizing residuals and observed data against model predictions were also used in the model comparison.

2.4: Results

Most of the relationships between variants of length measurements appeared to be linear (Figures 2.2a-g, 2j-o). Relationships with non-linearity/minor curvature appeared to be limited to partial length measurements, specifically, head measurements such as head length and preoral length (Figures 2.2h-i, 2p-q). There also seemed to be no difference in the relationship between sexes over the range of the length variants (Figure 2.2a-q).

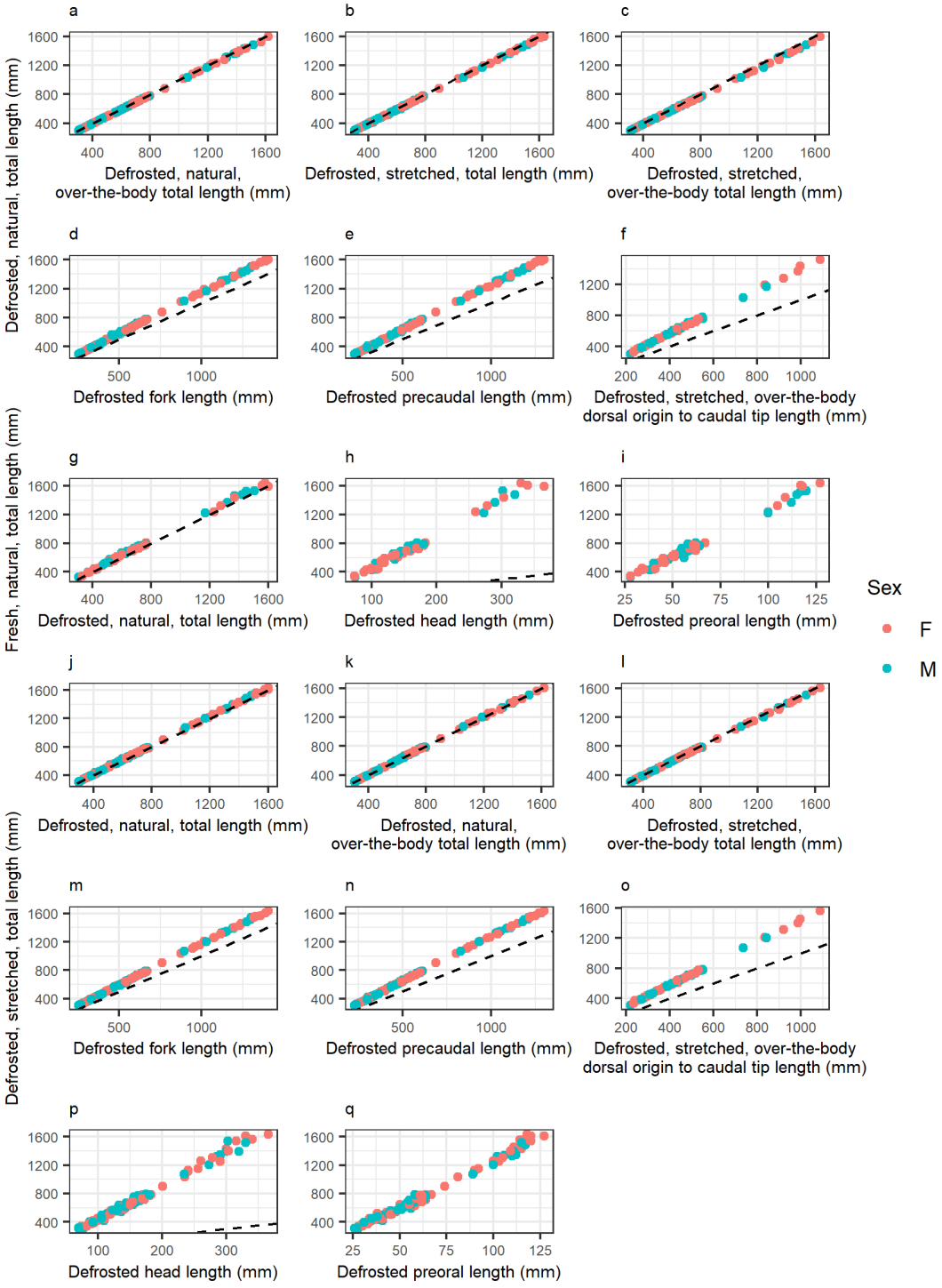


Figure 2.2: *The relationships between length variants being modelled. Defrosted variants are variants measured from defrosted animals, whereas fresh variants are variants measured from fresh/live animals. Definitions of each length variant are in Appendix 1.1. The dashed line is when x=y.*

The linear sigma and log-linear sigma models performed better than the models without in all but two conversions (Table 2.2; Figure 2.3). However, there appeared to be no evidence of a difference in the fit (Figure 2.4; Appendix 1.2) or predictable ability (Figure 2.3; Figure 2.5; Appendix 1.2) between the linear and log-linear models in most of the conversions. This resulted in the linear sigma model being selected due to its simplicity. There were four conversions where the log-linear sigma model performed and fit better (Figure 2.3; Figure 2.6) and was subsequently selected. The cases where the log-linear sigma model was selected included two relationships between partial and full body lengths that were non-linear (Figure 2.2). There were two conversions that lacked evidence of a difference between models with and without explicit heteroscedasticity, but this may be due to having limited data from larger individuals in these cases.

Table 2.2: *Model comparison results from the four models that convert between the 17 pairs of length measurement variants. Conversion are the conversions modelled with length variants expressed in concise subscript (defined in Appendix 1.1). Values in the table are the differences in the Expected Log Predictive Density (ELPD) of the four models from the model with the greatest ELPD (difference = 0), with standard errors of the difference. Models that were selected are highlighted in green. Models where the difference is less than the standard error are highlighted in brown.*

Conversion	Response variable	Predictor variable	Linear	Linear sigma	Log-linear	Log-linear sigma
fts~dts	Fresh, natural, total length	Defrosted, natural, total length	-18.1±8.8	-1.03±0.69	-16.3±8.3	0
fts~dpls	Fresh, natural, total length	Defrosted preoral length	-5.42±2.84	-2.97±1.30	-2.20±2.31	0
fts~dhls	Fresh, natural, total length	Defrosted head length	-15.8±7.4	-0.403±1.090	-16.4±8.6	0
dts~dto	Defrosted, natural, total length	Defrosted, natural, total length, over-the-body	-27.0±10.0	0	-27.5±10.0	-0.0896±0.1730
dts~dss	Defrosted, natural, total length	Defrosted, stretched, total length	-39.4±12.6	0	-39.8±12.3	-0.583±0.451
dts~dso	Defrosted, natural, total length	Defrosted, stretched, total length, over-the-body	-40.7±11.0	-0.172±0.403	-41.5±11.3	0
dts~dps	Defrosted, natural, total length	Defrosted precaudal length	-36.6±6.6	-6.06±2.51	-27.3±6.7	0
dts~dfs	Defrosted, natural, total length	Defrosted fork length	-11.7±4.7	-2.14±1.20	-7.95±4.62	0
dts~ddso	Defrosted, natural, total length	Defrosted, stretched, dorsal origin to caudal tip length, over-the-body	-7.40±4.74	-0.455±0.725	-7.62±5.27	0

Conversion	Response variable	Predictor variable	Linear	Linear sigma	Log-linear	Log-linear sigma
dss~dts	Defrosted, stretched, total length	Defrosted, natural, total length	-39.0±12.5	0	-39.1±12.3	-0.209±0.365
dss~dto	Defrosted, stretched, total length	Defrosted, natural, total length, over-the-body	-20.7±7.8	0	-20.6±7.9	-0.277±0.500
dss~dso	Defrosted, stretched, total length	Defrosted, stretched, total length, over-the-body	-23.2±8.8	0	-23.6±8.8	-0.477±0.381
dss~dps	Defrosted, stretched, total length	Defrosted precaudal length	-42.8±6.1	-8.85±2.48	-24.6±5.6	0
dss~dpls	Defrosted, stretched, total length	Defrosted preoral length	-21.2±6.1	-8.10±2.27	-11.6±5.6	0
dss~dhls	Defrosted, stretched, total length	Defrosted head length	-30.9±9.1	-5.21±1.43	-25.7±8.9	0
dss~dfs	Defrosted, stretched, total length	Defrosted fork length	-26.6±7.6	-2.21±1.29	-19.3±7.8	0
dss~ddso	Defrosted, stretched, total length	Defrosted, stretched, dorsal origin to caudal tip length, over-the-body	-3.59±2.92	-0.17±0.52	-3.82±3.11	0

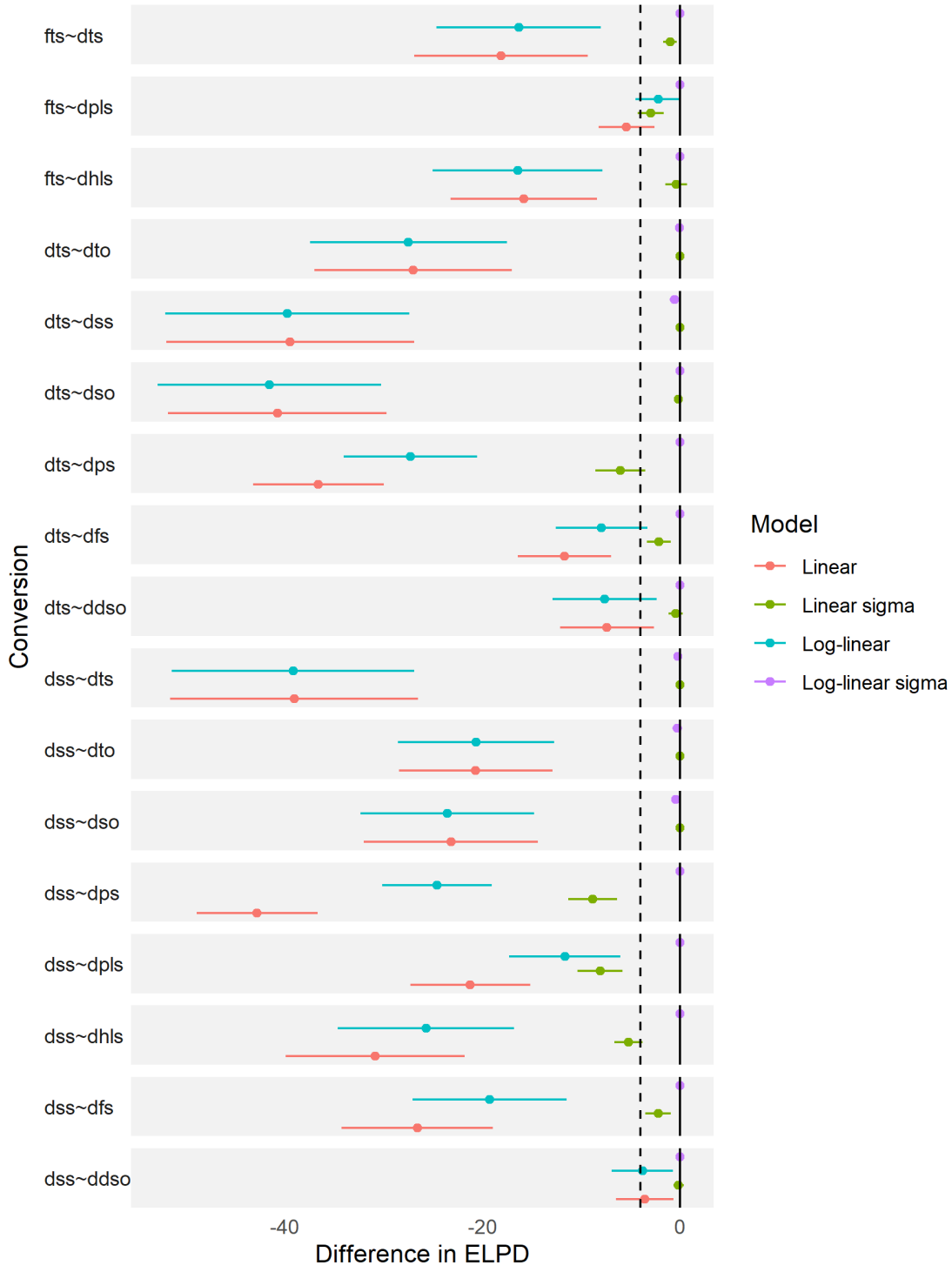


Figure 2.3: *Comparison of the difference in ELPD between the four models for each of the 17 length variant conversions. Conversions are the length variants given in concise subscript (see Table 2.2 and Appendix 1.1 for definitions). The horizontal lines are the standard errors of the difference. The solid vertical line represents a difference of 0, which is the model with the greatest ELPD. The vertical dashed line is a difference of 4. Any differences in model ELPD ≤ 4 can be taken as no evidence of a difference in the predictive accuracy of those models.*

Plots of fits and residuals of the four models across all conversions are available in Appendix 1.2. Point estimates (i.e., the mean of the posterior distribution of estimates) of the log-linear sigma model parameters to convert between the tested length variants are available in Table A1.3.1.

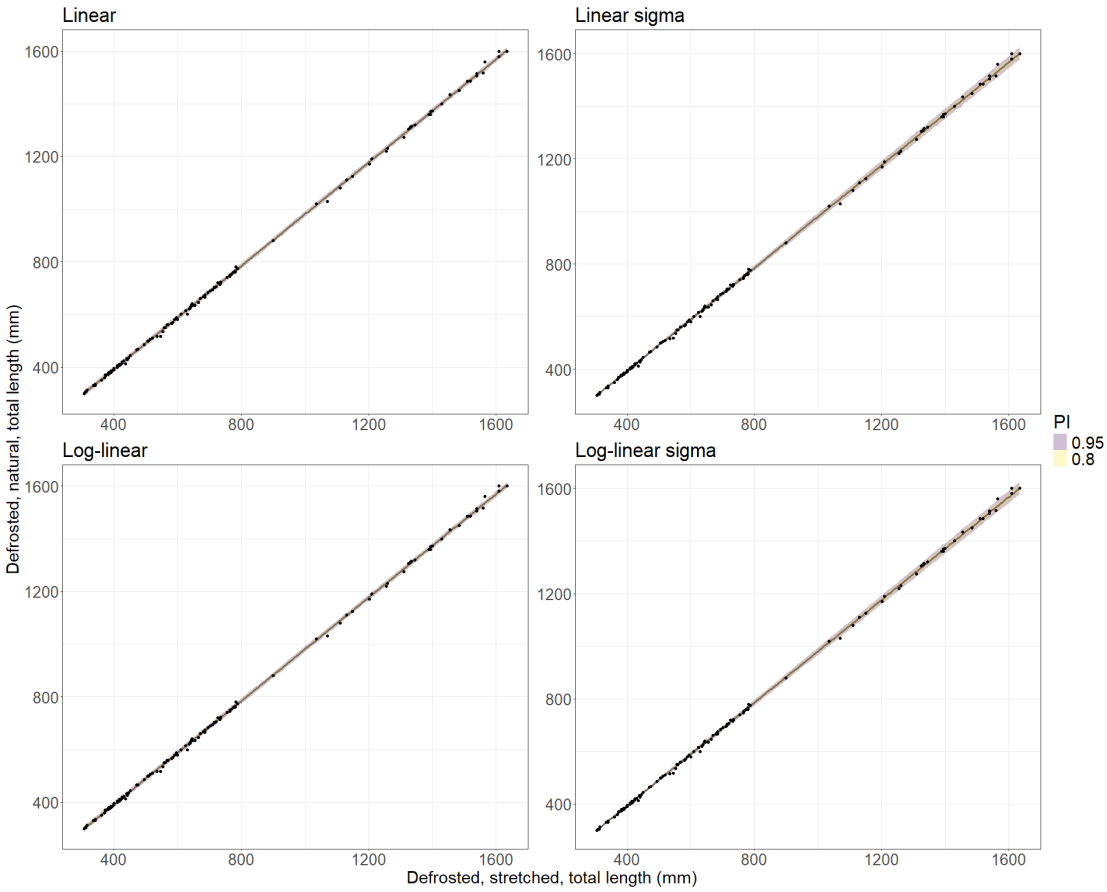


Figure 2.4: *Predicted fit of the four conversion models where there was no evidence of a difference in the ELPD between the models within the same error structure. PI corresponds to 80% and 95% posterior prediction intervals. Defrosted, stretched, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a stretched position. Defrosted, natural, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a natural position.*

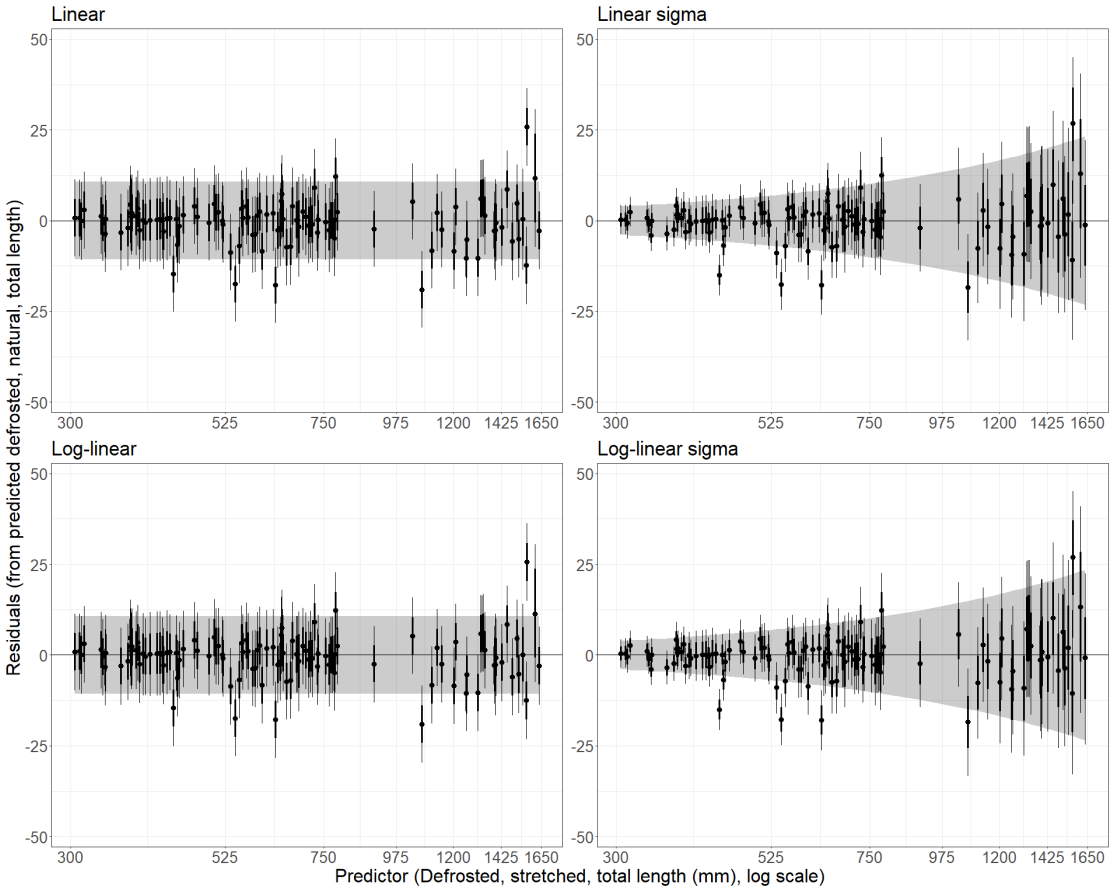


***Figure 2.5**: Residual plots of the four conversion models where there was no evidence of a difference in the ELPD between the models within the same error structure. Points represent the point estimates of the residual posterior distributions. Vertical lines indicate the 66% and 95% credible intervals of the residual posterior distributions. The shaded area is the 95% range of the residual variation, as determined by the model's error structure. Defrosted, stretched, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a stretched position. Defrosted, natural, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a natural position.*

Comparing the fit and ELPD scores of the heteroscedastic log-linear model with and without the inclusion of a sex covariate (average diff = -1.34, average SE = 1.41) showed no evidence of a difference between the models (Table A1.4.1; Figure A1.4.1).

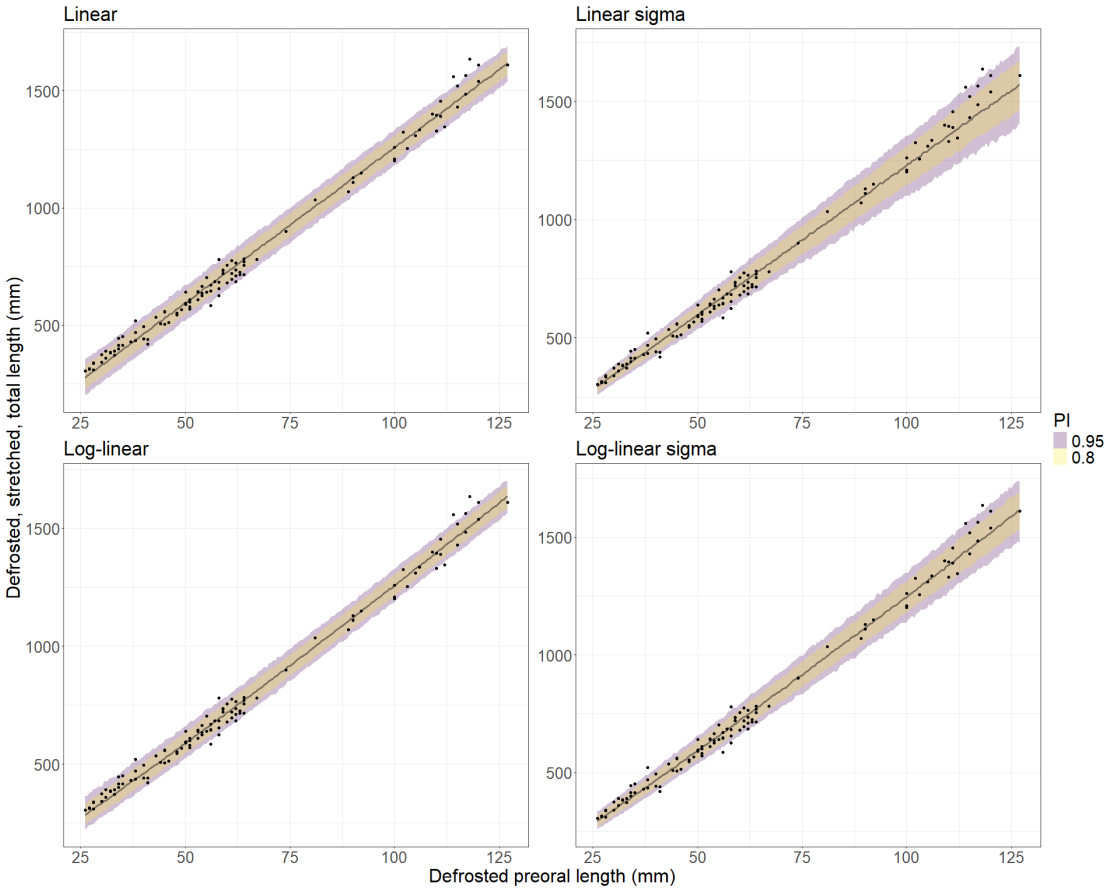
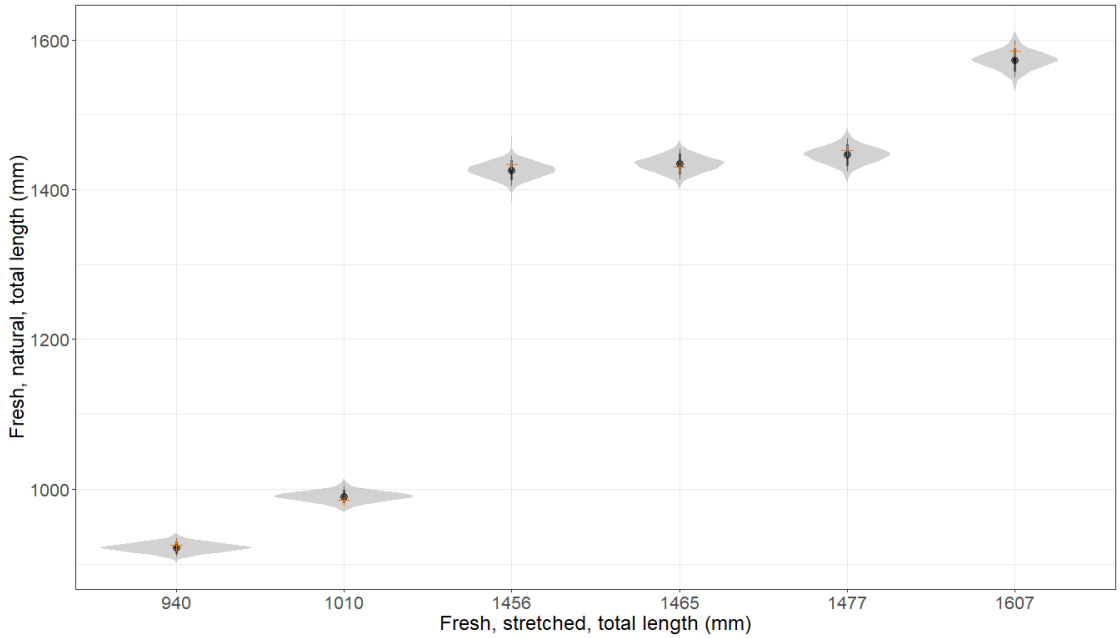
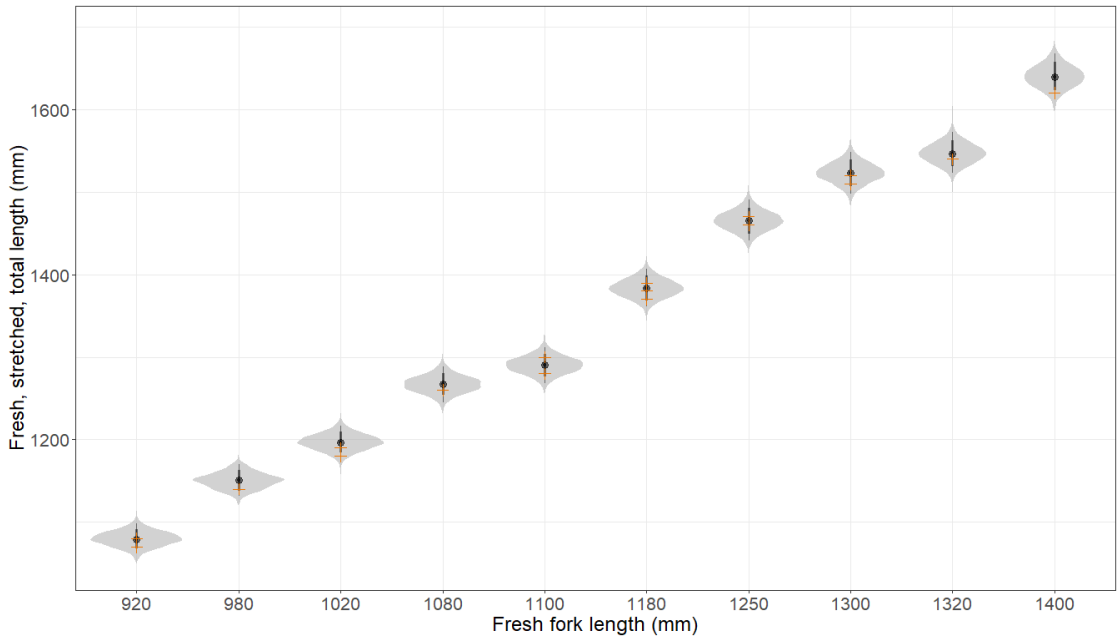


Figure 2.6: *Predicted fit of the four conversion models where there was evidence of a difference in the fit between all four models. PI corresponds to 80% and 95% posterior prediction intervals. Defrosted, stretched, total length is the total length measured from a defrosted shark in a straight line with the tail in a stretched position. Defrosted preoral length is the preoral length measured from a defrosted shark in a straight line.*

Given the disparity between the sample sizes of fresh and defrosted measurement variants of some length-length relationships (e.g., for total length natural ~ total length stretched, *n* = 6 for fresh vs *n* = 141 for defrosted), conversion models that used defrosted length variants performed well when used to convert between fresh variants of the same lengths. For most individuals, including data measured from a different population (Australia) by a different research group, the observed lengths were within the prediction error intervals of the predicted variant of the same length (Figure 2.7a and 2.7b; Appendix 1.5).



a)



b)

Figure 2.7: *Predictions for fresh measurement variants made from log-linear sigma models trained on the same variants measured from defrosted individuals. Fresh, natural, total length: total length, measured in a straight line, tail in natural position, measured from a fresh or live shark. Fresh, stretched, total length: total length, measured in a straight line, tail in stretched position, measured from a fresh or live shark. Fresh fork length: fork length, measured in a straight line, tail in natural position, measured from a fresh or live shark. The filled black circles are the point estimates of the predicted length variants. The black horizontal lines are the 80% and 95% prediction intervals. The*

grey distributions around the filled points and horizontal lines are the posterior distributions of the predicted length variants. The orange plus symbols are the observed values of the fresh variants.

2.5: Discussion

Relationships between partial and full body measurements for many elasmobranchs are typically modelled with linear models, on the arithmetic or log-scale, without a "sigma" model component that explicitly fits the residual error standard deviation as a function of the predictors (e.g., Francis, 2006). Yet, for all 17 of the conversion models presented here, one of the two models that included such a component gave the most accurate out-of-sample predictions (i.e., the linear sigma or log-linear sigma models; Table 2.2, Figure 2.3). The log-linear sigma model was favoured in 12 of those cases, and the linear sigma model was favoured in five cases; for six cases, the difference in ELPD between the two sigma models was less than the standard error of the difference, indicating that the out-of-sample predictive performance was generally very similar between the linear sigma and log-linear sigma models. In summary, explicitly modelling the error standard deviation led to better predictions in all cases.

Simply log-transforming the data and fitting a linear model does not always adequately account for heteroscedasticity (Carroll & Ruppert, 1988; Manning, 1998; Packard, 2017). In our study, even when the log-transformation was applied, including a model component for the error standard deviation resulted in superior out-of-sample predictive performance in all cases except for one (Table 2.2; Figure 2.3). The estimated slope of the sigma term was positive in all cases (Table A1.3.2), indicating that the log-linear models underestimated the degree of heteroscedasticity.

Like other shark species (e.g., De Wysiecki & Braccini, 2017; Natanson et al., 2022), there was little evidence of a difference in length conversion parameters between male and female school sharks. Therefore, it is recommended that the log-linear model with explicit heteroscedasticity (log-linear sigma model) and pooled sex data should be used for converting between body length variants of school sharks. This is due to the model being flexible to non-linear relationships, where they arise, and able to appropriately account for heteroscedasticity.

An important issue with measuring the lengths of sharks is whether the measurements were taken when the animal was fresh or after being frozen and defrosted (Francis, 1997; Francis & Francis, 1992; Olsen, 1954). Similar to patterns observed in other species (e.g., Francis, 1997 and Francis & Francis, 1992), length variants recorded from fresh school sharks were around 5% larger on average than the defrosted equivalents (Figure A1.6.1). Depending on how the animals are captured and processed, one usually obtains measurements either fresh or defrosted, and rarely both. In this study, there were fewer measurements from fresh animals than defrosted ones, and, as a result, conversion models for several variant pairs could not be built for fresh animals. However, when models trained on length data from defrosted animals were applied to convert between the same measurement variants from fresh animals, most of the observed (fresh) values were within the expected posterior distributions of predicted values (Figure 2.7; Appendix 1.5). This finding indicated that conversion models built with data from defrosted animals may be useful for converting within the same variant pairs taken from fresh animals. Of course, converting between fresh and defrosted would require different models to be built.

In summary, given the importance of length measurements to biological analyses, it is essential that conversions between length variants are accurate and unbiased. Using school sharks as a

case study, the log-linear model with explicit heteroscedastic error and non-sex-specific parameters was generally the best model to convert between length variants. Moreover, models constructed using length variants measured from defrosted animals can convert between length variants measured from fresh animals. However, to ensure accurate and unbiased conversions between length variants, and consistent with the recommendations of Francis (2006) and Natanson et al. (2022), it is vital that researchers clearly and thoroughly define the length measurements they used in a study. Furthermore, when building models to convert among measurement variants, it is recommended that a term that explicitly models the error standard deviation be included in the model because, while log-transforming the variables may go some way to account for heteroscedasticity, it did not do so sufficiently in the examples in this study.

Chapter 3: Variation in the life-history stage transitions among globally distributed populations of school shark (*Galeorhinus galeus*)

3.1: Abstract

An understanding of how life-history traits, such as growth and attainment of maturity, vary among geographically disparate populations of a species is useful for population-specific management. A novel hierarchical Bayesian generative classifier model was applied to a dataset of lengths and life history characteristics compiled from six populations of school sharks around the world to estimate the length at which school sharks transitioned between life-history stages at the species level and for each of the six school shark populations. While length-at-birth and female length-at-maturity could be estimated for three populations, though not the same three for each parameter, our analysis focused on male length-at-maturity, as sufficient data were available to estimate species level length-at-maturity and compare population-specific estimates among all six populations. The point estimate of species level length-at-maturity for male school sharks was estimated at 1273 mm total length (fresh total length, measured in a straight line, with the tail in a natural position; TL), and population-specific point estimates ranged between 1238 and 1306 mm TL. Most populations differed in length-at-maturity by at least 19 mm TL. Estimates were similar between the New Zealand and South African, and for the Northeast Atlantic and Southwest Atlantic populations; however, the estimates for the South African and Northeast Atlantic were predominantly larger than those for the New Zealand and Southwest Atlantic, respectively. Although the drivers of the observed variation could not be determined, population-specific length-at-maturity estimates for male school sharks are necessary for the ongoing management of school shark populations.

3.2: Introduction

Understanding the extent of geographic variation in life-history traits, such as length and age at maturity (attainment of maturity), is crucial for effective elasmobranch management. Since key population parameters (e.g., natural mortality, sensitivity, and recovery potential) depend on life-history traits, population-specific estimates may be necessary to inform local management decisions (Grant et al., 2020; Simpfendorfer et al., 2011; Smith et al., 1998). Inter-population variation in the attainment of maturity has been observed in many elasmobranchs, ranging from regionally distributed, dispersal-limited species to globally distributed, migratory species (e.g., Frisk & Miller, 2009; Grant et al., 2018; Lombardi-Carlson et al., 2003; Neer & Thompson, 2005). Multiple factors, such as adaptation to local biotic and abiotic conditions, environmental-latitudinal gradients, and responses to fishing pressures, have been offered as explanations for the observed inter-population variation (e.g., Cassoff et al., 2007; Rochowski et al., 2015; Stearns, 1992).

Although true inter-population variation in attainment of maturity exists, the extent of such variation may be masked or confounded by artefacts of the sampling design, biological trait measurement/assessment methods, and/or statistical methods (e.g., Walker, 2007; Walker et al., 1998). Datasets of captured specimens are often not representative of the full population due to the spatial and temporal (spatio-temporal) complexity of elasmobranch populations, spatio-temporal biases of sampling locations, and selectivity of sampling gear (Rufener et al., 2021; Walker, 2005; Walker et al., 1998). As a result, datasets used to estimate life-history parameters may overrepresent some length classes and demographic groups while underrepresenting others; for example, datasets used to estimate attainment at maturity may contain far more mature than immature individuals (Walker, 2007; Walker et al. 1998). Another common issue in broad-scale life-history studies, particularly those that combine different sources, arises from inconsistencies in the way traits are measured. Researchers often measure, assess, or determine biological traits differently, resulting in multiple variants of the same trait, such as age, length, and life-history stages (e.g., Beamish & McFarlane, 1995; Francis, 2006; Chapter 2). Failure to standardise trait variants before analysis can bias estimates of growth and maturity parameters (Beamish & McFarlane, 1995; Francis, 2006). To avoid such biases, it is necessary to identify and mitigate potential issues arising from non-representative data and inconsistent measurement methods.

Given the opportunistic nature of most life-history datasets, the statistical methods used to estimate maturity parameters may not always be appropriate. Logistic regression is commonly applied to estimating maturity parameters. Logistic regression is a “deterministic classifier”, directly estimating the probability of belonging to a certain class (e.g., mature) given a value of x (e.g., length), that is P(class|x) (Cox, 1958). As such, deterministic classifiers are sensitive to class imbalance because they base their estimates on the proportions of each class across values of x. If one class is over-represented in the data, then the estimated probabilities will be biased in favour of that class (Cramer, 1999; Oommen et al., 2011). An alternative approach is a “generative classifier”, such as Linear Discriminant Analysis (LDA) (Bouchard & Triggs, 2004). Generative classifiers first estimate P(x|class), the distribution of x values in each class, and then apply Bayes rule to obtain P(class|x) (Efron, 1975). This approach is less sensitive to class imbalance because the model first estimates the distribution of each class, placing classes on an “equal footing”. However, simple generative classifiers, such as LDA, rely on assumptions about the distribution of the data which may not be met. Furthermore, the required inference in studies of life-history transition is solely the point of transition; yet, generative classifiers may be strongly affected by data that are far away from the point of transition (Efron, 1975). Thus, there is a need for more careful consideration of the statistical methodology for life-history transition studies.

Biased estimates of life-history parameters arising from non-representative sampling designs, variable trait measurement and assessment methods, and non-robust statistical methods may lead to misinformed management decisions, increasing the risk of over-exploitation and population decline (Beamish & McFarlane, 1995; Devine et al., 2012; Grant et al., 2020; Taylor et al., 2016). For school sharks (*Galeorhinus galeus*), a globally distributed species, current estimates of inter-population variation in attainment of maturity are likely inaccurate or biased. This is due not only to the use of data with imbalanced classes and inappropriate statistical models (e.g., Lucifora et al., 2004) but also to conclusions being drawn from comparisons of published estimates derived from datasets that differ in measurement methods and representativeness of the population (e.g.,

Capapé et al., 2005; Peres & Vooren, 1991). For some populations, only ranges of attainment of maturity and length at birth have been reported (Table 3.1), and precise estimates for these parameters have yet to be determined. Given that accurate estimates of these life-history stage transitions help inform effective management, determining the extent of inter-population variation of life-history stage transitions is essential to assess whether population-specific parameters are required for the management of school sharks.

Table 3.1: *Estimates of school shark life-history stage transitions from available literature. Population is the population based on the definitions from Figure 3.1. Sources in* ***bold*** *indicate datasets also used in this study. Lengths are reported as fresh total length, measured in a straight line, with the tail in a natural position, converted from original lengths where necessary using models from Chapter 2. Confidence intervals represent the bounds of the 95% confidence interval for modelled estimates of length-at-maturity. Immature and mature length ranges are the length ranges of the life-history stages used to derive the estimates, with the sample size (n) of each stage in brackets where available. * represents estimates that were derived from modelling; ‡ represents the range of modelled estimates; † represents the lower confidence interval bound for the smaller estimate and the upper bound for the larger estimate.*

Population	Source	Length at birth	Sex	Length at maturity	Confidence intervals	Immature length range (n)	Mature length range (n)
Australia	Olsen (1954)	275-344	Female	1322-1410			
			Male	1176-1293			
Australia	**Walker (2005)**		Female	1321*	1312, 1330	<687-1469	1176-1663
			Male	1234-1285‡	1219, 1295†	<589-1468	1078-1663
New Zealand	Francis & Mulligan (1998)		Female	1322-1371			
			Male	1224-1322			
Northeast Atlantic	**Capapé et al. (2005)**	236-314	Female	1371		578-1342 (31)	1371-1948 (307)
			Male	1200-1234		491-1234 (35)	1200-1547 (307)
Northeast Pacific	**Ripley (1946)**	344-363	Female	1542		1273-1762 (89)	1518-1869 (1233)
			Male	1390		980-1615 (28)	1371-1713 (161)
South Africa	Freer (1992)	297	Female	1293			
			Male	1231			
South Africa	**Theron (2001)**	300	Female	1310			
			Male	1180			
South Africa	McCord (2005)		Male	975*	972, 978		
Southwest Atlantic	**Peres & Vooren (1991)**		Female	1156-1254			
			Male	1049-1146			
Southwest Atlantic	**Lucifora et al. (2004)**	310	Female	1247*		470-1290	1180-1520
			Male	1080-1200		490-1080	1180-1520
Southwest Atlantic	**Chiaramonte (2015)**	297	Female	1235*	1228, 1295	576-1325	1214-1475
			Male	1145*	1135, 1181	695-1220	1105-1470

Here, a new generative classifier model was applied to a global dataset of school sharks, incorporating data from multiple populations from around the world, to estimate the length school sharks transition between life history stages. Because the collated data included different methods for measuring length and assessing life-history stage, new techniques were applied to standardise these data so they were comparable. A hierarchical version of the generative model was then used to estimate length at life-history stage transition at the species and population level to assess the degree to which length at life-history stage transition varied across different populations. Finally, potential factors driving the observed variation in length at life-history stage transition among populations were examined based on the data and knowledge from each population, including whether the observed differences follow an environmental-latitudinal gradient by assessing the correlation between length at life-history stage transition estimates and latitude.

3.3: Methods

3.3.1: Definition of regional populations

For this study, seven populations of school sharks around the world were defined: namely, Australia, New Zealand, Northeast Atlantic, Northeast Pacific, Southeast Pacific, South Africa, and Southwest Atlantic (Figure 3.1). The distributions of the populations were based on data from Afonso & Priester (n.d.); Charvet (n.d.); De Wysiecki et al. (2022); Kabasakal & Türetken (2021); Hurst et al. (1999); Ministry for Primary Industries (2024a); Ministry for Primary Industries (2024b); Personius et al. (2024); Thorburn et al. (2019); and Walker et al. (2020). These populations were defined based on the lack of genetic and spatio-temporal (migratory) connectivity (Bester-van der Merwe et al., 2017; Chabot, 2015; Devloo-Delva et al., 2019; Hernández et al., 2015). In the case of Australia and New Zealand, though there has been some limited exchange between these two populations (Devloo-Delva et al., 2019; Hernández et al., 2015; McMillan et al., 2019; Chapter 5), the Australian stock has collapsed, whereas the New Zealand stock remains largely stable (Tremblay-Boyer, 2021; Woodhams et al., 2023). Given the differences in stock status and limited information on the extent of connectivity and exchange between stocks, Australia and New Zealand were treated as separate populations.

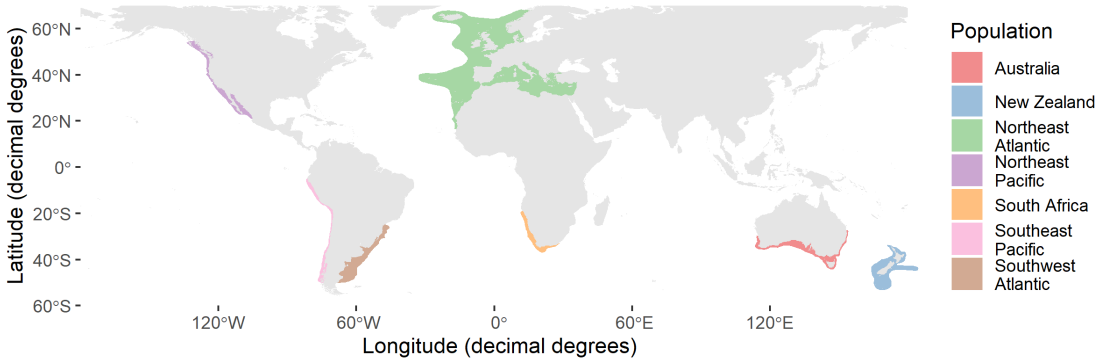


Figure 3.1: *The geographic distribution of the seven school shark populations defined in this study.*

3.3.2: Acquisition of data

Data associated with school shark life-history traits (length, sex, life-history stage, pregnancy information, neonate scar condition, and measurements of reproductive structures), along with specific details about how these traits were measured or assessed, and how the individuals were captured (gear type, capture date, approx. capture location) was sourced from various researchers and institutions around the globe (Table 3.2). In instances where requested data was not available from the source but available in published plots, Plotdigitizer (PORBITAL, 2024) was used to extract the relevant data.

Additional data for the New Zealand population was obtained from 286 school sharks captured between February 2020 and October 2023. Where possible, individuals were measured, sexed, weighed, and had life-history stage assessed (males only via clasper maturity assignment, Table A2.1.1) immediately after capture. 211 sharks were collected and had numerous external and internal morphometric measurements, sex, life-history stage, and total body and organ weights recorded during post-mortems. If present, *in utero* eggs and embryos had uteri of origin, uterus position (with respect to the posterior end of the uterus), and weight recorded. Embryo weight was split into weight with and without the yolk sac. Embryos also had total length (measured in a straight-line, with tail in a natural position) and sex recorded. All measurements were recorded to the nearest mm, where possible and, failing that, to the nearest 5mm. Weights were measured to the nearest gram. Sex was determined externally by the presence and absence of claspers, finger-like extensions of the pelvic fins used for copulation (Figure A2.1.7). The life-history stage of an individual was determined through macroscopic examination of all organs and structures used for reproduction and, if present, the neonate/umbilical scar (located between the pectoral fins). Each structure was assessed individually (Table A2.1.1) and life-history stage was determined based on the collection of these assessments (see section *'3.3.3: Life-history stage definitions'* for details). The exception to this was for *in utero* embryos, which were assigned as "prenate". Samples of all tissues and whole reproductive structures (including *in utero* eggs and embryos) were collected from each individual and stored in a tissue archive at $-20^{\circ}C$ for future study.

To examine the extent of variation in the latitudinal distribution between populations, minimum, maximum, and median latitude values for each population were extracted from distributions shown in Figure 3.1.

3.3.3: Life-history stage definitions

Sharks were classified into one of three life-history stages: prenate, immature, and mature.

An individual was classified as mature when they reached sexual maturity, which was defined as having the ability to produce, transport, and fertilise gametes, and, in the case of females, encase fertilised ova and gestate embryos.

For males, individuals were classified as mature when individuals had enlarged, lobular, vascularised testes with negligible epigonal gland tissue; rigid, fully calcified claspers that were longer than the pelvic fin and could be rotated anteriorly, and seminal vesicles with thickened opaque walls (Figure A2.1.1). When available, additional metrics, such as the appearance of the epididymides and vas deferens, were used to assist with determining maturity. In general,

assessments of the testes, seminal vesicles, and claspers were all required to determine maturity. However, there were two exceptions: (1) when only the seminal vesicles (with sperm present) or testes were assessed, as long as claspers were also evaluated; and (2) when only the claspers were assessed, as they are the last reproductive structure to mature in males (Figure A2.2.1). Though sperm may be present and suggest maturity, assessments of the structures that produce and/or transport gametes were needed to sufficiently determine maturity in males.

For females, sexual maturity was reached when oviducal glands were enlarged and heart-shaped and uteri were uniformly enlarged, tubular structures, contained ova or embryos, or distended, flaccid, and potentially vascularised structures (Figure A2.1.2). Ovaries were not part of the main maturity definition as mature females in a resting phase have ovaries similar in appearance to the ovaries of immature females (Nosal et al., 2021; Peres & Vooren, 1991; Figures A2.1.8b and A2.1.8c). Therefore, stating that mature females only have ovaries in a state of vitellogenesis is incorrect and could lead to misidentification. However, ovary condition was used to assist with assigning maturity; ovaries in a state of vitellogenesis were an additional sign of maturity. Assessments of the three structures by themselves were not sufficient to determine sexual maturity, and there was insufficient data to assess potential exceptions based on the timing of structure maturation. The only exception was if individuals were carrying *in utero* ova/eggs or embryos (Figure A2.1.10d and A2.1.10e) or had distended, flaccid, and, potentially, vascularised uteri (indicating a recent pregnancy), which were deemed mature.

An individual was classified as immature if any of the reproductive structures used to determine maturity were deemed immature or maturing and as prenate if the individual was still *in utero* at the time of capture. If data was lacking to sufficiently classify life-history stage, an individual's life-history stage was classified as unknown.

3.3.4: Data standardisation

In this study, different methods of measuring the length of a shark are referred to as "length variants". The global dataset compiled here included 11 length variants (Table 3.2). Fresh total length, measured in a straight-line with the tail in a natural position (fresh, natural, total length), was chosen as the basis for analyses for two primary reasons: (1) the total length captures the full body length, and (2) straight-line lengths with the tail in natural position can be measured from sharks observed in situ (e.g., calibrated stereo video footage).

To convert measurements made using the other 10 length variants to our chosen length variant, a linear model with a natural log-normal error distribution and a model component that related the error standard deviation to the length to explicitly model heteroscedasticity was used (see Chapter 2 for details). In some cases, information describing the measured length variant was incomplete, for example, not specifying whether the tail was in a natural or stretched position. When necessary, missing details were inferred from regional measurement practices (Francis, 2006).

In addition to length variants, the dataset also included life-history stage classifications based on 12 different maturity scales. To convert between life-history stage classifications, a source's life-history stage definitions were compared to the life-history stages defined above and/or Table A2.1.1 and then determined based on this comparison. An individual's life-history stage was classed as unknown when (1) a source's life-history stage definitions did not align with any of the definitions or

exceptions listed above, as the likelihood of the individual's stage being mis-classified was high, or (2) an individual's life-history stage was not assessed.

In some cases, although an individual's maturity stage was classified as unknown, measurements of reproductive structures were recorded. To include these individuals in the analysis, a Bayesian logistic regression was used to convert reproductive measurements into the standardised life-history stage scores. Only measurements of clasper inner length (defined in Table A2.1.2) and testes weight had sufficient data to construct the required models. A description of the logistic regression model, including the rationale for its selection over the generative model described below, along with details on the priors and prior simulations for the clasper inner length and testes weight conversion models, is available in Appendix 2.3.

Table 3.2: *Sources of data for the various school shark populations used in this study. Sample size is the size of the useable data from a source after length and life-history stage data were standardised. Length variant is the length variant(s) present in the source data. Length variants are defined in Appendix 1.1. Year range is the range of years the sharks were captured in. n.d. refers to no date for the source.*

Source	Population	Sample size	Year range	Length variant
Braccini (n.d.) & Braccini et al. (2009)	Australia	758	1993 - 2008	Fresh fork length; Fresh precaudal length; Fresh, stretched, total length
Hernández Muñoz (2013)	Australia	64	2009 - 2010	Fresh, natural, total length
McMillan et al. (2019) & McMillan (n.d.)	Australia	350	2015 - 2019	Fresh precaudal length; Defrosted, natural, total length; Fresh, natural, total length
Walker (2005)	Australia	2960	1973 - 2001	Fresh, stretched, total length
This study	New Zealand	198	2020 - 2023	Defrosted head length; Defrosted, natural, total length; Fresh, natural, total length
Duffy (n.d.)	New Zealand	55	1998 - 2014	Fresh, stretched, total length
Francis et al. (2012)	New Zealand	274	2011	Fresh, stretched, total length
Hernández Muñoz (2013)	New Zealand	301	2009 - 2012	Fresh, natural, total length
Fisheries New Zealand Observer Services (n.d.)	New Zealand	157	2022 - 2024	Fresh head length; Fresh, natural, total length
Ministry for Primary Industries (2024a)	New Zealand	4535	1986 - 2023	Fresh, natural, total length
Afonso & Priester (n.d.)	Northeast Atlantic	42	2019	Fresh, natural, total length, over-the-body

Source	Population	Sample size	Year range	Length variant
Biton-Porsmoguer (n.d.)	Northeast Atlantic	51	2009 - 2021	Fresh, natural, total length, over-the-body
Centre for Environment, Fisheries & Aquaculture Science (n.d.)	Northeast Atlantic	173	1963 - 2021	Fresh, stretched, total length
Capapé et al. (2005)	Northeast Atlantic	96	1970 - 2000	Fresh, stretched, total length
Thorburn (n.d.)	Northeast Atlantic	136		Fresh, stretched, total length, over-the-body
Torres (n.d.)	Northeast Atlantic	95	2013	Fresh, stretched, total length
Fisheries and Oceans Canada (n.d.)	Northeast Pacific	5	2012 - 2019	Fresh, stretched, total length
King (n.d.)	Northeast Pacific	9	2019 - 2022	Fresh, stretched, total length
Nosal (n.d.)	Northeast Pacific	31	2010 - 2020	Fresh fork length; Fresh, stretched, total length
Ripley (1946)	Northeast Pacific	124	1942 - 1944	Fresh, stretched, total length
da Silva (n.d.)	South Africa	1384	1993 - 2022	Defrosted, stretched, dorsal origin to caudal tip length, over-the-body; Fresh, stretched, dorsal origin to caudal tip length, over-the-body; Fresh, stretched, total length, over-the-body
McClusky (1988)	South Africa	7	1986 - 1987	Fresh fork length; Fresh, natural, total length
Theron (2001)	South Africa	72	1998 - 2000	Fresh, natural, total length
Bovcon (n.d.)	Southwest Atlantic	234	2008 - 2023	Defrosted, natural, total length; Fresh, natural, total length; Fresh, stretched, total length, over-the-body
Charvet (n.d.)	Southwest Atlantic	125	1989 - 1992	Fresh, natural, total length
Chiaramonte (2015)	Southwest Atlantic	704	1991 - 1997	Fresh, natural, total length
Elías et al. (2005)	Southwest Atlantic	144	1994 - 2002	Fresh, stretched, total length, over-the-body
Lucifora et al. (2004)	Southwest Atlantic	273	1999 - 2001	Fresh, natural, total length
Peres & Vooren (1991)	Southwest Atlantic	67	1980 - 1986	Fresh, stretched, total length

All measurement standardisation and subsequent analyses were carried out in R and R Studio (Posit team, 2024; R Core Team, 2024). Models were constructed using the brms (Bürkner, 2017) and rstan (Stan Development Team, 2024) packages.

3.3.5: Statistical modelling

3.3.5.1: Uniform-Gaussian model

For the purposes of this study, length at life-history stage transition (i.e., length-at-birth and -maturity), herein referred to as length-at-transition, is defined as the mean length at which the probability of observing each stage is equal (i.e. probability = 0.5).

A novel statistical method, the Uniform-Gaussian Generative Classifier (UGGC), developed by Smith (2025), was applied to estimate length-at-transition. The UGGC classifies observations into two categories, $y \in \{0,1\}$, based on the value of x relative to a transition point (m_{50}). For this study, the two categories are prenate or immature ($y = 0$) and immature or mature ($y = 1$) for length at birth and maturity, respectively. Furthermore, the transition point is either length at birth or maturity. This UGGC model fits a mixture of a uniform distribution and a scaled half-Gaussian distribution to x. For $x|y = 0$, the model fits a uniform distribution between a specified lower truncation value up to a value μ_0; above μ_0 the model fits a half-Gaussian distribution. Similarly, for $x|y = 1$, the model fits a uniform distribution from a specified upper truncation value down to a value μ_1; below μ_1 the model fits a half-Gaussian distribution.

More specifically, the plateau distribution is described by the following unnormalised probability density functions (PDF, adapted from Lau & Krumscheid, 2022) for x given y:

$$f(x_i|y_i = 0, \mu_0, \sigma, L) = \begin{cases} 0 & \text{if } x_i < L \\ 1 & \text{if } L \le x_i \le \mu_0 \\ \exp\{-\dfrac{(x_i - \mu_0)^2}{2\sigma^2}\} & \text{if } x_i > \mu_0 \end{cases}$$

$$f(x_i|y_i = 1, \mu_1, \sigma, U) = \begin{cases} \exp\{-\dfrac{(x_i - \mu_1)^2}{2\sigma^2}\} & \text{if } x_i < \mu_1 \\ 1 & \text{if } \mu_1 \le x_i \le U \\ 0 & \text{if } x_i > U \end{cases}$$

where μ_0 and μ_1 are the means of the two half-Gaussian distributions, respectively; σ is the standard deviation of the two half-Gaussian distributions; L and U are the lower and upper truncation bounds, respectively.

The overall likelihood contribution of each observation is:

$$\text{loglikelihood for } y_i = 0: \quad \log\big(f(x_i|y_i = 0)\big) - \log(C_0)$$

$$\text{loglikelihood for } y_i = 1: \quad \log\big(f(x_i|y_i = 1)\big) - \log(C_1)$$

where C_0 and C_1 are normalization constants that ensure that the unnormalised densities of each category integrate to 1:

$$C_0 = \sqrt{2\pi} \cdot \sigma/2 + (\mu_0 - L)$$

$$C_1 = \sqrt{2\pi} \cdot \sigma/2 + (U - \mu_1)$$

When fitting the model, the parameters μ_0 and μ_1 of m_{50} and d satisfy:

$$\mu_0 = m_{50} - \frac{d}{2}, \quad \mu_1 = m_{50} + \frac{d}{2}$$

such that m_{50} is the mid-point between μ_0 and μ_1, and represents the estimated length-at-transition; and d is the difference between μ_0 and μ_1.

A hierarchical version of this model was applied to allow the parameter of interest, m_{50}, to vary for population j , as follows:

$$m_{50,j} \sim \mathcal{N}(m_{50}, \sigma_\alpha)$$

where σ_α is the standard deviation of the population transition points.

3.3.5.2: Estimating length-at-transition

The hierarchical UGGC model variant was applied here to estimate the length at which male school sharks attain maturity in six globally distributed populations. Unfortunately, there was insufficient data to model length-at-maturity for the seventh population, the Southeast Pacific, as only two individuals had useable data, and total lengths and external clasper measurements could not be extracted from the provided images. Priors for the model parameters m_{50}, d, σ, and σ_α were based on prior simulations (Figure A2.4.1), with code adapted from (Wesner & Pomeranz, 2021). The mean of the m_{50} parameter prior was based on the median of the range of length-at-maturity reported for male school sharks in the literature. The priors used for modelling length-at-maturity for male school sharks were as follows:

$$\begin{aligned} m_{50} &\sim \mathcal{N}(1275,50) \\ d &\sim \mathcal{N}(0,100) \\ \sigma &\sim \mathcal{N}^+(0,50) \\ \sigma_\alpha &\sim \mathcal{N}^+(0,50) \end{aligned}$$

The lower and upper truncation values were chosen as:

$$\begin{aligned} L &= 1025 \\ U &= 1525 \end{aligned}$$

The diagnostics of the model are available in Appendix 2.4.

Posteriors of male length-at-maturity at the species level and for each population were summarised as point estimates (i.e., the mean of the posterior distribution) with associated standard deviations and 95% credible intervals. The variation in male length-at-maturity among

populations was assessed by examining the estimate of σ_{α}. Differences in length-at-transition between populations were estimated by examining the posterior distribution of the difference between the estimates of m_{50} for the two populations being compared.

A Pearson correlation coefficient between length-at-maturity estimates and the median latitude of each population was calculated to examine if there was a latitudinal gradient in the length-at-maturity estimates.

The hierarchical UGGC model variant was also used to estimate length-at-birth and female length-at-maturity for school sharks. However, since there was sufficient data around the point at transition for only three populations, though not the same three in each case, estimates of length-at-birth and female maturity further are not discussed further due to a lack of data from other populations. In Appendix 2.5 (female length-at-maturity) and Appendix 2.6 (length-at-birth), the priors and truncation values for the estimation of these two life-history parameters are provided. Moreover, estimates of length-at-birth and female length-at-maturity for populations where parameters could be modelled, as well as possible transition points for populations that could not be modelled, are also available in these supplementary text.

3.4: Results

A total of 2,791 male school sharks from six populations were included in the analysis of the length-at-maturity for school sharks. Data imbalance between immature and mature life-history stages varied across populations, with the maximum immature length varying between 1361-1440mm TL (fresh, natural, total length; defined in section '*3.3.4: Data standardisation*'), and minimum mature length varying between 1105-1225mm TL (Figure 3.2). For some populations, school sharks were captured using diverse gears, spatial scales, and months, whereas in other populations, captures were more restricted to specific months, gears, and/or locations (Figures 3.3a and 3.3b). Additionally, while there was some temporal overlap in school shark captures across populations, certain populations were predominantly sampled during specific time periods (Figures 3.3a and 3.3b).

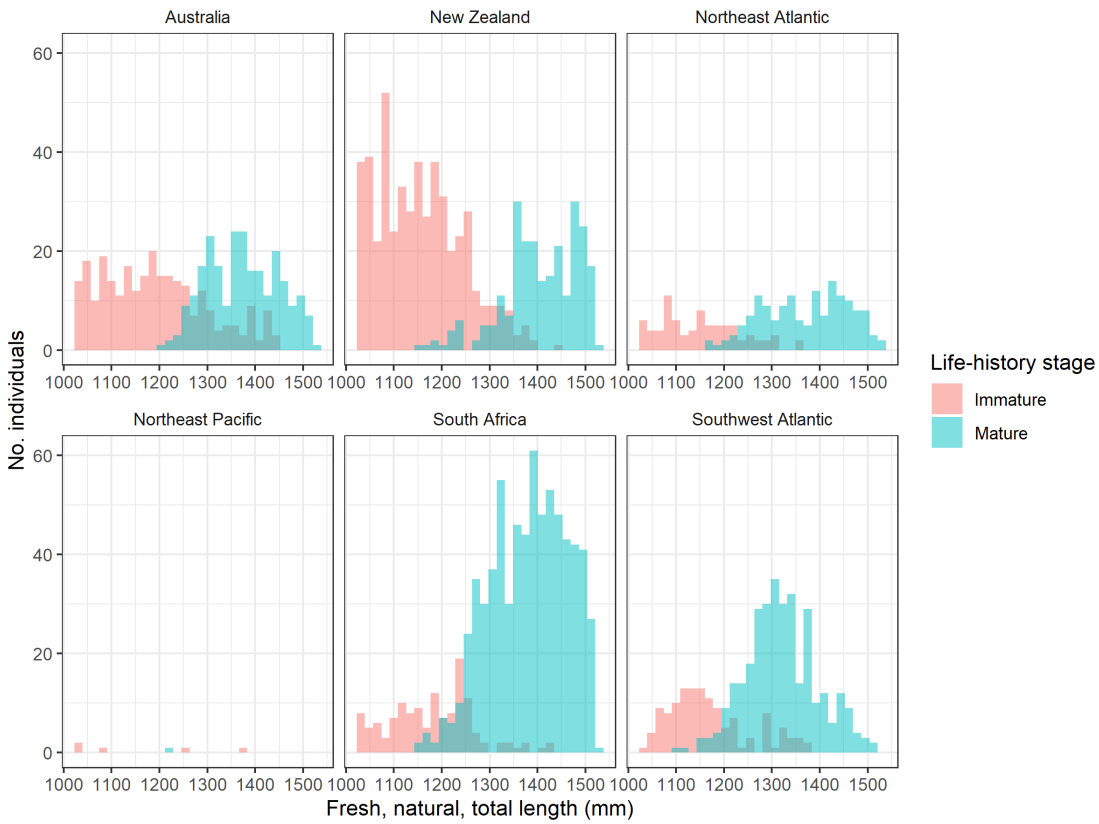
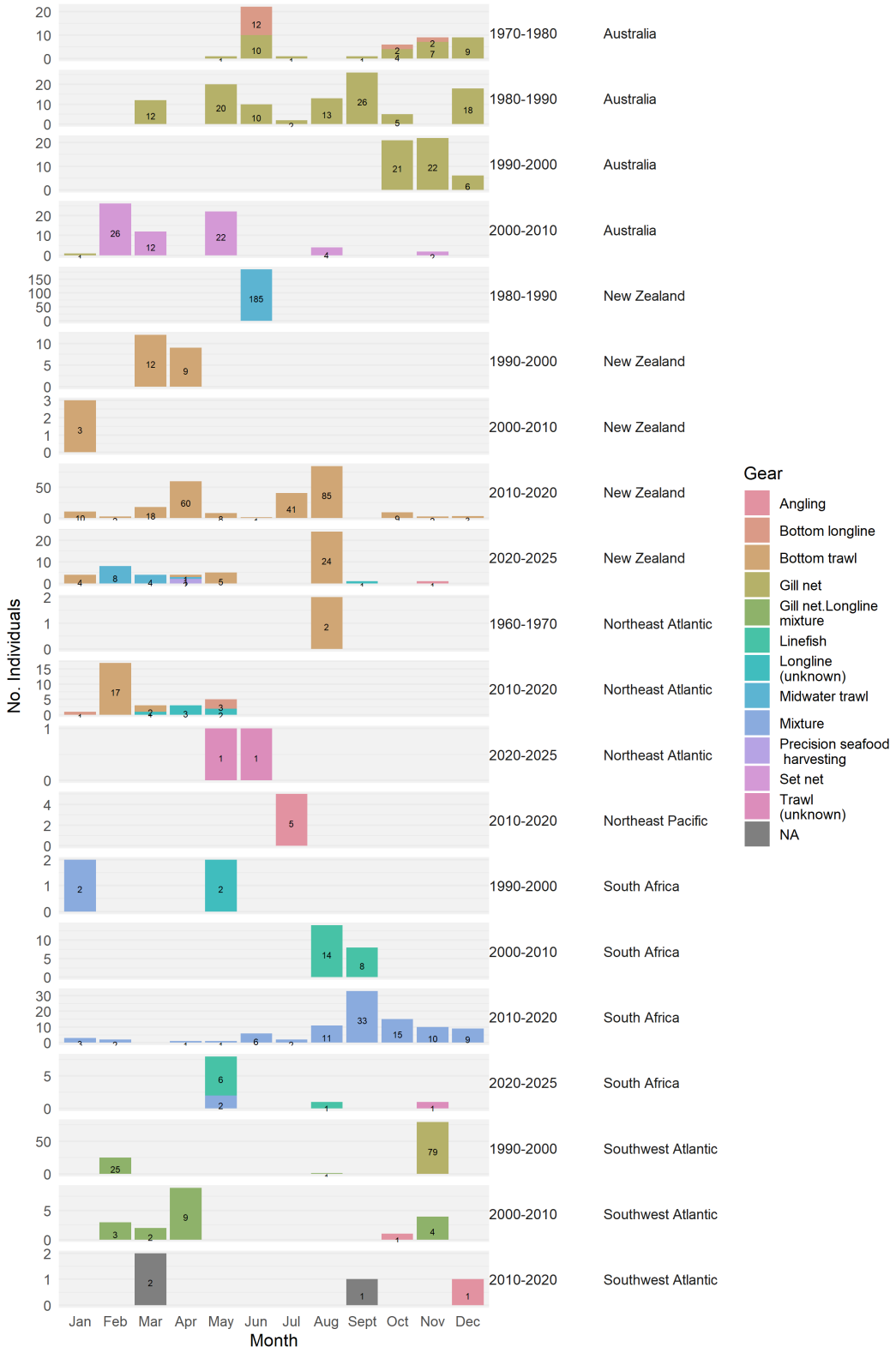
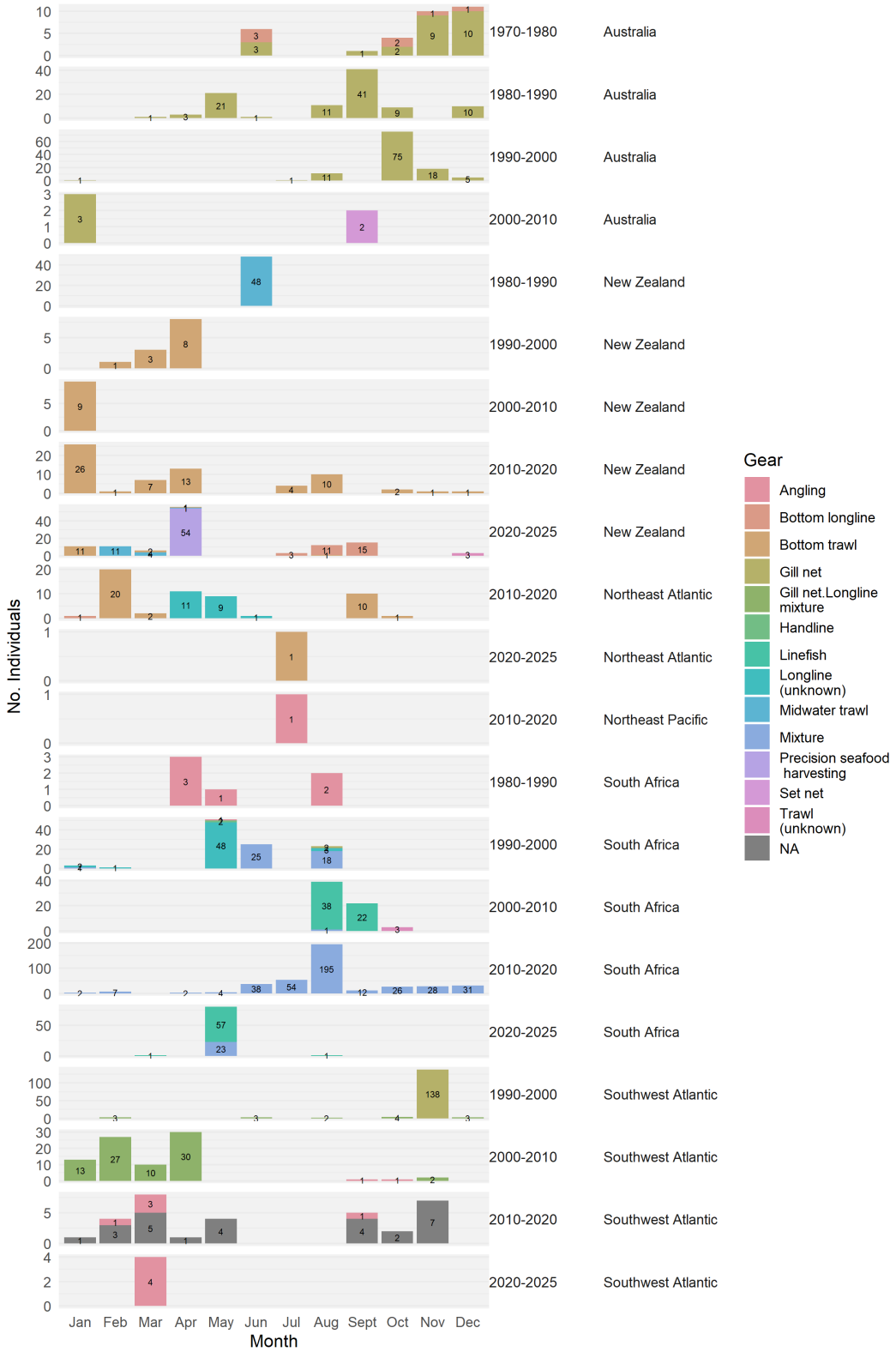


Figure 3.2: *Distribution of lengths of immature and mature male school sharks for each population, within the truncation bounds. Fresh, natural, total length is the total length measured in a straight line from a fresh animal, with the tail in a natural position.*


No. Individuals
Month
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sept
Oct
Nov
Dec
1970-1980
Australia
1980-1990
Australia
1990-2000
Australia
2000-2010
Australia
1980-1990
New Zealand
1990-2000
New Zealand
2000-2010
New Zealand
2010-2020
New Zealand
2020-2025
New Zealand
1960-1970
Northeast Atlantic
2010-2020
Northeast Atlantic
2020-2025
Northeast Atlantic
2010-2020
Northeast Pacific
1990-2000
South Africa
2000-2010
South Africa
2010-2020
South Africa
2020-2025
South Africa
1990-2000
Southwest Atlantic
2000-2010
Southwest Atlantic
2010-2020
Southwest Atlantic
Gear
Angling
Bottom longline
Bottom trawl
Gill net
Gill net.Longline mixture
Linefish
Longline (unknown)
Midwater trawl
Mixture
Precision seafood harvesting
Set net
Trawl (unknown)
NA

a) Immature



b) Mature

Figure 3.3: *Number of male school sharks captured per gear type, month, and time period in each population.*

At the species level, male length-at-maturity for school sharks was estimated at 1273mm TL, on average (Figure 3.4). The estimate of σ_α suggests that population-specific estimates of male length-at-maturity typically deviated from the species level estimate by 33mm TL, on average (Table A2.4.1). Alternatively, that 95% of the population-specific estimates were expected to occur with 66mm TL (i.e., $\pm$ 2 standard deviations) of the species level estimate. Point estimates (i.e., the mean of the posterior distribution of estimates) of male length-at-maturity for each population varied between 1238 mm TL and 1306 mm TL (Figure 3.4, Table 3.3). Pairwise differences between population estimates range from 7mm (New Zealand vs South Africa) to 68mm TL (Australia vs Southwest Atlantic), with most populations differing from one another by at least 19mm TL (Figure 3.5). The posterior distributions for the differences in length-at-maturity between the New Zealand and South African populations, as well as the Northeast and Southwest Atlantic populations, partially overlapped zero (Figure 3.5). However, estimates still suggested that the South African population matured at a larger length than the New Zealand population 76.8% of the time and that the Northeast Atlantic population matured at a larger length than the Southwest Atlantic population 92.6% of the time (Figure 3.5). Differences between the Northeast Pacific and the other populations were not calculated due to high uncertainty in its length-at-maturity estimate resulting from small sample sizes.

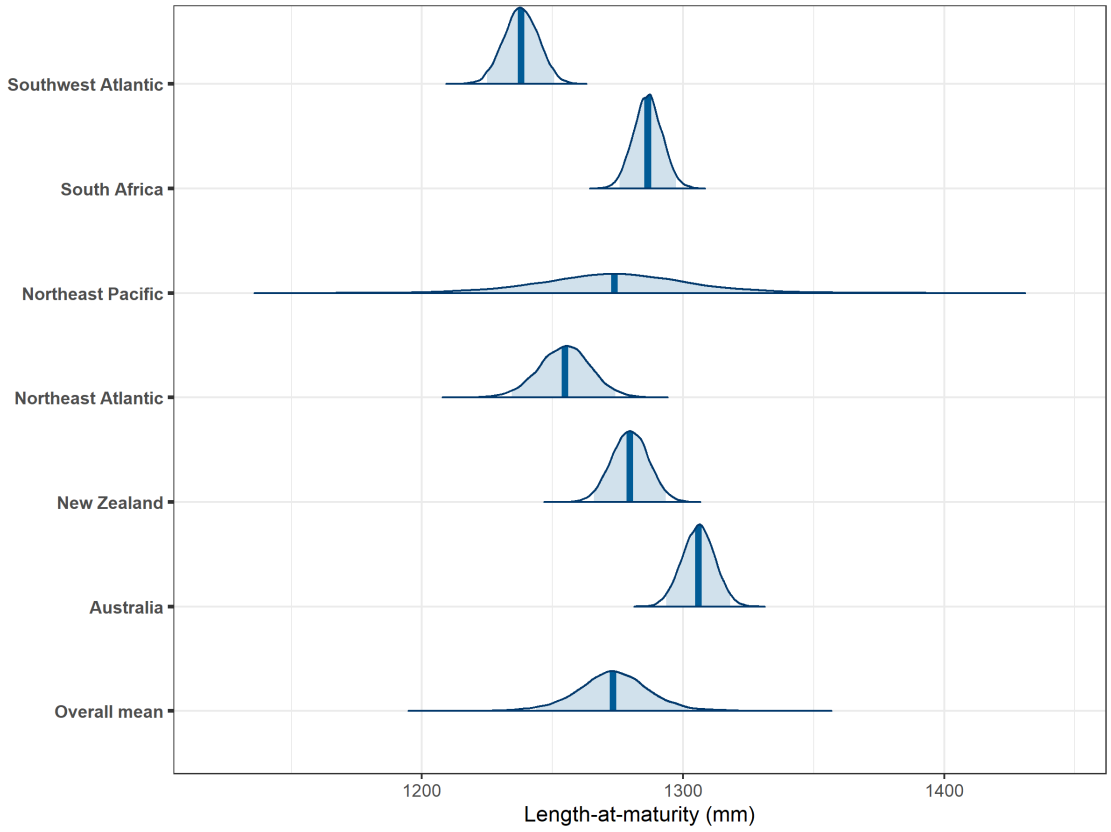


Figure 3.4: *The overall/species level and population-specific posteriors of the length-at-maturity for male school sharks. Solid lines indicate the point estimates of length-at-maturity. The light blue shading under the curve visualises the 95% credible interval of the length-at-maturity estimate.*

Table 3.3: *Point estimates of length-at-maturity (mm TL; ± standard deviation, SD) for male school sharks for each of the modelled populations.* LCI_{95} *is the lower bound of the 95% credible interval.* UCI_{95} *is the upper bound of the 95% credible interval. Maturity length range is the total length range (mm, fresh, natural, total length) of mature individuals from the datasets received for each population for this study.*

Population	Length-at-maturity (±SD)	LCI_{95}	UCI_{95}	Maturity length range
Australia	1306±6	1294	1318	1205 - 1678
New Zealand	1280±7	1266	1293	1155 - 1680
Northeast Atlantic	1255±10	1234	1274	1166 - 1694
Northeast Pacific	1274±29	1215	1333	1225 - 1918
South Africa	1286±6	1276	1297	1151 - 1899
Southwest Atlantic	1238±7	1225	1251	1105 - 1551

When comparing estimates of length-at-maturity for male school sharks from this study to those reported in literature, most of the estimates from this study lay outside the ranges or confidence intervals of earlier studies (Tables 3.1 and 3.3). The only exceptions were for the New Zealand and Australian populations, where the estimates or credible intervals from this study fell within the previously reported ranges (New Zealand) or estimated confidence intervals (Australia; Tables 3.1 and 3.3).

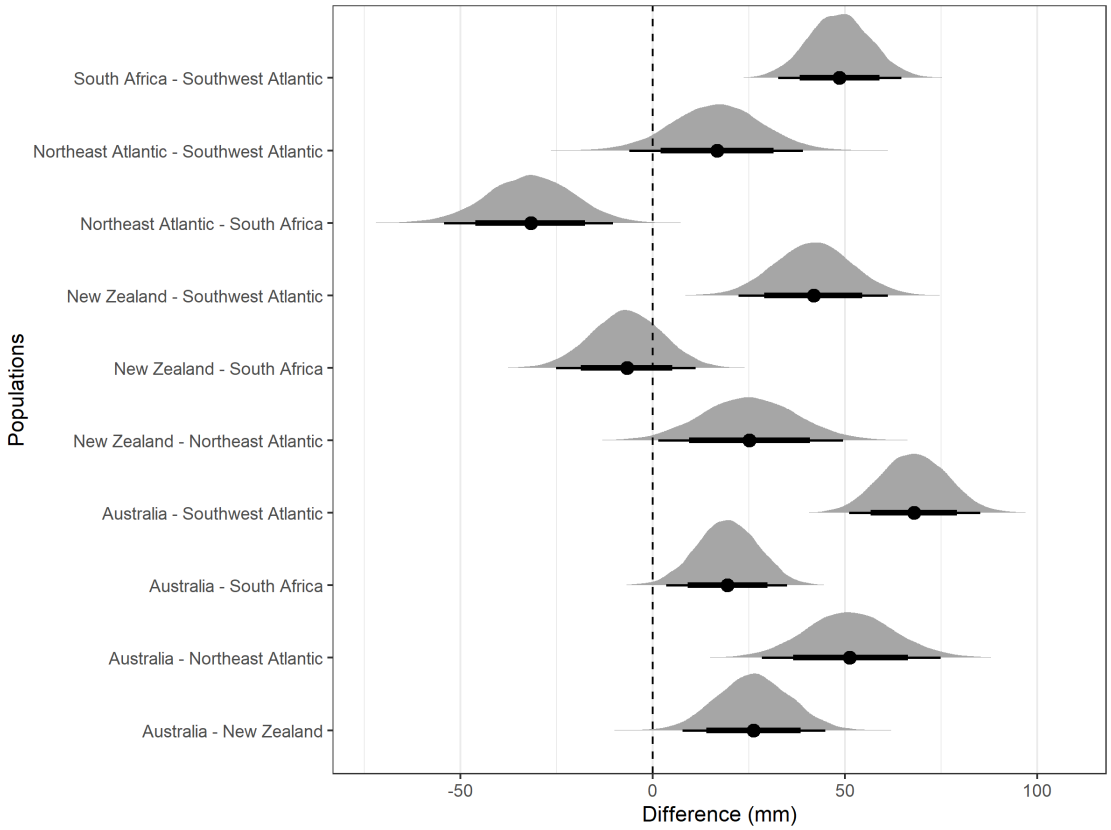


Figure 3.5: *Posterior distributions of the differences in length-at-maturity for male school sharks between pairs of populations. The points are the average difference between populations, the thicker lines are the 80% credible intervals, and the thinner line are the 95% credible intervals.*

There was a weak, negative correlation between the estimated length-at-maturity for male school sharks and the median latitude of the populations (-0.36, Figure 3.6). In addition, we note the large overlap in the latitudinal ranges among the populations (Figure 3.6).

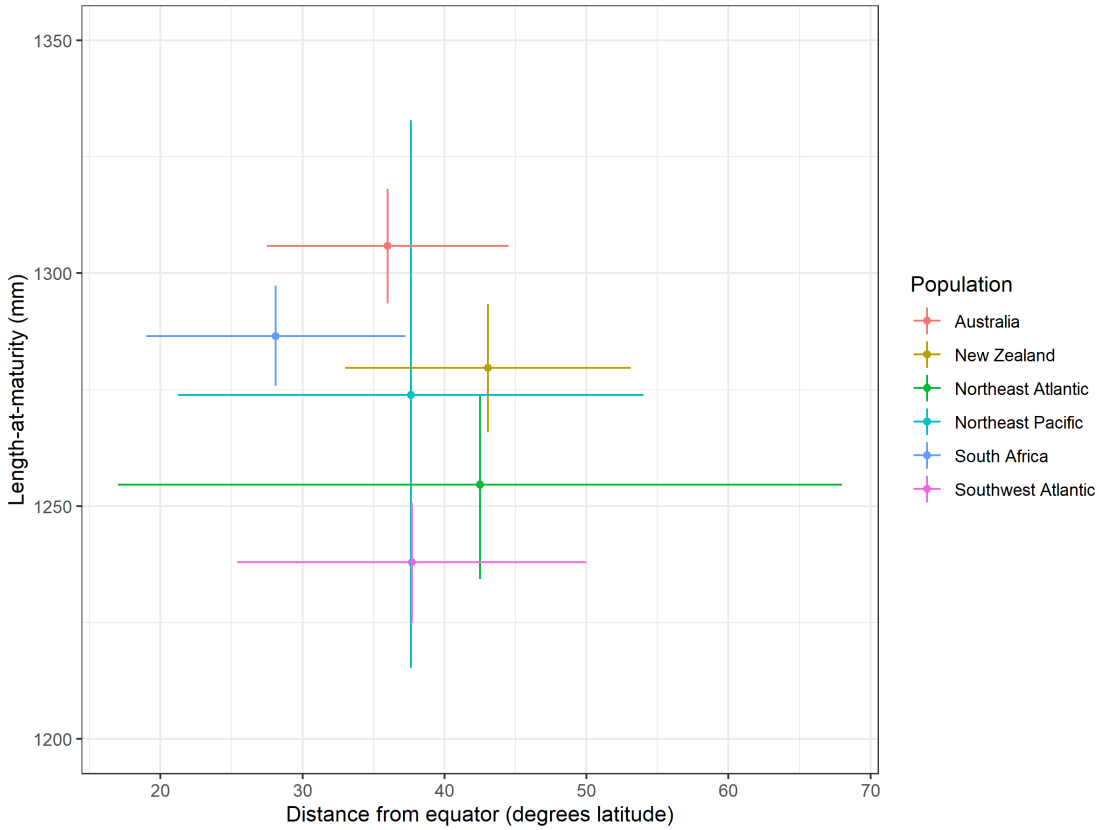


Figure 3.6: *Length-at-maturity for male school sharks vs latitude. The points for latitude are the median latitude of the population. The horizontal lines show the latitudinal range of each population. The vertical lines are the 95% credible intervals of the length-at-maturity estimates.*

3.5: Discussion

Estimating the lengths at which animals transition from one life-history stage to another poses myriad challenges due to non-representative data, the use of different methods to measure or assess biological traits, and statistical models that are sensitive to class imbalance (e.g., Cramer, 1999; Francis, 2006; Rufener et al., 2021). To address some of these challenges, this study compiled data from multiple school shark populations across various sources, and applied novel methods to standardise length and life-history stage data that were measured or assessed by different methods. Additionally, a new generative classifier model was used, designed to be non-sensitive to class imbalance and limit the influence of data away from the transition zone, which are known issues with commonly used deterministic classifiers (e.g., logistic regression) and standard generative models (Cramer, 1999; Efron, 1975; Oommen et al., 2011). Furthermore, the hierarchical version of the generative model leveraged data from multiple populations compiled from across the globe to offer new insights into inter-population variation in maturity and length at birth for school sharks. Unlike previous studies that relied on comparisons of published estimates, our approach directly modelled variation among populations. Notably, this method also allowed us to generate the first estimates of these parameters that were previously unknown for some populations, such as New Zealand. For data-limited populations, the hierarchical framework produced reasonable estimates by borrowing strength from global data, and these estimates are made with an appropriate level of uncertainty given the global population. While the new generative

model is yet to be formally tested against alternatives, this work is underway, and we are confident that the model used here represents the best available option for the present study.

Our results present the first global study that estimates inter-population differences in length-at-maturity for male school sharks. Based on the estimated standard deviation of the population transition points (σ_α), 95% of the population-specific estimates of male length-at-maturity were expected to occur within 66mm TL (fresh, natural, total length; defined in section '*3.3.4: Data standardisation*') of the species level estimate (Figure 3.4, Table A2.4.1). Population-specific point estimates ranged from 1238mm and 1308mm TL (Figure 3.4, Table 3.3), with most populations differing from one another by at least 19mm TL (Figure 3.5). Although estimates for the New Zealand and South African populations, as well as the Northeast and Southwest Atlantic populations, showed some similarity (Figure 3.5), estimates of the South African and Northeast Atlantic populations were predominantly larger than the New Zealand and Southwest Atlantic populations, respectively (Figure 3.5). Estimates for the Northeast Pacific population were accompanied with high uncertainty, preventing meaningful comparisons with the other populations (Figure 3.4). The geographic variation in estimates of length-at-maturity for males suggests that population-specific life-history parameters may be necessary for the management of school sharks.

When compared with previous studies, the estimates of male length-at-maturity from this study generally lay outside the reported ranges or confidence intervals for most populations, except for New Zealand and Australia (Tables 3.1 and 3.3). These differences likely reflect variation in data representativeness and the statistical models applied. While some of the data used in earlier studies were incorporated here (Tables 3.1 and 3.2), this study drew on data spanning broader spatio-temporal scales for each population (Figure 3.3; Table 3.2), rather than relying on localised datasets. Most previous studies reported only ranges of length-at-maturity for male school sharks, and those that produced modelled estimates typically applied logistic regression to limited and/or imbalanced datasets (Table 3.1). By contrast, the hierarchical generative model used here was not only less sensitive to the known issues with logistic regression but also partially pooled population-specific estimates towards the global mean, with data-poor populations experiencing greater shrinkage towards the global mean to provide reasonable estimates. However, since the data used in this study were collected across multiple decades, including periods before and after population collapses (Figure 3.3; Table 3.2), temporal variation could also be contributing to the observed differences between estimates from this and previous studies. Similar temporal effects on maturity estimates have been previously reported for school sharks (Walker, 2005) and gummy sharks (*Mustelus antarcticus*; Walker, 2007).

It has been proposed that, with increasing latitude, elasmobranchs have slower growth rates, larger maximum lengths, and attain maturity at larger lengths and older ages (e.g., Blackburn et al., 1999; Lombardi-Carlson et al., 2003; Rochowski et al., 2015). Within each population, school sharks are generally exposed to a range of different conditions due to their migratory nature (Blackburn et al., 1999; De Wysiecki et al., 2022; Thorburn et al., 2019; Chapter 5). However, young juveniles (<3 years) are confined to particular local conditions for prolonged periods, due to their limited dispersal abilities and/or residency in nursery or important non-nursery habitats, which can influence their growth in length and condition (Hurst et al., 1999; McAllister et al., 2015; McMillan et al., 2021; Chapter 4). If juveniles grow slower or faster in a particular region, and that region is a major contributor to the recruitment to the population, the population could have a larger or

smaller attainment of maturity, respectively. Therefore, if the regions that contributed the most juveniles to each population varied in latitude, a latitudinal gradient in attainment at maturity may be possible. Yet, no evidence of a relationship between latitude and length-at-maturity for male school sharks; although a weak negative correlation existed, the substantial overlap in the latitudinal ranges among populations (Figure 3.6) suggests that a latitudinal gradient in length-at-maturity is likely absent. However, given the inter-population differences observed here, some regions may have more favourable conditions than others. Variation in local conditions has been attributed to geographic variation in life-history parameters for other elasmobranchs (e.g., Bradley et al., 2017; Branstetter, 1990; Carlson & Baremore, 2003; Di Battista et al., 2007). Therefore, differences in juvenile growth and recruitment contributions within and among populations clearly warrant further study.

Geographic variation in attainment of maturity for elasmobranchs may be due, in part, to density-dependent effects, which may vary among populations with different levels of fishing pressure (e.g., Carlson & Baremore, 2003; Cassoff et al., 2007; Farrell et al., 2010). Some have suggested that the remaining individuals of heavily fished populations may have faster growth rates, resulting in a decrease in the attainment of maturity (e.g., Bradley et al., 2017; Devine et al., 2012; Sharpe & Hendry, 2009; Walker et al., 2021). However, in many studies, it is unclear whether the differences attributed to fishing pressure are truly density-dependent responses or a result of methodological limitations, such as non-representative data caused by gear selectivity (Walker et al., 1998; Walker, 2005, 2007). To examine whether fishing pressure has influenced life-history parameters (e.g., growth and attainment of maturity), comparisons before and after exploitation, or between fished and unfished states, are required. In our study, the data that was used was collected over a long time period (61 years), including before and after populations collapsed but, unfortunately, not before populations were exploited. Therefore, the extent to which fishing pressure is contributing to the geographic variation in attainment of maturity for male school sharks remains uncertain. Other anthropogenic factors, such as climate change or broader temporal effects (e.g., Walker, 2007), may also play a role in the observed differences, but again, these were beyond the scope of this study.

Age-at-maturity is also a key parameter for estimating population parameters, in some cases more informative than length-at-maturity (e.g., Au et al., 2008; Petersma et al., 2024). In this study, age-at-maturity could not be directly estimated due to insufficient data on the ages of individuals. For school sharks, growth parameters have been estimated for several populations, where some populations have multiple estimates (Table A2.7.2). However, there were differences in data representativeness and methods used to measure lengths and assign ages to individuals between growth studies (Table A2.7.3 and Table A2.7.4). Moreover, the growth models that were used to estimate the growth parameters in these studies were sensitive to unrepresentative data (Table A2.7.1; Francis & Francis, 1992; Thorson & Simpfendorfer, 2009; Walker et al., 1998), resulting in apparent differences in growth parameters between populations (Walker et al., 1998). If these population-specific growth parameters were used to calculate age-at-maturity for school sharks from the estimates of length-at-maturity, the observed variation (e.g., Figure A2.7.1) would likely stem from methodological inconsistencies instead of true inter-population differences. The effect that artefacts of the methodology can have on growth parameter estimation highlights the importance of critically assessing how growth parameters were calculated before use and, where

possible, estimating age-at-maturity directly (Braccini et al., 2015; Cortés, 2004). Moreover, further study is required to better estimate the true variation of growth parameters and age-at-maturity among school shark populations.

To facilitate global comparisons of life-history parameters, it would be advantageous for researchers and institutions to standardise the methods by which they measure life-history traits. This would include moving towards more deterministic criteria for assigning life-history stage and age and agreeing on a "gold standard" method for measuring length for each species. For life-history stage classification, it is recommended that reproductive structures are assessed individually and then life-history stage is assigned based on the criteria that were used in this study. If age is to be assigned by vertebral band counts, band deposition rates before, during, and after sexual maturation for each sex should be validated and considered when assigning an age of an individual (e.g., Walker et al., 2001).

Determining whether population-specific life-history parameters are necessary is crucial for the effective management of elasmobranchs. In the first study of its kind, data collected from school shark populations around the world were compiled and standardised, and a novel generative classifier model was used to estimate the extent of inter-population variation in the life-history stage transitions of male school sharks. Our findings suggest that length-at-maturity for male school sharks varied between 1238 and 1308mm (fresh total length, measured in a straight line, with the tail in a natural position) and differed among all six of the modelled populations. Although the drivers of the observed variation could not be determined, population-specific length-at-maturity estimates for male school sharks are necessary for the ongoing management of populations. To improve the accuracy of life-history parameter estimation and geographic variation assessments, researchers need to improve the representativeness of sampling methods, standardise data that were measured or assessed with different methods before use, and apply models that are less sensitive to unbalanced datasets.

Chapter 4: Extent of geographic variation in the growth of juvenile school sharks

4.1: Abstract

Variation in life-history traits has predominantly been studied between rather than within elasmobranch populations, despite intra-population variation playing a key role in shaping a population's life-history traits and subsequent management. A new vertebral band counting technique (image stacking) and novel Bayesian models were used to investigate whether rates of somatic (increase in body length with age) and hepatosomatic growth (increase of energy stores in the liver with age) varied between regions of importance to the early life-history of school sharks (*Galeorhinus galeus*), namely the Canterbury Bight, Kaipara Harbour, Kapiti Coast, and Tasman and Golden Bays. Somatic and hepatosomatic growth for school sharks from the Kapiti Coast could not be analysed due to insufficient data. While there was little difference in somatic growth among the Canterbury Bight, Kaipara Harbour, and Tasman and Golden Bays, individuals from the Canterbury Bight were generally in a better body condition compared to those in the other two regions. However, further work is needed to confirm the patterns observed in this study.

4.2: Introduction

Variation in life-history traits, such as length- and age-at-maturity, among populations of the same species has been observed in many chondrichthyans (e.g, Lombardi-Carlson et al. (2003); Neer & Thompson (2005); Chapter 3). Yet, few studies have examined the extent of trait variation within populations (e.g., Di Battista et al., 2007; Francis, 1997; Walker et al., 1998) despite various factors influencing life-history traits at different scales (Blackburn et al., 1999; Bradley et al., 2017; Devine et al., 2012; Visser & Gienapp, 2019). Intra-population variation in life-history traits can occur when, during specific life-history stages, a species segregates into a few distinct geographical areas, creating temporary subpopulations. If these areas differ in terms of the quality and quantity of important habitats and food resources, as well as environmental conditions, then these subpopulations may differ with respect to important traits, such as rates of somatic growth (increase in body length with age) and hepatosomatic growth (increase of energy stores in the liver with age) (Di Battista et al., 2007; Dmitriew, 2011; Heithaus, 2007; Lyons et al., 2020; Weideli et al., 2019; Yates et al., 2012). Thus, the population may comprise of sets of individuals that can be different in terms of their length-at-age, overall health, and resilience to pressures, resulting in areas having differential importance to the health and productivity of the overall population (Benard & McCauley, 2008; Lyons et al., 2020; Yates et al., 2012; Chapter 3). Areas can vary not only in terms of their quality, but also in terms of size, thereby varying the contribution in terms of overall numbers of individuals to the population (Beck et al., 2001; Heithaus, 2007). A large area that has a relatively poor-quality habitat might be important to the overall population by providing large numbers of relatively poorly provisioned individuals, especially during times when conditions are generally favourable for the species. Indeed, the contributions of different areas may vary over time. In some years, conditions may be more or less favourable in particular areas due to annual

climate variability or local disturbances (Schlaff et al., 2014). Having several areas contributing to the population may increase long-term stability and resilience at the population level, a phenomenon known as the "portfolio effect" (Figge, 2004; Yates et al., 2012). The contributions of geographically separate temporary subpopulations to the long-term persistence of a population are dynamic and complex. Fully understanding these dynamics is difficult, requiring long-term datasets from multiple geographical areas. Yet, failure to account for intra-population variation can limit our ability to manage populations effectively.

School sharks (*Galeorhinus galeus*) are a globally distributed, migratory species that has apparent inter-population differences in growth rate across their life-history (Table A2.7.2). However, the extent of intra-population variation in somatic and hepatosomatic growth has yet to be examined, despite juvenile school sharks being observed to prioritise growth and reside in various nursery and important non-nursery areas for up to two years, resulting in rapid growth in periods of prolonged exposure to local conditions (McAllister et al., 2015; McMillan et al., 2021; Olsen, 1954; Stevens & West, 1997). In New Zealand, juvenile school sharks have rapid growth, limited dispersal abilities, and potentially reside in one of several areas of importance in the first few years after birth (Blackwell & Francis, 2010; Francis, 2010; Francis et al., 2012; Francis & Mulligan, 1998; Hurst et al., 1999; Tindale Marine Research Charitable Trust unpublished data), although little is known about the biology of school sharks in New Zealand, especially juveniles. The New Zealand population presents a useful opportunity to study the biology of school sharks as, unlike other school shark populations around the globe, the New Zealand population is largely stable (Finucci et al., 2019; Tremblay-Boyer, 2021; Walker et al., 2020). To help ensure the ongoing stability of the New Zealand school shark population, and potentially assist with the recovery of the other populations, there is a need to confirm whether somatic and hepatosomatic growth of juvenile school sharks vary between several habitats of likely importance.

Using a novel ageing methodology and hierarchical Bayesian models, the aim of this study is to estimate the somatic and hepatosomatic growth for juvenile school sharks in New Zealand. More specifically, the study examines the extent to which somatic and hepatosomatic vary between males and females, as well as regions of likely importance to juvenile school sharks.

4.3: Methods

4.3.1: Study areas

For the purposes of this study, regions were selected based on their likely importance to the early life-history of school sharks (based on repeated observations of newborns, young juveniles (0-3 years), and pregnant females) and the degree of spatio-temporal connectivity of juveniles between regions. The Kaipara Harbour, Kapiti Coast, Tasman and Golden Bay, and the Canterbury Bight (Figure 4.1) were selected as newborns, young juveniles, and pregnant female school sharks have been observed in these regions over multiple years (Coxon, 2018; Hernández Muñoz, 2013; IUCN SSC Shark Specialist Group, 2024c, 2024a; Morrison, Lowe, et al., 2014; Paul & Bradford, 2000; Chapter 6; A. Burton unpublished data; C. Duffy unpublished data; Tindale Marine Research Charitable Trust unpublished data; M. Griffiths personal observations; M. Cryer personal observations). Furthermore, mark-recapture data has shown no evidence of connectivity between the regions until individuals reach c. ~ four years old (Francis, 2010; Hurst et al., 1999; Chapter 5; Tindale Marine Research Charitable Trust unpublished data); the lack of connectivity is likely due to

the long distances between regions and oceanographic features, such as the Cook Strait, restricting dispersal. Golden and Tasman Bays were treated as one region as there are possibly multiple important habitats contained in each bay, and individuals around two years old can traverse between these two bays (Francis, 2010; Hurst et al., 1999; Chapter 5).

The Kaipara Harbour (Figure 4.1) is a large estuarine harbour containing a wide variety of inter- and sub-tidal habitats important to the life-history of many species, including rig (*Mustelus lenticulatus*), bronze whaler (*Carcharhinus brachyurus*), smooth hammerhead (*Sphyrna zygaena*), and white (*Carcharodon carcharias*) sharks (Francis et al., 2012; Hewitt & Funnell, 2005; IUCN SSC Shark Specialist Group, 2024b; Morrison, Lowe, et al., 2014; A. Burton unpublished data). The Kaipara receives water input from multiple waterways in its catchment where land is primarily used for agriculture (Morrison, Lowe, et al., 2014).

The Kapiti Coast (Figure 4.1) is a section of coast consisting of mud and sand sediment and an offshore island that has a complex hydrodynamic system of currents (Bostock et al., 2019; Stevens et al., 2021). This region is influenced and supplied with nutrients via the D'Urville Current as well as multiple waterways which allow the region to support many species including providing possible reproductive habitats for the New Zealand carpet (*Cephaloscyllium isabellum*) and smooth hammerhead sharks (iNaturalist, 2024a; Stevens et al., 2021; Stevens & Forrest, 2019).

Tasman and Golden Bays (Figure 4.1) are a pair of gradually shoaling bays that consist of mud and sand sediment, as well as a range of biogenic habitats, that provide essential habitat for a variety of species including carpet and rig sharks as well as the New Zealand rough skate (*Zearaja nasuta*) (Bostock et al., 2019; iNaturalist, 2024b; IUCN SSC Shark Specialist Group, 2024c; Jones et al., 2016). Both bays receive water input and nutrients via the D'Urville Current as well as multiple waterways in the catchment, which flow through a mixture of vegetation, agriculture, and urban areas (Newcombe, 2016; Zeldis & Swaney, 2018).

The Canterbury Bight (Figure 4.1) is a large section of coast that primarily consists of sand and gravel and is influenced and supplied with nutrients from the Southland Current as well as multiple rivers within alpine and agriculturally dominated catchments (Bostock et al., 2019; Environment Canterbury, 2024; Leckie, 2003; Stevens et al., 2021). The region is able to support essential habitats for a range of species including elephantfish (*Callorhynchus milii*), southern spiny dogfish (*Squalus acanthias*), carpet sharks, and rough skates (Francis, 1997; iNaturalist, 2024c; IUCN SSC Shark Specialist Group, 2024a; Jones et al., 2016; Morrison, Jones, et al., 2014).

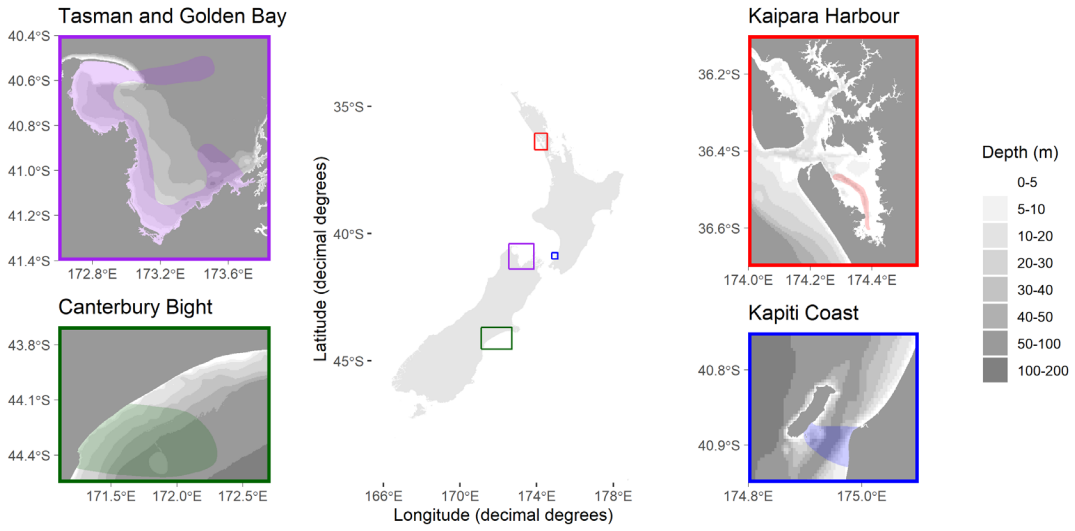


Figure 4.1: *Map of the regions sampled for juvenile school sharks. Shaded areas in each region represent the areas from which school sharks were sampled.*

4.3.2: Specimen collection

To examine the variation in somatic and hepatosomatic growth, individuals up to 1000mm total length were collected from across the four regions between 2020 and 2023, either during dedicated research surveys or via opportunistic sampling. An upper length restriction on sampling in target regions was used to ensure the capture of 0-3 year old sharks, which are the age classes that are typically range-restricted and have been reported as large as 1000mm total length (Moulton et al., 1992). Additional specimens captured in New Zealand's exclusive economic zone during the sampling period were used to develop ageing methods and train vertebral band count readers. Where possible, specimens were measured, sexed, weighed, and had life-history stage assessed (males only via clasper maturity assignment as defined in Table A2.1.1) immediately after capture. Specimens were frozen whole at -20°C shortly after capture and then defrosted prior to post-mortem.

During post-mortems, numerous external and internal morphometric measurements (including several variants of total length; see Appendix 1.1), sex, life-history stage, and total body, liver, and stomach weights were recorded. All measurements were recorded to the nearest mm, where possible and, failing that, to the nearest 5mm. Weights were measured to the nearest gram. Life-history stage was determined according to criteria described in section *'3.3.3: Life-history stage definitions'* of Chapter 3.

A sample of thoracic vertebrae from under the origin of the first dorsal fin to the pelvic fins, following Francis & Mulligan (1998), was extracted and stored at -20°C until further processing. Samples of all other tissues, including cervical and precaudal vertebrae (as defined by Officer et al., 1996), were also retrieved and stored in a frozen tissue archive. Two of the largest vertebrae from the thoracic vertebral sample were used for ageing. These vertebrae were used because the thoracic region contains the largest vertebrae, which have been reported to have higher band counts and greater band resolution than vertebrae sampled from cervical and precaudal regions in school sharks (Officer et al., 1996).

4.3.3: Vertebra preparation and counting

After thawing, the two largest vertebrae from each individual were separated and had bulk connective tissue, as well as the haemal and neural arches, removed. Vertebra were then boiled in Milli-Q water (Milli-Q EQ 7000, Millipore Corporation) for between 0.5-5 minutes, depending on the size of the vertebra, and manually cleaned to remove as much of the remaining soft tissue before bleaching to reduce the risk of overbleaching. Samples were then submerged in bleach (4% Sodium Hypochlorite, made from 13.5% Hyperstat Sodium Hypochlorite (Ecochem) and Milli-Q water) until any remnants of soft tissue were removed. This lasted up to one hour, depending on the size of the vertebra, where samples were checked every 5-10 minutes for signs of overbleaching. After bleaching, vertebrae were initially rinsed and then soaked in Milli-Q water for at least 12-24 hours to remove any traces of the bleach. Samples were then individually air-dried for a week under negative pressure. This was done at room temperature and away from direct sunlight. After drying, maximum vertebral length and diameter were recorded, and vertebrae were frozen at -19°C, in cell and tissue culture plates (6 and 24 well, Biofil), until vertebrae were bisected.

Once allowed to thaw to room temperature, vertebrae were affixed to metal rods (6mm, stainless steel) for bisecting. To ensure that the cutting plane was in the same plane as the vertebral focus, vertebrae that had cones that differed in diameter were placed in a gluing stand (Figure 4.2). The nylon screws (RS Components) were adjusted so that the vertebral focus plane was parallel to that of the bench. The rod was then fixed in position using epoxy resin (5-min Araldite epoxy adhesive, Selleys). Vertebrae that were too small to be supported by the nylon screws were affixed atop of the rods using the same resin without support from a stand. The resin was left to set for 0.75-1 hour. Vertebrae were bisected frontally through the medio-lateral plane (Figure 4.3) using a diamond coated cutting disc (987P, 48mm diameter, 0.33mm thick, Komet Dental) attached to a Dremel rotary tool (Dremel 4000 with flex shaft attachment, speed: 7,000-10,000 RPM). Bisecting was done on a custom-built XY stage and cooled by Type 3 water (Suez Water Technologies) (Figure 4.4). Vertebrae were positioned so that their anterior-posterior axis was perpendicular to the bench (Figure 4.4), and cutting was continuous to prevent any cutting marks hampering the visibility of the vertebral bands in the sectioned face. The vertebral halves were dried overnight and stored at -19°C, in cell and tissue culture plates, until vertebrae were imaged.

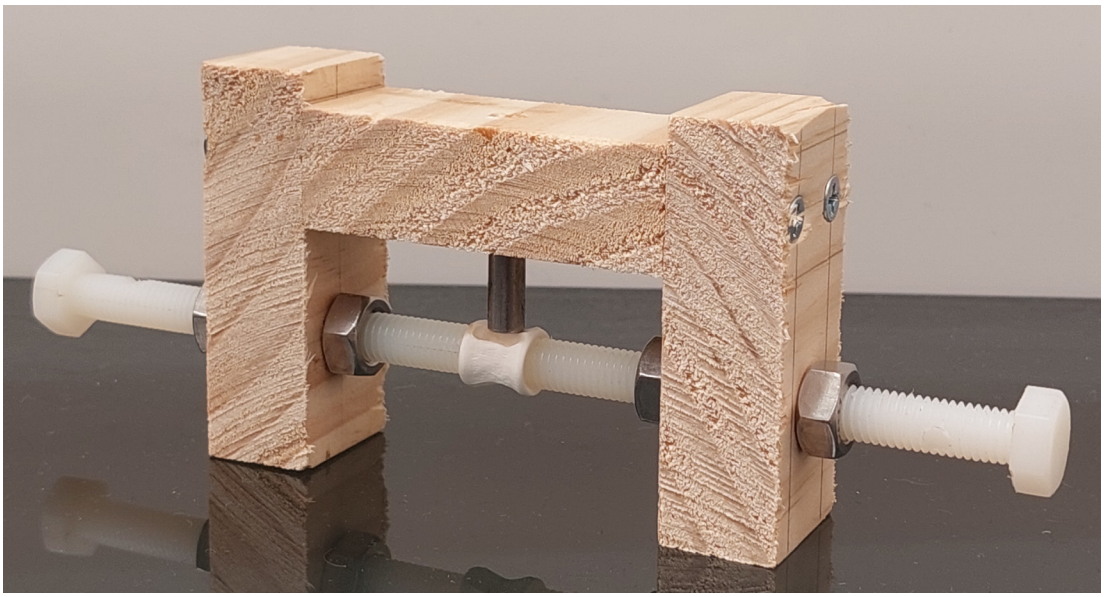


Figure 4.2: *Custom made gluing stand to ensure that the cutting axis was in line with the focal axis of the vertebrae.*

Various methods were trialled to get the best amplification of the vertebral bands. The methods that had the best band amplification were micro-CT of whole vertebrae (viewing a vertebral half in processed images) and image stacking of both the conical (in reflected light) and sectioned faces (in transmitted light) of vertebral halves. Due to financial constraints, image stacking of vertebral halves was the method chosen to amplify vertebral bands.

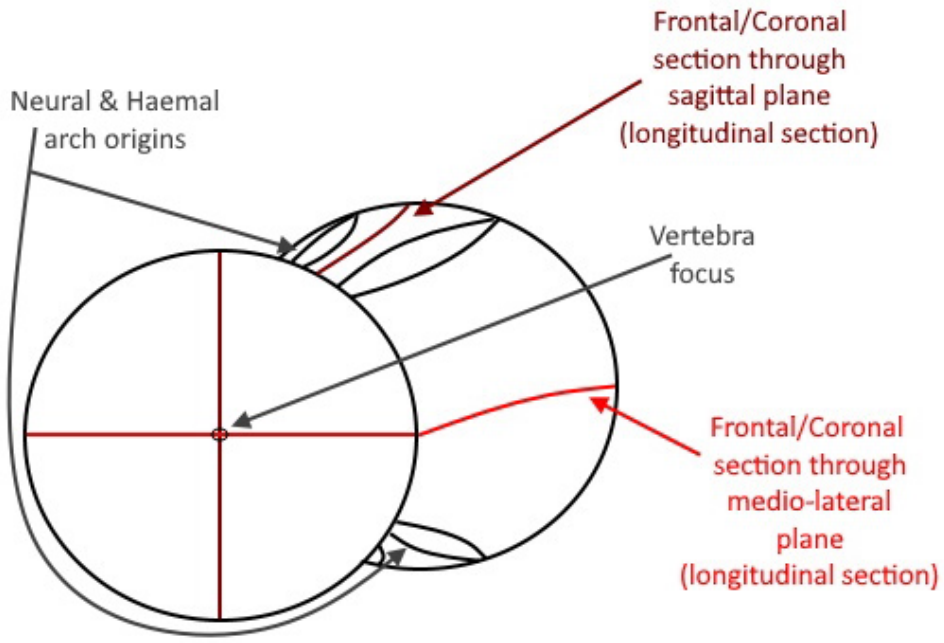


Figure 4.3: *Cutting planes through a carcharhiniform shark vertebra*.

Images of vertebrae for counting were captured using automated and manual image stacking techniques in dark rooms. Automated image stacking involved illuminating the vertebral half positioned on a glass petri dish (2.5mm) and coverslip (0.16-0.19mm, Citoglass) with fibre optic lights (Leica CLS 150x fibre optic lights, 240v, 150w) (Figure 4.5a). Images were then taken using the imaging stacking function of a Tough TG-6 camera (Olympus) and manipulated in ImageJ (Schneider et al., 2012) to make the bands clearer. Manual image stacking involved illuminating the vertebral half, with fibre optic lights (Schott fibreoptic lights, 12v, 150w), and manually moving the tethered camera (Camera: Canon EOS Kiss X7i, Lens: Cannon EF-S 60mm macro lens with 21mm extension tube, Tether program: DSLR Remote Pro (Breeze Systems., 2023)), attached to a custom XY stage, in 200μm steps (Figure 4.5b). Camera movement steps were determined by the depth of field and focus of the camera to ensure the right amount of resolution was being captured for each vertebra. Images were then processed using Photoshop (Adobe Inc., 2019) and Zerene Stacker (Zerene Systems., 2023) to make the bands clearer and merge the stacked images together.

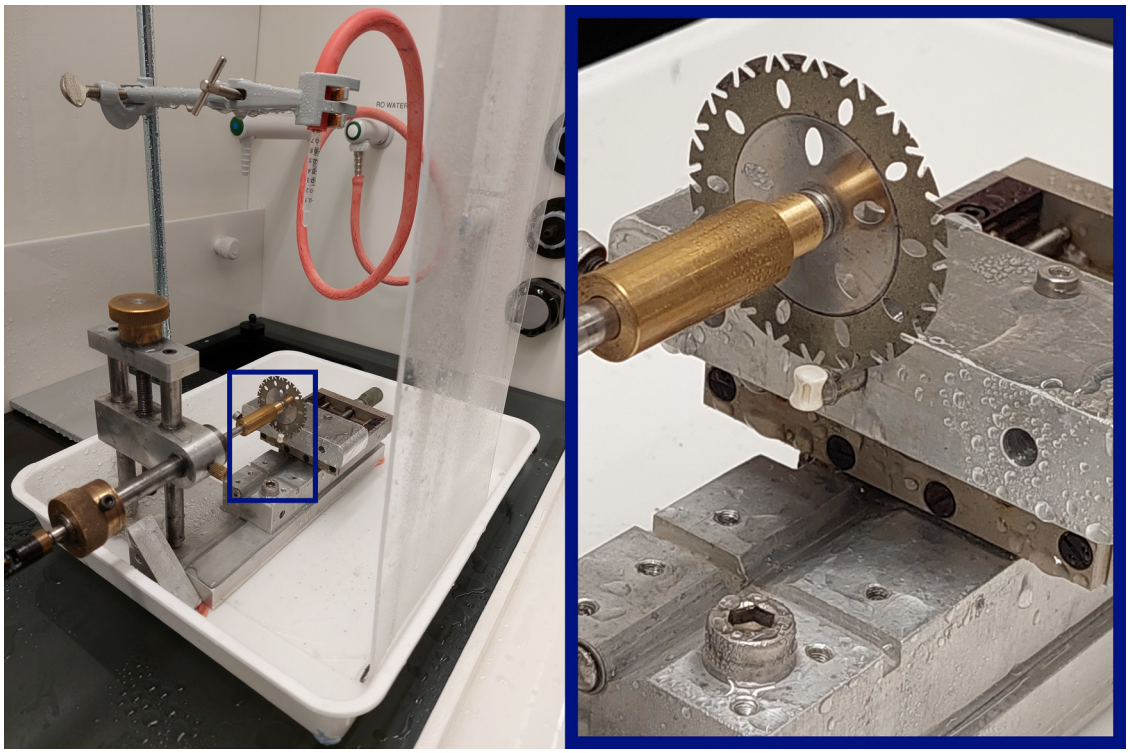
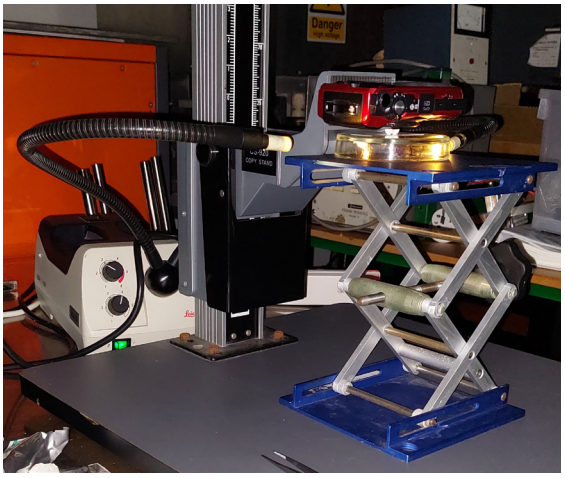


Figure 4.4: *Custom vertebra cutting set up.*

Due to additional timing constraints, the manual image stacking technique was used to capture images to be used for training, as it had better clarity and resolution of vertebral bands compared to the automatic image stacking technique. Vertebrae imaged by manual image stacking were also imaged by automatic image stacking to compare the appearance of bands between methods (Figure 4.6). This comparison verified the appearance of bands in the automatic image stacking images, allowing us to count bands in vertebrae that were captured by automatic image stacking due to time limitations.



(a)

(b)

Figure 4.5: *Amplification techniques to visualise vertebral bands. a) Automated image stacking. b) Manual image stacking.*

Vertebral bands consist of a pair of hypo- and hyper-mineralised bands in the corpora calcareum (Cailliet & Goldman, 2004; Ferreira & Vooren, 1991; Walker et al., 1995). Unfortunately, limited sampling throughout the year and small sample sizes prevented validation of vertebral band deposition rates for juvenile school sharks in New Zealand. However, vertebral bands have been validated to form annually in cervical vertebrae, until age at maturity, and have been used to age school sharks (Ferreira & Vooren, 1991; Francis & Mulligan, 1998; Thomson et al., 2020; Walker et al., 2001). Given the small difference in band counts between cervical and thoracic vertebrae observed in Officer et al. (1996) (average = 0.37-0.43), bands in thoracic vertebrae were assumed to form annually and were used in this study to approximate the age of an individual. Bands of hyper-mineralised growth, which form in the austral winter (Ferreira & Vooren, 1991; Walker et al., 1995), were the bands that were counted and are herein referred to as major bands.

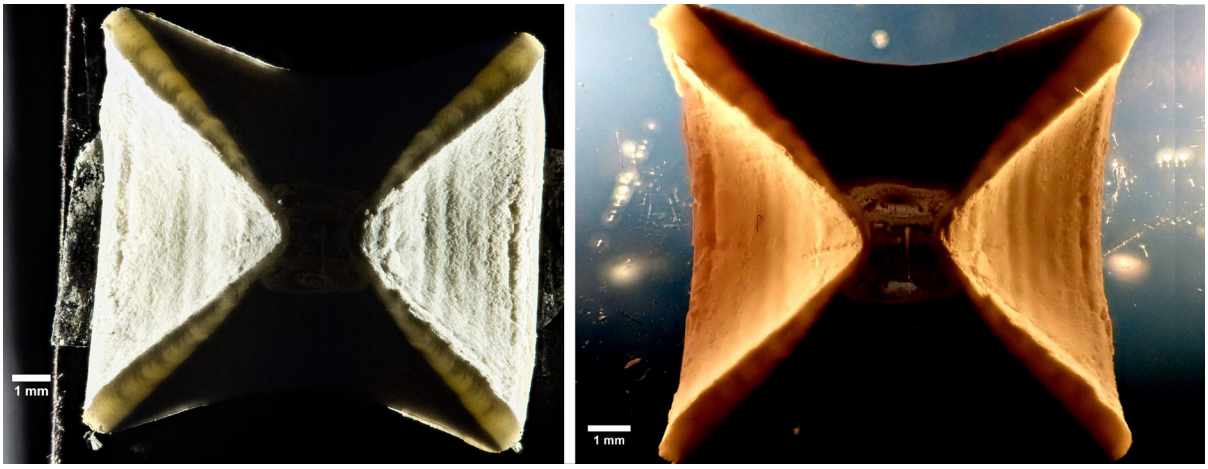


Figure 4.6: *Examples of the manual and automatic techniques used to amplify growth rings. Left: Manual image stacking image taken by D. Gerneke. Right: Automatic image stacking image taken by A. Burton. Both images were of the same vertebral half, and the estimated age was 6.8 years.*

Using the image stacking techniques described above, major bands appeared as optically translucent bands (Ferreira & Vooren, 1991) in the sectioned face and coincided with changes in the angle of the corpora calcareum (Figure 4.6). In the conical face, major bands appeared as raised lighter bands (Figure 4.6). The spacing and thickness of the bands were also used to aid in major band identification; that is, major bands had similar spacing and thickness (Ferreira & Vooren, 1991; Officer et al., 1996; Walker et al., 1995). The first major band in school sharks has not been observed to be laid down until the first winter after birth (Ferreira & Vooren, 1991; A. Burton personal observation of newborns). Therefore, the birth mark was considered as the initial change in the angle of the corpus calcereum as it shows a difference between the fast intra-uterine and slower post-natal growth (Walter & Ebert, 1991). Only major bands observed after the birth mark were counted.

Table 4.1: *Vertebrae readability scores modified from Geraghty et al. (2014) and Officer et al. (1996).*

No	Definition
1	Bands are well defined, and interpretation is unambiguous.
2	Bands have diminished clarity; however, interpretation is unambiguous.
3	Most bands are visible. The indicated count is most likely.
4	Bands visible, majority difficult to interpret. The recorded count is the best estimate.
5	Vertebra is unreadable; no band count is possible.

Images of amplified vertebral halves were read by two readers. Reader 1 had no prior experience with reading structures used to age elasmobranchs, fish, or cetaceans. Reader 2 had prior experience reading growth bands from cetacean teeth. Given the lack of experience in reading shark vertebrae, initial training consisted of viewing vertebral images, with knowledge of an individual's length and sex and vertebra size, that had also been counted by an experienced otolith ager and an experienced shark vertebral band counter. What followed was both readers practiced counting vertebral images from a subset of individuals whilst knowing the length and sex of the

individual, capture date, and size of the vertebra. Final counts consisted of readers undertaking randomised blind reads of the rest of the vertebrae; that is, readers did not know the length, sex, or capture date of the animal, nor the size of the vertebra. All non-training counts were conducted independently, and all images that were counted had a readability score (Table 4.1) assigned. If there were disagreements in the counts between readers, both readers would re-read the images with knowledge of their first count. If readers still disagreed on the count of a vertebra, both readers reviewed and discussed the interpretation of the image and agreed on a final count.

The observed age of an individual was given by the following equation:

$$\text{Age}_i = c_i + (-1 \times w_i) + P_{year}$$

where c_i is the number of bands counted for a given vertebra; w_i is an indicator for whether the winter band would have been deposited in the vertebra based on the capture date; w_i accounted for the lag between the major band formation and potential birth date of an individual, which can be between two and six months (Ferreira & Vooren, 1991; Walker et al., 1995); and P_{year} is the portion of the year between the capture date and the arbitrary birth date. For this study, the arbitrary mean birth date was the 1st of January as the peak of pupping occurs in December and January (Francis & Mulligan, 1998; McMillan et al., 2018; Moulton et al., 1992; Olsen, 1954; Stevens & West, 1997). However, the pupping season in Australia is November to February and likely the same in New Zealand (Olsen, 1954; Stevens & West, 1997; A. Burton personal observation). Variation around the 1st of January was accounted for by including a measurement error term in the model (see section *'4.3.5: Statistical analysis'* for details).

Reader bias and precision were examined by count-bias plots as well as the Index of Average Percentage Error (Beamish & Fournier, 1981) and Coefficient of Variation (Campana et al., 1995; Chang, 1982) (Table 4.2). Count-bias plots consisted of comparisons of counts between readers and between readers and agreed counts. Counts used for individual readers are the counts after the second read.

Table 4.2: *Metrics used to assess the precision of readers.*

Precision metric	Equation
Index of Average Percentage Error	$\frac{1}{N}\sum_{j=1}^{N}\left[\frac{1}{R}\times\sum_{i=j}^{R}\frac{\lvert X_{ij}-X_j\rvert}{X_j}\right]$
Coefficient of Variation	$100\times\frac{\sqrt{\sum_{i=1}^{R}\frac{(X_{ij}-X_j)^2}{R-1}}}{Xj}$

N is the number of vertebrae that have been read. R is the number of readings (based on the number of readers). X_{ij} is the ith band count of the jith shark. X_j is the average band count for the jth shark.

4.3.4: Body condition

To approximate the body condition of individuals, the relative liver weight, more commonly referred to as the hepatosomatic index (HSI_i), was used. This metric was selected as the body condition (herein referred to as condition) of an individual is dependent on the balance between food consumed and the energetic demands at a given time (Gallagher et al., 2014; Hussey et al., 2009). If an individual exhausts its energy reserves, then it is likely not consuming enough prey to meet energy demands of key biological processes such as growth or migrations, which can hinder such processes (Dmitriew, 2011). Thus, those with greater energy reserves are in a better condition as they are more equipped to undertake key processes. The liver is the primary organ for energy storage in sharks (Lauter et al., 1968; Oliver, 1948; Pethybridge et al., 2010), hence, individuals with heavier livers at a given length will have more energy and be in better condition.

$$HSI_i = W_{L_i}/W_{T_i} \times 100$$

W_{L_i} and W_{T_i} are the total liver weight and total body weight of an individual, respectively. When calculating the hepatosomatic index, the state (fresh/defrosted) of an individual was taken into account to minimise bias from freezing on the weight ratios. For example, when liver weight was measured fresh, fresh total body weight was also used in the calculation. Stomach content weight was not excluded from total body weight when calculating the hepatosomatic index, as for most sampled individuals, the weight of stomach contents accounted for a small percentage of the total body weight (range: 3.1-18.0%, proportion of range < 10%: 0.8).

4.3.5: Statistical analysis

All data visualisations, measurement standardisation, and analyses were carried out in R and R Studio (Posit team, 2024; R Core Team, 2024). Bayesian models were fit using the brms (Bürkner, 2017) and rstan (Stan Development Team, 2024) packages.

4.3.5.1: Data standardisation

The total length used in this study was defined as total length measured from a fresh shark, in a straight line, with the tail in a natural position (fresh, natural, total length). However, for some individuals, this specific total length measurement was unavailable, and alternative full and partial body length variants (as defined in Chapter 2 and Appendix 1.1) were recorded instead. To ensure consistency across measurements, a linear model, with a natural log-normal error distribution and a model component that related the error standard deviation to the length to explicitly model heteroscedasticity, was used to convert alternative length variants to our chosen total length variant (see Chapter 2 for details).

4.3.5.2: Bayesian models

Bayesian linear, von Bertalanffy (von Bertalanffy, 1983), and Gompertz (Ricker, 1975) growth models (Table 4.3) were fit to length-at-age and condition-at-age data to estimate and determine the shape of somatic and hepatosomatic growth of juvenile school sharks. All three models were designed to account for the variation in length at and timing of birth using informative priors (see below) and the inclusion of measurement error for ages, respectively. Measurement error assigned to ages was a standard deviation of 0.1 based on the four month pupping period, that is 95% of births would occur within 60 days of the arbitrary birth date, January 1st. Visual examination of residuals revealed no evidence of heteroscedasticity for any of the models.

Table 4.3: *Models used to model somatic and hepatosomatic growth for juvenile school sharks.*

Data	Model variant	Mathematical notation	Priors
Length-at-age	Linear	$L_i \sim \mathcal{N}(\mu_i, \sigma)$ $\mu_i = L_0 + \beta_1 A_{\text{True},i}$ $A_{\text{Obs},i} \sim \mathcal{N}(A_{\text{True},i}, 0.1)$	$L_0 \sim \mathcal{N}(300,10)$ $\beta_1 \sim \mathcal{N}(100,10)$ $\sigma \sim \mathcal{U}(0,100)$
Length-at-age	von Bertalanffy	$L_i \sim \mathcal{N}(\mu_i, \sigma)$ $\mu_i = L_0 + (L_\infty - L_0)(1 - e^{-kA_{\text{True},i}})$ $A_{\text{Obs},i} \sim \mathcal{N}(A_{\text{True},i}, 0.1)$	$L_0 \sim \mathcal{N}(300,10)$ $L_\infty \sim \mathcal{N}(2000,400)$ $k \sim \mathcal{U}(0.05,0.2)$ $\sigma \sim \mathcal{U}(0,100)$
Length-at-age	Gompertz	$L_i \sim \mathcal{N}(\mu_i, \sigma)$ $\mu_i = L_0 e^{\left(\ln\left(\frac{L_\infty}{L_0}\right)\left(1-e^{-kA_{\text{True},i}}\right)\right)}$ $A_{\text{Obs},i} \sim \mathcal{N}(A_{\text{True},i}, 0.1)$	$L_0 \sim \mathcal{N}(300,10)$ $L_\infty \sim \mathcal{N}(2000,400)$ $k \sim \mathcal{U}(0,0.7)$ $\sigma \sim \mathcal{U}(0,100)$
Condition-at-age	Linear	$H_i \sim \mathcal{N}(\mu_i, \sigma)$ $\mu_i = H_0 + \beta_1 A_{\text{True},i}$ $A_{\text{Obs},i} \sim \mathcal{N}(A_{\text{True},i}, 0.1)$	$H_0 \sim \mathcal{N}(3,1)$ $\beta_1 \sim \mathcal{N}(0.5,0.5)$ $\sigma \sim \mathcal{U}(0,10)$
Condition-at-age	von Bertalanffy	$H_i \sim \mathcal{N}(\mu_i, \sigma)$ $\mu_i = H_0 + (H_\infty - H_0)(1 - e^{-kA_{\text{True},i}})$ $A_{\text{Obs},i} \sim \mathcal{N}(A_{\text{True},i}, 0.1)$	$H_0 \sim \mathcal{N}(3,1)$ $H_\infty \sim \mathcal{N}(20,4)$ $k \sim \mathcal{U}(0,0.3)$ $\sigma \sim \mathcal{U}(0,10)$
Condition-at-age	Gompertz	$H_i \sim \mathcal{N}(\mu_i, \sigma)$ $\mu_i = H_0 e^{\left(log\left(\frac{H_\infty}{H_0}\right)\left(1-e^{-kA_{\text{True},i}}\right)\right)}$ $A_{\text{Obs},i} \sim \mathcal{N}(A_{\text{True},i}, 0.1)$	$H_0 \sim \mathcal{N}(3,1)$ $H_\infty \sim \mathcal{N}(20,4)$ $k \sim \mathcal{U}(0,0.3)$ $\sigma \sim \mathcal{U}(0,10)$

L_i is the length of a given individual, H_i is the hepatosomatic index (condition) of a given individual, L_0 is the length-at-birth, L_∞ is the asymptotic length, H_0 is the condition-at-birth, H_∞ is the asymptotic condition, β_1 is the growth coefficient for the linear model, k is the growth coefficient for the non-linear growth models, $A_{\text{Obs},i}$ is the observed age of an individual, $A_{\text{True},i}$ is the true age of an individual, σ the standard deviation of the posterior.

In addition, varying intercept and slope variants of the selected model (see section '*3.5.5.3: Model comparison'* for selection criteria) with different parameters for each sex and region were also fit to the data to assess the extent of variation between sexes and regions. Examples of the linear model with sex- and region-specific parameters are presented in Table 4.4.

Table 4.4: *Hierarchical Bayesian linear models with sex and region parameters.*

Data	Parameter	Intercept	Slope	Mathematical notation
Length-at-age	Sex	Fixed	Variable	$L_i \sim \mathcal{N}(\mu_i, \sigma)$ $\mu_i = L_0 + \beta_{\text{Sex}[i]} A_{\text{True},i}$
Length-at-age	Region	Variable	Fixed	$L_i \sim \mathcal{N}(\mu_i, \sigma)$ $\mu_i = L_{0_{\text{Loc}[i]}} + \beta_1 A_{\text{True},i}$
Length-at-age	Region	Variable	Variable	$L_i \sim \mathcal{N}(\mu_i, \sigma)$ $\mu_i = L_{0_{\text{Loc}[i]}} + \beta_{\text{Loc}[i]} A_{\text{True},i}$
Condition-at-age	Sex	Fixed	Variable	$H_i \sim \mathcal{N}(\mu_i, \sigma)$ $\mu_i = H_0 + \beta_{\text{Sex}[i]} A_{\text{True},i}$
Condition-at-age	Region	Variable	Fixed	$H_i \sim \mathcal{N}(\mu_i, \sigma)$ $\mu_i = H_{0_{\text{Loc}[i]}} + \beta_1 A_{\text{True},i}$
Condition-at-age	Region	Variable	Variable	$H_i \sim \mathcal{N}(\mu_i, \sigma)$ $\mu_i = H_{0_{\text{Loc}[i]}} + \beta_{\text{Loc}[i]} A_{\text{True},i}$

$L_{0_{\text{Loc}[i]}}$ is the length-at-birth for a given region, $H_{0_{\text{Loc}[i]}}$ is the condition-at-birth for a given region, $\beta_{\text{Sex}[i]}$ is the slope for a given sex, $\beta_{\text{Loc}[i]}$ is the slope for a given region.

The priors for length-at-birth L_0 and asymptotic length L_∞ were based on estimates from Appendix 2.6 and the maximum, globally observed standardised total length of school sharks (Appendix 2.5; C. Duffy unpublished data), respectively. The priors for condition-at-birth H_0 and asymptotic condition H_∞ were based on observations of conditions of individuals around length-at-birth (near-term embryos and newborns) and adults with the largest HSI (Ripley, 1946; A. Burton unpublished data), respectively. Priors for other model parameters (e.g., β_1, k, σ) were determined by prior simulations using code adapted from Wesner & Pomeranz (2021). The length-at-age von Bertalanffy and Gompertz models and the condition-at-age Gompertz model did not converge with informative priors for σ and were allocated non-informative, uniform, priors instead. To allow for consistency between models, non-informative, uniform, priors for σ were adopted for all length- and condition-at-age models. Prior simulations for parameters are available in Appendix 3.1.

4.3.5.3: Model comparison

Leave-One-Out cross-validation techniques, such as Expected Log Predictive Density (ELPD), as well as the fit of the model, were used to compare the linear, von Bertalanffy, and Gompertz models as well as establish whether somatic and hepatosomatic growth varied between sexes and regions. ELPD is a measure of predictive accuracy for out-of-sample data, which is estimated using Pareto-Smoothed Importance Sampling (Vehtari et al., 2017). Differences in ELPD < 4 and/or the standard deviation of the difference was greater than the difference in ELPD indicated there was no evidence in the difference of the predictive ability of a model (McLatchie & Vehtari, 2024; Sivula et al., 2020). When there was no evidence of a difference in predictive ability or the fit between the models, the simplicity of a model was used to select a model.

4.4: Results

Thoracic vertebrae were sampled from 99 juveniles captured across the Kaipara Harbour, Kapiti Coast, Tasman and Golden Bays, and Canterbury Bight, with individuals ranging in length from 316-1075mm total length (TL, fresh, natural, total length; Table 4.5). Individuals captured in Tasman and Golden Bays, as well as the Canterbury Bight, were primarily captured via bottom trawls, whereas those captured in the Kaipara Harbour and Kapiti Coast were caught by linefishing (longlines and angling; Figure 4.7). Images of amplified vertebral halves from all sampled individuals were deemed readable and, thus, could be used to estimate somatic and hepatosomatic growth. However, because juvenile school sharks typically leave nurseries after 2-3 years (McAllister et al., 2015), growth analyses were restricted to individual < 4 years old to reduce the bias from non-location bound individuals. An example of growth analyses including older individuals is shown in Figure A3.2.1. Due to the small sample size, individuals sampled from the Kapiti Coast were excluded from analyses (Figure 4.7; Table 4.5). Capture year and season were also excluded from analyses due to the lack of sufficient sampling in each region throughout and between years (Figure 4.7).

Table 4.5: *Summary of the biological information related to juveniles sampled in the Kaipara Harbour, Kapiti Coast, Tasman and Golden Bays, and Canterbury Bight. Length range is the range of total length measured in a straight line, with the tail in a natural position.*

Location	Sex	Year range	Sample size	Length range	Age range
Canterbury Bight	Female	2022 - 2022	18	379 - 879	0.4 - 5.4
Canterbury Bight	Male	2022 - 2022	17	347 - 892	0.4 - 5.4
Kaipara Harbour	Female	2020 - 2023	10	345 - 655	0.1 - 3.7
Kaipara Harbour	Male	2020 - 2023	8	325 - 680	0.1 - 3.6
Kapiti Coast	Female	2022 - 2022	4	561 - 738	2.5 - 4.8
Kapiti Coast	Male	2022 - 2022	2	738 - 1075	2.8 - 4.7
Tasman/Golden Bay	Female	2021 - 2023	20	334 - 920	0.2 – 4.0
Tasman/Golden Bay	Male	2021 - 2023	26	316 - 999	0.0 - 4.2

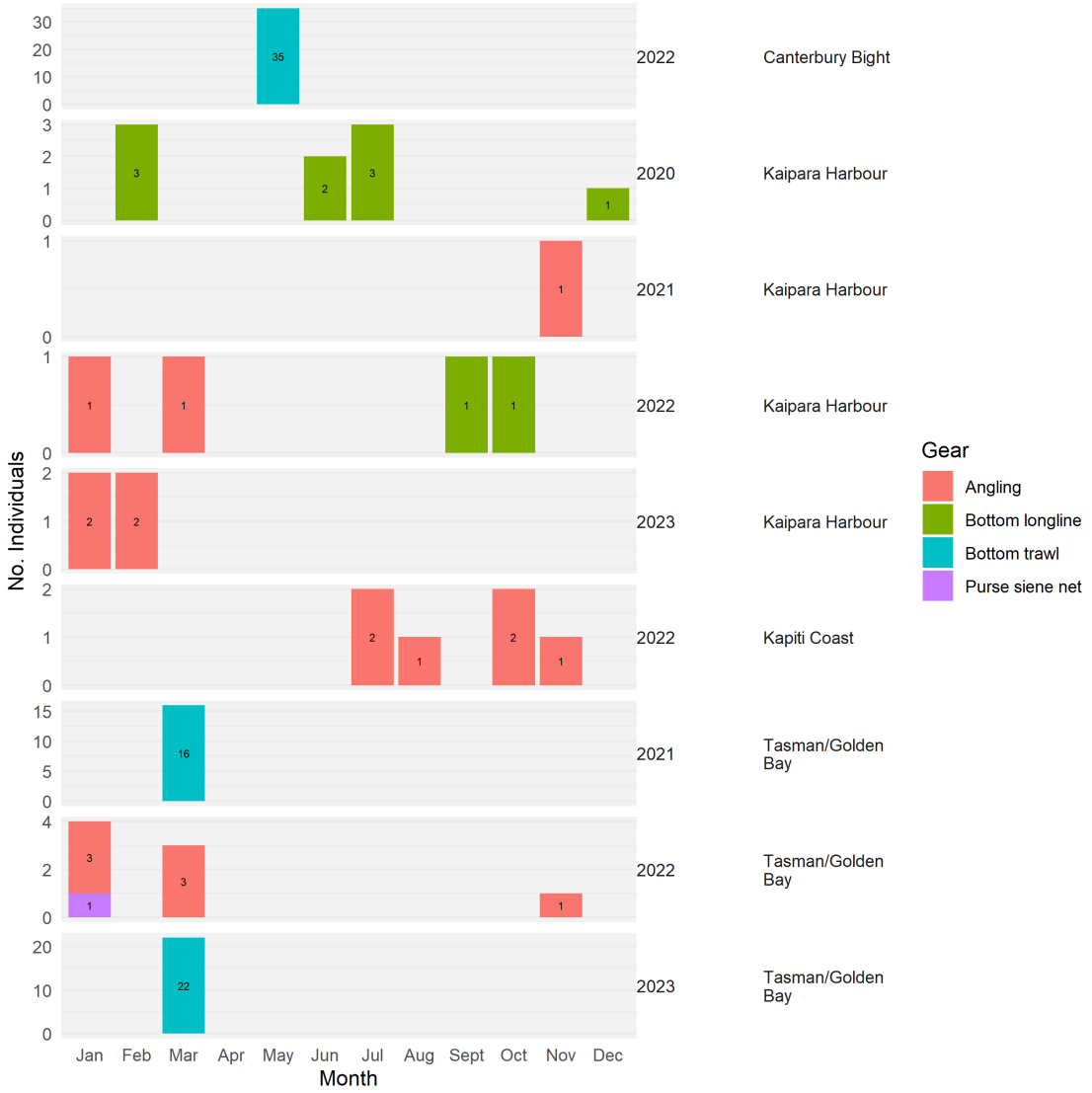


Figure 4.7: *Number of juvenile school sharks captured per gear type, month, and year in the Kaipara Harbour, Kapiti Coast, Tasman and Golden Bays, and Canterbury Bight.*

Precision in vertebral counts between readers was low (Overall: Index of Average Percentage Error = 36%, Coefficient of Variation = 44.7%), particularly for counts between 0 and 2, where both precision metrics were above 25% (Figure 4.8). However, 98.5% of counts were within 2 bands, 75% were within 1 band, and 25% of counts agreed. From count-bias plots, there appeared to be some bias between readers, with reader two on average estimating approximately one band more than reader one when reader one counted zero or one band (Figure 4.9). Both readers tended to have higher counts compared to the agreed final count (Figure 4.9), where agreement with the final count was 59.7% for reader one and 38.1% for reader two.

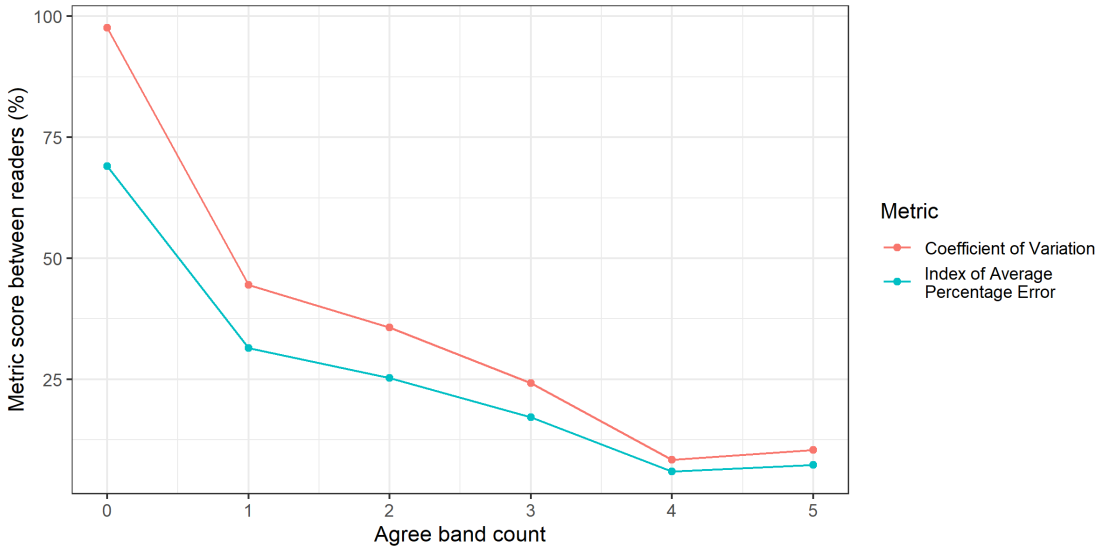


Figure 4.8: *Extent of error in readings between the two readers over the agreed final count.*

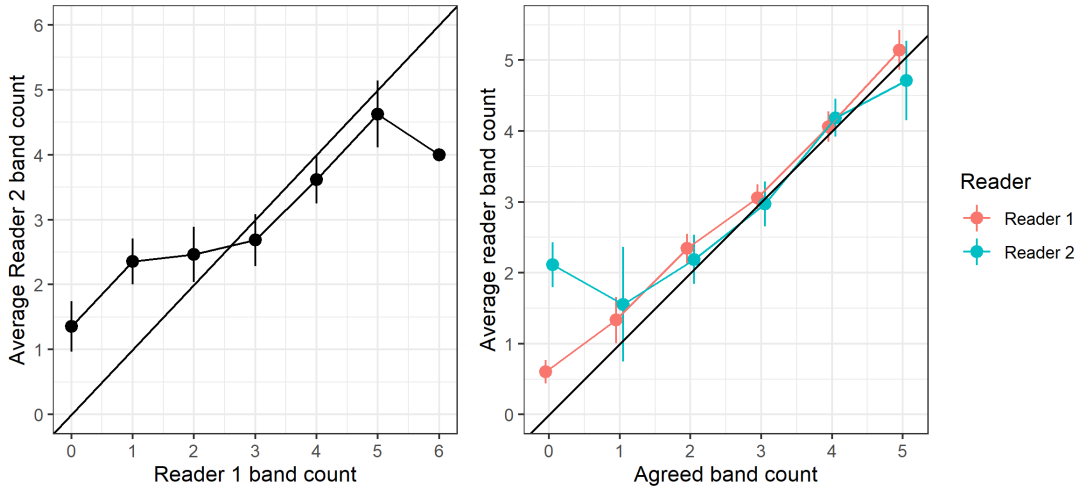
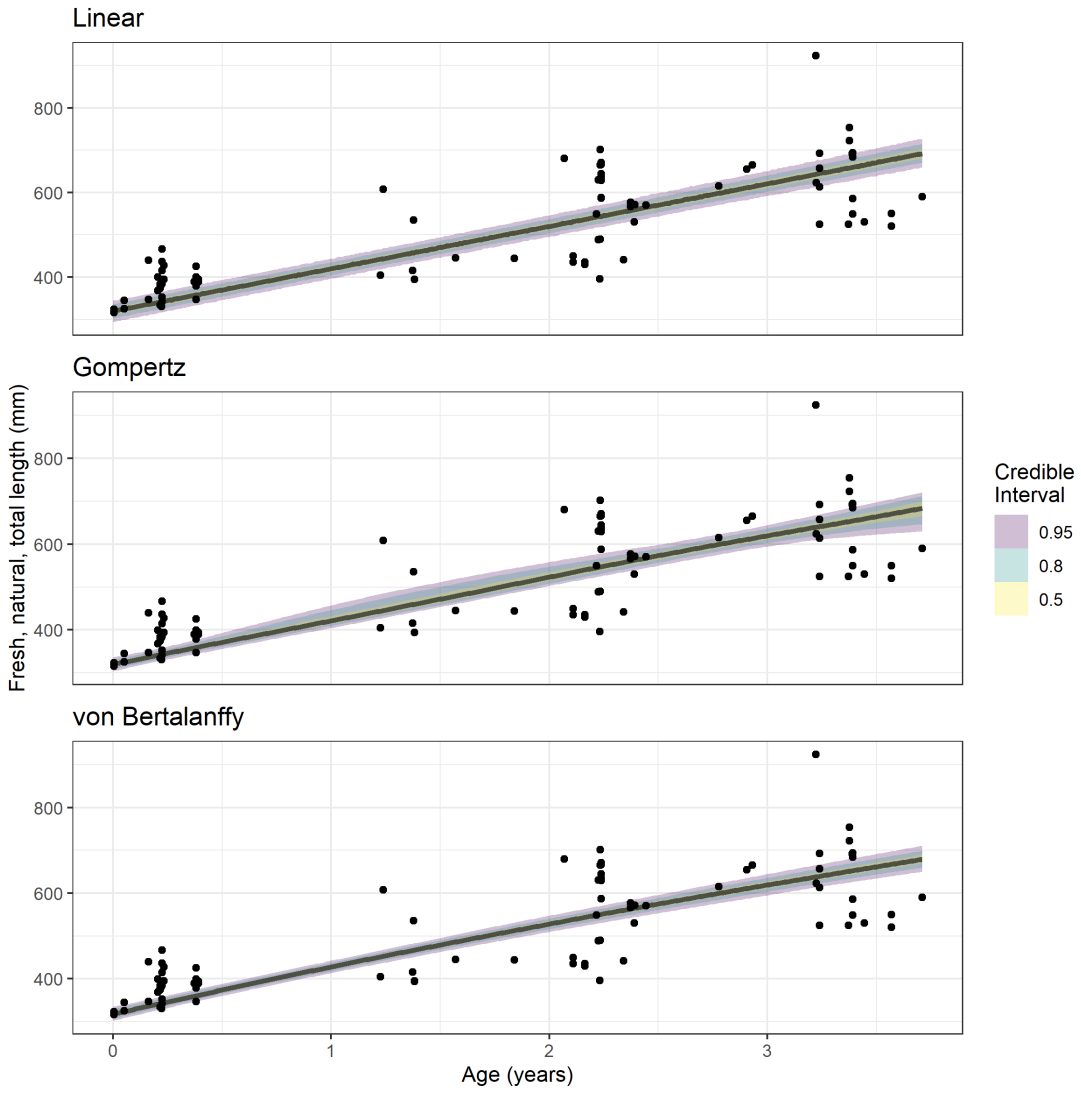


Figure 4.9: *Count-bias plots between reader counts (left) and readers' and the agreed counts (right). Vertical lines represent 95% confidence intervals of the average band count. The solid black line represents the 1:1 relationship between band counts.*

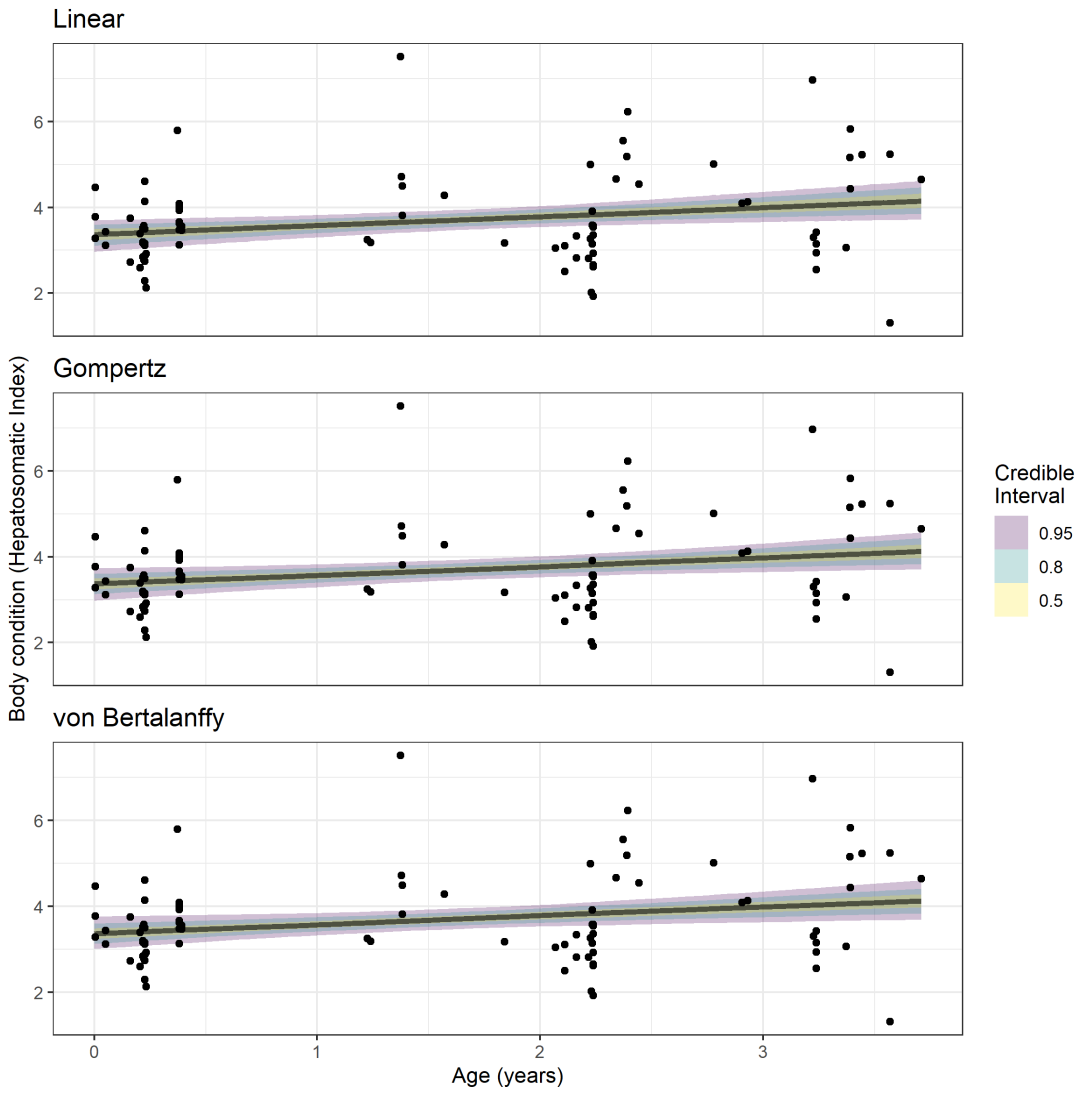
The von Bertalanffy growth model appeared to perform better than the other growth models for length-at-age and condition-at-age data (Table 4.6). However, there was no evidence of a difference in predictive ability and fit between the three growth models for either data set, and the linear model was selected in both cases due to its simplicity (Table 4.6 and Figure 4.10).

Table 4.6: *Model comparison results for the linear, Gompertz, and von Bertalanffy growth models. Model is the model used to estimate somatic and hepatosomatic growth. Values are the differences in the Expected Log Predictive Density (ELPD) of the three growth models from the model with the greatest ELPD (difference = 0) with standard errors of the difference. Models initially selected are highlighted in green.*

Model	Response variable	Predictor variable	Linear	Gompertz	von Bertalanffy
TL~Age	Total length	Age	-0.609±0.778	-1.419±0.214	0
HSI~Age	Hepatosomatic Index	Age	-0.071±0.063	-0.011±0.068	0



a)



b)

Figure 4.10: *The predicted fit of the three growth models to a) length-at-age and b) condition-at-age data. Fresh, natural, total length is the total length measured from a fresh shark, in a straight line, with the tail in a natural position. Credible interval represents the 50%, 80%, and 95% credible intervals.*

Comparing the fit and ELPD scores of the linear model with and without varying slopes for sex showed no evidence of a difference in somatic and hepatosomatic growth (Table 4.7, 95% credible intervals of sex parameters included zero). Due to a lack of evidence of an effect of sex, combined sex data was used to examine whether somatic and hepatosomatic growth varied between regions.

For somatic growth, the linear model with varying slopes for location was selected by ELPD scores, whereas the linear model with varying intercepts for location was selected for hepatosomatic growth (Table 4.7). When examining model fit for somatic growth, there was no evidence of a difference between the three regions (Figure 4.11, zero inclusive 95% credible intervals). In contrast there was evidence of individuals from the Canterbury Bight having larger livers relative to their total

body weight compared to the Kaipara Harbour and Tasman and Golden Bays (Figure 4.11, non-zero 95% credible intervals). However, despite some variation in the rates of hepatosomatic growth (Figure 4.11), there was no evidence of a difference in the hepatosomatic growth rates between the three regions (zero inclusive 95% credible intervals).

Table 4.7: *Model comparison results for linear models with and without varying intercepts and slopes for sex or location. Model is the model used to estimate somatic and hepatosomatic growth. Values are the differences in the Expected Log Predictive Density (ELPD) of the three models from the model with the greatest ELPD (difference = 0) with standard errors of the difference. Models initially selected are highlighted in green.*

Model	Response	Predictor	Varying intercepts: Location	Varying slopes: Location	Varying slopes: Sex	Linear without varying slopes
TL~Age	Total length	Age	-0.733 ± 0.433	0	-4.521 ± 7.362	-0.855 ± 0.484
HSI~Age	Hepatosomatic Index	Age	0	-1.086 ± 1.806	-9.676 ± 4.389	-8.495 ± 4.397

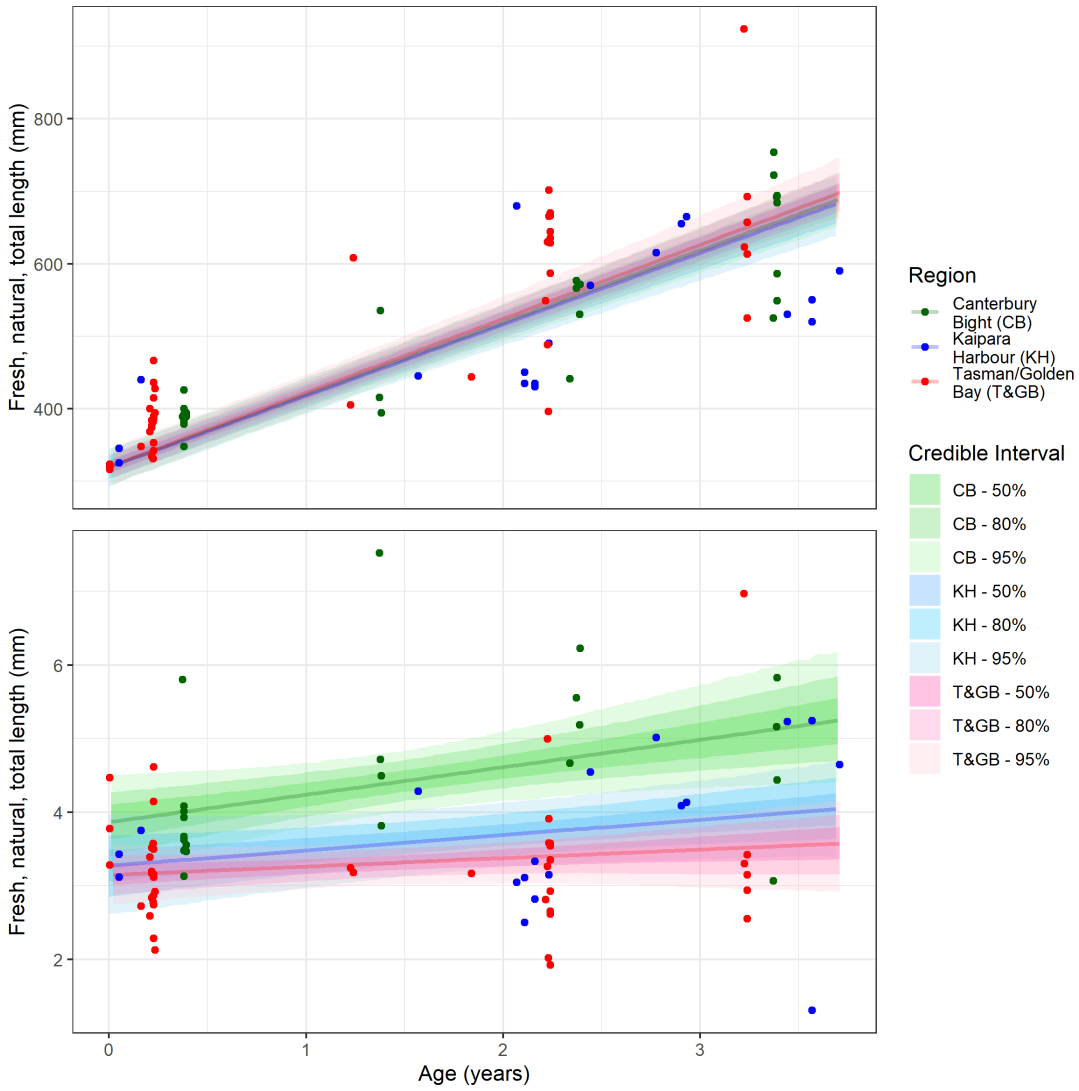


Figure 4.11: *The predicted fit of the linear model with varying slopes for location to length-at-age (above) and condition-at-age data (below). Fresh, natural, total length is the total length measured from a fresh shark, in a straight line, with the tail in a natural position. Credible interval represents the 50%, 80%, and 95% credible intervals.*

4.5: Discussion

For some elasmobranch species, the growth of juveniles is faster in the first few years after birth compared to later years (e.g., Finucci & Ó Maolagáin, 2022; Geraghty et al., 2014; Harry et al., 2019). A similar pattern was observed in juvenile school sharks, which steadily grow and gain energy reserves in the first four years after birth (Figure 4.10). Since there was no evidence of a difference between the three growth models for length-at-age data, results would suggest that the growth of juvenile school sharks occurs at a constant rate. While growth rates with other studies could not be directly compared, steady, constant somatic growth of juvenile sharks has previously been observed in the Australian and New Zealand school shark populations (Francis & Mulligan, 1998; Stevens & West, 1997) as well as great white sharks (*Carcharodon carcharias*; Finucci & Ó

Maolagáin, 2022) and some carcharhinid species (e.g., Geraghty et al., 2014; Simpfendorfer, 2000). Despite, also exhibiting steady, constant, hepatosomatic growth, there was some potential loss of body condition in juveniles, between 0 and 4 months old, sampled from Tasman and Golden Bays (Figure 4.11). The potential loss of condition may be linked to juvenile school sharks using reserves they gained over gestation whilst they are learning how to hunt effectively (Hussey et al., 2010; Lyons et al., 2020; Weideli et al., 2019). However, the limited data from the first year after birth makes it difficult to determine if young school sharks are using reserves whilst they are learning to hunt, which led to the selection of a linear growth model. Although steady growth and gain in energy reserves in juvenile school sharks has been linked to timely dispersal from important habitats and/or reduction in the risk of predation when exploiting more energetically rewarding habitats (McAllister et al., 2015; McMillan et al., 2021), the specific causes for the New Zealand population remain unknown.

Like other elasmobranchs (e.g., Contreras-Reyes et al., 2021; Geraghty et al., 2014; Holmes et al., 2015), there was little evidence of a difference in somatic and hepatosomatic growth between juvenile males and females (Table 4.7). The similarity could be due to juvenile males and females attempting to reach a similar length and condition that will allow for dispersal and/or habitat exploitation whilst experiencing similar trade-offs between growth and local conditions (e.g., Dmitriew, 2011; Heithaus, 2007; Hussey et al., 2017).

Abiotic conditions, such as available habitats and nutrient supply, are known to vary between the Kaipara Harbour, Tasman and Golden Bays and the Canterbury Bight (Bostock et al., 2019; Environment Canterbury, 2024; Hewitt & Funnell, 2005; Morrison, Lowe, et al., 2014; Newcombe, 2016; Stevens et al., 2021; Stevens & Forrest, 2019); yet there was little difference in the somatic growth of juvenile school sharks among regions despite individuals from the Canterbury Bight generally being in better body condition (Figure 4.11). It is possible that the trade-offs between life-history traits and local pressures that shape the somatic growth are similar between regions. For example, juveniles from each location were able to gain surplus energy/increase in condition over time, with individuals from the Canterbury Bight being better provisioned than those from Tasman and Golden Bays and the Kaipara Harbour (Figure 4.11). Without any growth limiting factors, sharks that consume greater quantities of energy can grow faster (e.g., Cortes & Gruber, 1994). Yet, there was little difference in somatic growth across regions despite a difference in body condition (Figure 4.11). It is therefore possible that other growth limiting factors, such as size-specific predation (e.g., Di Battista et al., 2007; Matich et al., 2021), occur and impact somatic growth similarly in all three regions. However, because life-history traits are shaped by complex interactions between biotic, abiotic, and anthropogenic factors (Bradley et al., 2017; Devine et al., 2012), specific studies are required to identify the factors influencing somatic and hepatosomatic growth of juvenile school sharks in the Kaipara Harbour, Tasman and Golden Bays and the Canterbury Bight. These studies must also disentangle methodological limitations that may obscure these patterns.

There are multiple methodological limitations that may have contributed to our observations. Despite efforts, only small sample sizes, greatly affected by age, length, and spatio-temporal selectivity of the sampling gear, were obtained and resulted in the selection of specific length-age classes (Walker et al., 1998) and lack of temporal sampling. Additionally, the vertebral ring count method used had some degree of imprecision. Low sample sizes, unrepresentative data (caused by gear selectivity), and use of vertebral count methods, especially with inexperienced readers, are known to greatly affect growth curves (Francis & Francis, 1992; Harry, 2018; Officer et al., 1996;

Thorson & Simpfendorfer, 2009; Walker et al., 1998). Combined with limited knowledge on the biology of juvenile school sharks in the study regions, further work is needed to confirm the patterns observed in this study and identify the non-method and non-modelling factors that are contributing to the observed patterns.

Differences in ageing methods between studies prevented direct comparison of the ages and growth of juvenile school sharks from this study with those from other populations or historical data from New Zealand, a problem recognised in elasmobranch ageing studies due to biases in vertebral band count methods (Harry, 2018; Natanson et al., 2018). To allow for comparisons between studies, it would be beneficial for researchers and institutions to standardise the methods to assign ages to individuals. This would include moving towards a more deterministic method for assigning the age of individuals for each species (Natanson et al., 2018), for example, using measurements of the neonate scar to determine the age of newborns (e.g., Debaere et al., 2023). If vertebral counts are used to assign age, it is recommended that the position and appearance of the birth mark in relation to the vertebral bands, as well as the band deposition rate before, during, and after maturation for both sexes, are validated for a species before using counts to assign age (e.g., Walker et al., 2001). The manual image stacking method used in this study showed promise as a readily deployable, cost-effective method for counting vertebral bands and, with further development, could be used as a standard method to count vertebral bands.

Accurate knowledge of the extent of regional variation in somatic and hepatosomatic growth is crucial for the management of elasmobranch populations, as it helps determine if region-specific model parameters and management actions are necessary. Additionally, such knowledge provides insight into a population's resilience to different pressures, such as habitat degradation. Using a novel ageing method and hierarchical Bayesian modelling, our results suggest that juvenile school sharks steadily grow in length and gain energy reserves in the first few years after birth. While there was little evidence of a difference in somatic and hepatosomatic growth rates across regions, body condition varied between regions of likely significance to juvenile school sharks in New Zealand. However, methodological limitations, including low sample sizes, gear selectivity, poor temporal representation, and subjectivity of the ageing method, highlight the need for further research to confirm the patterns observed in this study. Future studies should improve the representativeness of sampling methods, adopt standardized, species-specific age and body condition assessment methods that are more deterministic and non-lethal, and consider the use of Bayesian models to enhance the accuracy of growth estimates and regional variation assessments.

Chapter 5: Beyond the Kaipara Harbour: Connectivity and Three-Dimensional Movement of New Zealand School Sharks

5.1: Abstract

Like other migratory species, school sharks (*Galeorhinus galeus*) have spatio-temporally complex behaviours, which can make it difficult to manage a population without appropriate knowledge. Spatial protections of habitats important to school sharks have been implemented to help prevent population declines. However, these protections have been ineffective. School sharks are now classified, globally, as Critically Endangered due to all but the New Zealand population having collapsed as a result of overfishing. Effective management and recovery of school shark populations requires a better understanding of the spatial-temporal complexity of populations, especially the movement of individuals among habitats key to the life-history of a population, and incorporation of such knowledge into management decisions. Using satellite telemetry and mark-recapture data, we assess the degree of connectivity between the Kaipara Harbour and other habitats of likely importance to the life-history of school sharks in Australia and New Zealand. The Kaipara Harbour was found to be one of many important interconnected habitats used for feeding and reproduction for the New Zealand population. Moreover, multiple potentially important feeding and reproductive habitats for the New Zealand population were identified, which were also used by school sharks that migrated to and from Australia. Further work is needed to determine the drivers of the migrations, as well as why school sharks use these habitats. However, this work provides the first in-depth knowledge on the spatio-temporal behaviours of New Zealand school sharks, which will aid with improving the management of the New Zealand school shark population.

5.2: Introduction

Like other migratory species, school sharks (*Galeorhinus galeus*) have three-dimensional, spatio-temporally complex behaviours that span vast distances and multiple jurisdictional boundaries (Andrzejaczek et al., 2022; Hurst et al., 1999; McMillan et al., 2019; Schaber et al., 2022; Thorburn et al., 2019; Walker et al., 2008). Some of these behaviours include extended residency in and periodic site fidelity to important habitats such as nurseries (McAllister et al., 2015) and gestation grounds (Nosal et al., 2021). To help stem population declines caused by overfishing, inshore spatial protections based on school shark residency behaviours have been implemented in Australia; however, these protections so far have only been effective at protecting newborns within nurseries (McMillan et al., 2019; Stevens, 2002). Unfortunately, all but the New Zealand population have been overfished to the point of collapse (Chiaramonte et al., 2016; Holts, 1988; Molfese et al., 2014; Pondella & Allen, 2008; Thomson et al., 2020; Winker et al., 2019), leading to school sharks being classified, globally, as Critically Endangered by the International Union for the Conservation of Nature (Walker et al., 2020), and added to Appendix II of the Convention on the Conservation of Migratory Species of Wild Animals (2020). Incorporation of accurate knowledge on the spatio-

temporal complexity of a population into management decisions is key to a population's effective management and recovery (Andrzejaczek et al., 2022; Braccini et al., 2016; Kessel et al., 2014; Martin et al., 2007; Simpfendorfer et al., 2011; Walker et al., 2008); however, for many school shark populations, this knowledge is limited. Hence, there is a need for a greater understanding of the spatio-temporal behaviours of school sharks to help improve the management and recovery of school shark populations worldwide.

New Zealand is home to the last stable school shark population (Tremblay-Boyer, 2021) where school sharks can migrate to habitats throughout New Zealand's main and offshore islands and southern Australia (Brown et al., 2000; Francis, 2010; Hurst et al., 1999; Lédée et al., 2021; McMillan et al., 2019; Walker et al., 2008). Though there is some exchange between biological stocks (e.g., Devloo-Delva et al., 2019; Hurst et al., 1999; McMillan et al., 2019; Walker et al., 2008), the Australian stock has collapsed, whereas the New Zealand stock remains largely stable (Tremblay-Boyer, 2021; Woodhams et al., 2023). Limited information on exchange between biological stocks, combined with differing stock statuses, suggests two separate populations, resulting in the management of national stocks. While our current understanding of school shark movements in New Zealand is limited to connectivity between release and recapture locations, there is evidence of movement towards several areas of likely significance to school sharks in New Zealand, such as the Kaipara Harbour (Francis, 2010; Hurst et al., 1999; Morrison, Jones, et al., 2014). The Kaipara Harbour hosts a wide variety of habitats and large biodiversity of species, including a seasonal abundance of adult female and year-round abundance of juvenile school sharks (Morrison, Lowe, et al., 2014; A. Burton unpublished data; Tindale Marine Research Charitable Trust unpublished data). Given the notable lack of adult males, it is suspected that the Kaipara Harbour may be acting as a nursery, gestation, and/or feeding ground for school sharks (Hernández et al., 2014; IUCN SSC Shark Specialist Group, 2024b; Morrison, Lowe, et al., 2014; C. Duffy unpublished data; A. Burton, C. Duffy, and S. Tindale personal observations;). However, it is unclear how important the Kaipara Harbour is to the New Zealand population and how it is connected to other habitats of likely significance. Given the concerns that the New Zealand population is starting to show signs of decline (Tremblay-Boyer, 2021), it is important to gain a greater understanding of the spatial movements of school sharks among key habitats in New Zealand, especially those that are important to reproduction and, therefore, the sustainability of the population.

The aim of this study was to investigate the spatio-temporal movements of large female school sharks in New Zealand using satellite telemetry, with a focus on assessing the degree of connectivity between the Kaipara Harbour and other locations that are of likely significance to the species. Based on previous evidence, the Kaipara Harbour is suspected to be connected to various habitats around New Zealand and even Australia. However, assessing habitat importance and connectivity requires knowledge of where and when sharks are residing and how they are using different areas. Hence, the specific objectives of this study are to:

1. Describe the movement patterns and habitat use (depth and temperature) of large female school sharks over the course of one year.
2. Identify where & when school sharks predominantly reside and whether the locations that are occupied are of likely significance to the species.

5.3: Methods

5.3.1: Tagging

Satellite tags were fitted to 25 female school sharks, >1m total length (TL), which were caught around the heads of the Kaipara Harbour between March 2021 and December 2022. Captures occurred during drifting and anchored angling sessions from a vessel. Burley, consisting of assorted fish frames and/or burley bombs, was used to attract sharks at anchored sites. Sharks were captured using traces, consisting of 8/0-16/0 barbless circle hooks, stainless steel trace (7x7, 316 grade) and 80lb leader (0.8mm, Black Magic tough trace), baited with fresh or frozen grey mullet (*Mugil cephalus*), kahawai (*Arripis sp.*), jack mackerel (*Trachurus sp.*), skipjack tuna (*Katsuwonus pelamis*), or bullet tuna (*Auxis rochei*).

Once animals were brought alongside the vessel, they were lifted onto the deck and placed on a wet foam mattress with a towel over their eyes to minimise stress. Out-of-water handling time was kept to a minimum, generally lasting less than three minutes. Sharks were then measured (total length, straight line, tail in natural or stretched position, to the nearest 5mm), sexed, and assessed for tagging suitability. Only sharks that were greater than 1m total length (TL, measured in a straight line with tail in the natural position), lively, and free of life-threatening injuries (e.g., excessive bleeding from the gills) and signs of undue stress were tagged.

MiniPAT satellite tags (Wildlife computers) were attached by inserting a “small” titanium anchor (45mm x 14mm x 1.3mm, Wildlife Computers), perpendicular to the first dorsal fin, through the pterygiophores (cartilaginous radials at the base of the first dorsal fin) and into the dorsal musculature on the adjacent side of the fin (~100mm, Figure 5.1). Anchors were inserted using a stainless steel applicator (sterilized with isopropyl alcohol) at a shallow angle, no more than 45°, to prevent the anchor from piercing the vertebral column or the body cavity. To set the tag, the applicator was twisted towards the posterior of the animal and the tag’s tether was tugged on gently. The tags were checked visually to ensure that no more than the anchor crimp was visible (Figure 5.1). Tag tethers consisted of a mixture of 7x7 stainless steel and 400lb mono between 120mm and 230mm (Table A4.1.1).

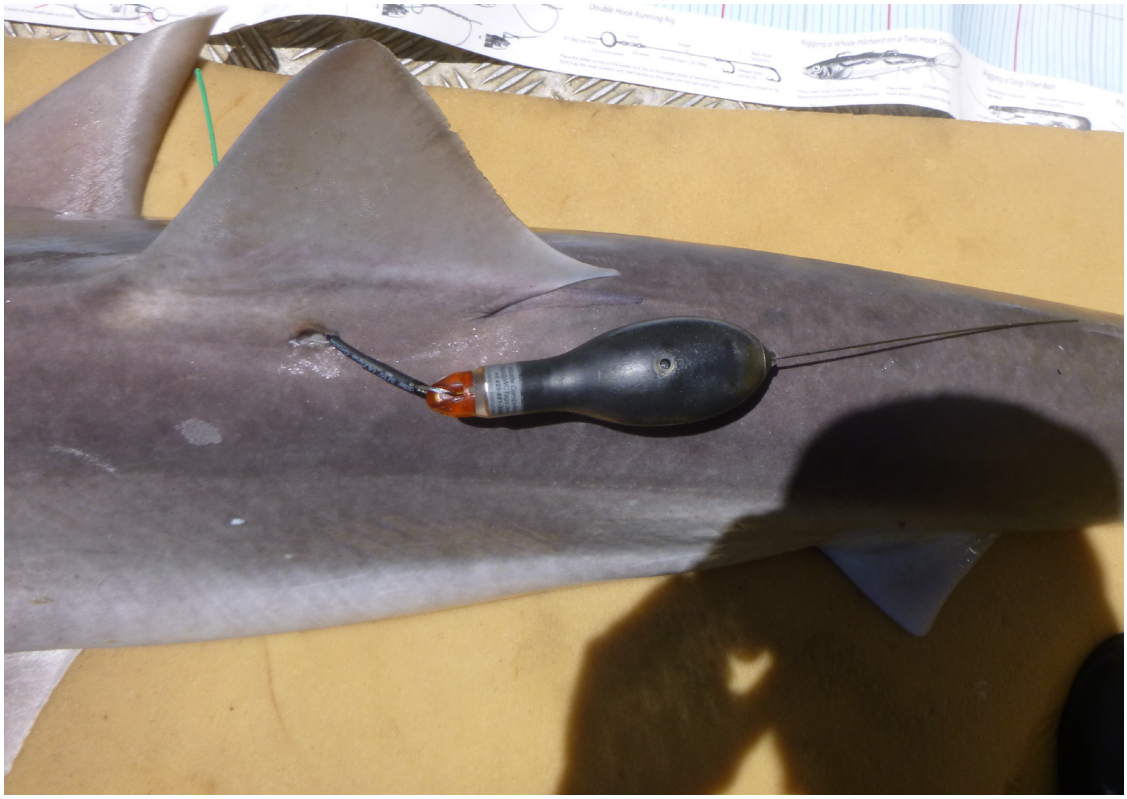


Figure 5.1: *A female school shark on a wet foam mattress with a Mini-PAT satellite tag and dart tag attached.*

Some of the satellite tagged sharks were also tagged with a Tindale Marine Research Charitable Trust (TMRCT) inshore tagging program elastomer/dart tag in the pterygiophores but on the opposite side of the dorsal fin (Figure 5.1). This was so that sharks could be identified if they were caught after the satellite tag deployment period.

Once tagged, sharks were placed back in the water, held upright, facing into the current, until signs of strong activity/liveliness were evident. Sharks were monitored after release to ensure they were swimming properly. Once released, the release location, animal condition (Table A4.2.1), depth, and sea surface temperature (SST) were recorded.

5.3.2: Programming

MiniPAT tags were programmed to detach 365 days after deployment. During deployment, tags measured and archived measurements of depth (accuracy: $\pm$ 1%), temperature (accuracy: $\pm$ 0.1°C), and light (range: 5×10^{-12}W cm^{-2} to 5×10^{-2}W cm^{-2}) every five seconds. At the end of a deployment, tags transmitted summaries of the archived data via satellite. To maximise the amount of data received via satellite transmissions, tags sampled archived depth and temperature measurements (in five-minute intervals) every day for the first 90 days of the deployment and then every second day after that for the remainder of the deployment. Furthermore, the tags generated summary messages of time at depth and temperature and daily activity every 12 and 24 hours, respectively. These additional summary messages were to help reduce the possible number of gaps in the transmitted data.

Once a tag reached the end of its deployment, stayed at a constant depth (± 1m) for more than three days, or dived to >1700m, the tag would detach from the animal, float to the surface, and start transmitting summaries of the archived data to the ARGOS satellite network. Detached tags also pinged a radio beacon every two seconds to assist with its recovery using an IC-R30 receiver (ICOM) and yagi antenna (Model: 401.68-3, Arrow Antennas). Transmitted data summaries received by the ARGOS satellite network and recovered tag data archives were both processed using the Wildlife Computers Data Portal.

If a tag was recovered and had its data archive downloaded, then the archived data was used for analysis. Otherwise, data summaries retrieved from the ARGOS satellite network were used.

5.3.3: Data analysis

Maximum likelihood positions and temporary residency distributions of sharks were estimated using the Global Position Estimator 3, hidden Markov, state-space model (GPE3, Wildlife Computers) utilising a 0.25°x0.25° grid. Model parameters included a constant swimming speed. A range of swimming speeds have been used to model school shark tracks (e.g., McMillan et al., 2019; Rogers et al., 2017; Schaber et al., 2022). Given that the swimming speed variable is fixed, various swimming speed assumptions were compared using model scores (the averaged likelihood of the model estimates given the data) and the likelihood the shark migrated along the modelled track (based on comparisons between estimated position and recorded depth data). The swimming speed with the best model score and greatest likelihood were selected. GPE3 models for all sharks assumed a swimming speed of $1ms^{-1}$.

Maximum likelihood positions were derived by fitting estimated geolocations and observations of twilight, SST, and swimming depth from an individual's tag against known sea surface temperatures (NOAA OI SST V2 High Resolution dataset; Huang et al., 2021), depth (ETOPO1-bedrock; Amante & Eakins, 2009), and locations.

A hidden Markov smoothing algorithm within the GPE3 was used to determine the likely temporary residency of an individual in a given location and time (Pedersen et al., 2011; Thygesen et al., 2009). This involves estimating the probability of an individual being in a resident or transient behavioural state at a given time and place based on the posterior distribution of an individual's behavioural state. For each individual, areas with probabilities of modelled residency ≥ 0.2 (i.e., areas where sharks were estimated to spend at least 20% of the deployment) were considered to be areas of temporary residency for that shark. To look at temporary residency patterns across all tagged sharks, the probabilities of modelled residency of all sharks were averaged. Areas where the average probability of modelled residency > 0.08 were classified as temporary residency "hot spots" as this value corresponds to at least 4 individuals estimated to spend at least 20% of the tag deployment in that area.

For all individuals, the maximum likelihood tracks and temporary residency distributions also included the drift of the tag due to using the first ARGOS location as the end location in the GPE3 model. Due to the detachment programming (see section '*5.3.2: Programming'* for details) and/or the transmission settings (only transmit data summaries and location when tag sensor detects its dry after at least one dry reading), the tags likely drifted between the true detachment and the first ARGOS location. To counter the presence of drift, tracks and temporary residency patterns after the

time the tag detached from the shark were removed to show an accurate representation of these two results.

Given the large degree of error associated with geolocations, even with refinement through state-space models, only tracks for sharks that travelled ≥ 120km or ~1 degree of latitude away from the original tagging site are presented (Braun et al., 2015; Gatti et al., 2021). This is because the error can exceed the actual movement made over short distances.

Visualisations and comparisons of the GPE3 output and mark-recapture data (see below) were conducted in R and R Studio (Posit team, 2024; R Core Team, 2024). The GEBCO 2024 15-Arc second bathymetry grid (GEBCO Compilation Group, 2024) and ggOceanMaps package (Vihtakari, 2024) were used for bathymetry visualisations. rnaturalearth (Massicotte & South, 2023) and southernMaps (Burge, 2017) packages were used for land visualisations.

Connectivity of the Kaipara Harbour to other possibly important locations within Australia and New Zealand was examined by comparing movements and temporary residency of the satellite tagged females with mark-recapture data from the Southern Shark tagging database as well as the NIWA shark, New Zealand Gamefish, and TMRCT inshore tagging programs. Connectivity between regions from mark-recapture data was visualised using the circlize package (Gu et al., 2014) and regions defined in Table A4.3.1 and Figure A4.3.1. The life-history stage of individuals undertaking migrations between regions was determined by the life-history stage at recapture. Seasonal abundances of released and recaptured school sharks were used to determine if school sharks were present in the same region and time the satellite tagged school sharks were temporarily residing there. Seasonal abundance was calculated, using a hexagonal grid, as the number of school sharks released or recaptured in each grid cell divided by the total number of school sharks released or recaptured in a season.

The tagging programs included in the Southern Shark tagging database are described in Brown et al. (2000). Data from the Southern Shark tagging database was limited to records up to 2008, whereas data from the other programs extended through to 2024. The NIWA shark and New Zealand Gamefish tagging programs are described in Francis (2010) and Hurst et al. (1999), and Holdsworth et al. (2016), respectively. The TMRCT inshore tagging program consists of tagging fish and chondrichthyan species with plastic anchor dart tags by recreational and commercial fishers. Upon release or recapture of an animal, the GPS coordinates, depth, and date of capture are recorded, as well as the length of the animal. For school sharks, specifically, the recording of the sex and maturity of animals was also recorded. In the NIWA and TMRCT programs, maturity was only assessed for males and was derived by examination of the claspers (as described in Table A2.1.1). For individuals in the Southern shark tagging database, females that were not re-released and had in-utero eggs or embryos present were deemed mature. If maturity of an individual could not be determined at release or recapture in any of the tagging programs, individuals greater than the estimated length-at-maturity (New Zealand (M:1280mm TL, F:1375mm total length), Australia (M:1306mm TL, F:1399mm total length), Chapter 3; Appendix 2.5) were deemed mature. While lengths were unable to be validated as part of this study, we have high confidence that the length recorded at release of the NIWA tagging program and at release and recapture of the TMRCT inshore tagging program reflect the total length of the animal unless otherwise specified.

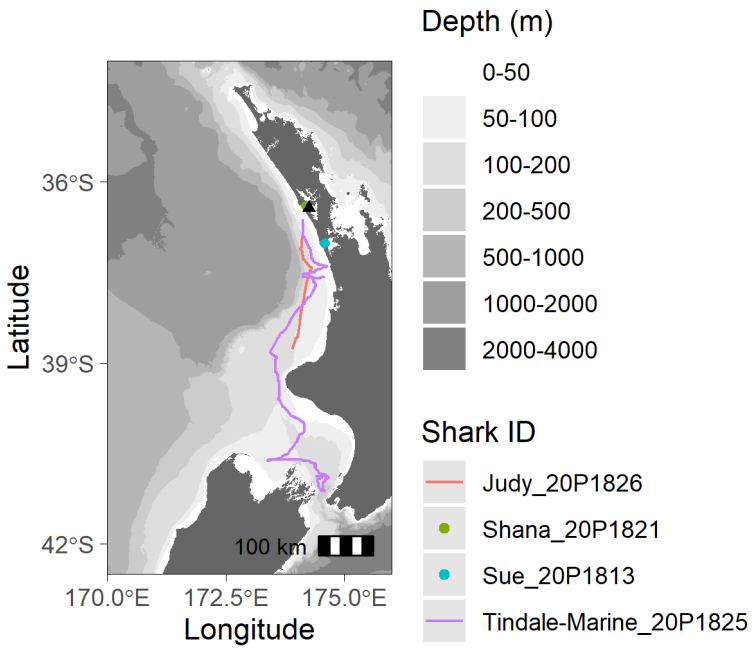
5.4: Results

Female school sharks that were tagged with MiniPAT tags ranged in length from 1370mm to 1650mm total length (TL), with most being above the estimated length-at-maturity (1375mm TL) for the New Zealand population (Appendix 2.5, Table 5.1). None of the captured females appeared to be heavily pregnant or have mated recently based on external assessments and lack of bruising and swelling of the cloaca. Data from 14 tags were excluded from analyses due to mortality, premature releases that occurred within five days of release, sharks not travelling >120km away from the tagging site, or tags not reporting nor being recovered (Table 5.1). Premature releases within five days of release were either likely due to wounding or predation by predators (e.g., Great White sharks (*Carcharodon carcharias*), Sc. Tindale personal observation) or the anchors coming loose. Mortality of one individual was confirmed by recorded temperatures being approximately 4°C warmer than the surrounding water (Figure A4.6.5) and a lack of light readings for multiple days, indicating the tag had been ingested.

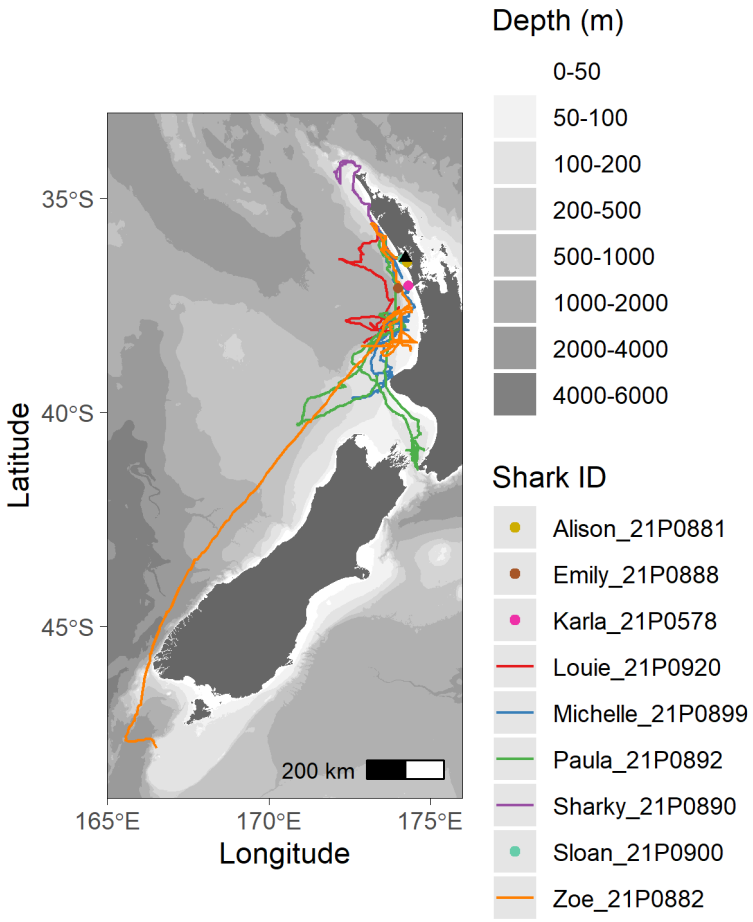
Table 5.1: *Details of sharks tagged with MiniPAT satellite tags. Shark ID's in* ***bold*** *denote individuals included in the analysis. Total length is the total length measured in a straight line, with the tail in a natural position. "*" denotes initial total length measurements that were converted to the total length variant reported in the table using models from Chapter 2. Tag date is the date the shark was tagged and tag latitude and longitude are the release coordinates. End date is when the tag popped off or was removed from the shark if it was captured. Detachment indicates how the tag detached. "+" denotes if a prematurely released tag's pin was intact at the time the tag released from the shark. Time at liberty is the time the tag was attached to the shark. Retrieved indicates whether a tag was recovered.*

Shark ID	Total length (mm)	Sex	Tag date	Tag Latitude	Tag Longitude	End date	Detachment	Time at Liberty (days)	Retrieved
Judy (20P1826)	1650	F	01-03-2021	-36.4311	174.2388	12-03-2021	Premature+	11	N
Sue (20P1813)	1460	F	01-03-2021	-36.4349	174.2441	05-03-2021	Premature+	4	Y
Eleanor (20P1812)	1570	F	01-03-2021	-36.4338	174.2419	05-06-2021	No report	96	N
Shana (20P1821)	1445	F	01-03-2021	-36.4298	174.2384	03-03-2021	Premature+	2	N
Ruth (20P1824)	1460	F	02-03-2021	-36.4344	174.2408		No report		N
Tindale-Marine (20P1825)	1440	F	02-03-2021	-36.4406	174.2480	13-08-2021	Premature+	164	Y
Sharky (21P0890)	1565	F	04-01-2022	-36.3869	174.2246	05-06-2022	Capture	152	Y
Lorraine (21P0893)	1530	F	04-01-2022	-36.3869	174.2246	07-02-2023	No report	399	N
Sloan (21P0900)	1580	F	08-01-2022	-36.3865	174.2226	08-01-2022	Premature+	0	Y
Alison (21P0881)	1570	F	08-01-2022	-36.3865	174.2226	14-01-2022	Mortality	0	Y
Natalie (21P0911)	1520	F	08-01-2022	-36.3865	174.2226		No report		N
Zoe (21P0882)	1510	F	08-01-2022	-36.3865	174.2226	09-01-2023	Scheduled	366	N
Emily (21P0888)	1550	F	08-01-2022	-36.3865	174.2226	20-01-2022	Premature+	12	N
Dianne (21P0884)	1540	F	08-01-2022	-36.3865	174.2226		No report		N
Michelle (21P0899)	1470	F	08-01-2022	-36.3865	174.2226	08-01-2023	Scheduled	365	N
Karla (21P0578)	1510	F	08-01-2022	-36.3865	174.2226	11-01-2022	Premature+	3	Y
Paula (21P0892)	1460	F	08-01-2022	-36.3865	174.2226	09-01-2023	Scheduled	366	N
Louie (21P0920)	1490	F	08-01-2022	-36.3865	174.2226	31-07-2022	Premature+	204	Y
Anna (21P0912)	1550	F	20-12-2022	-36.3970	174.1279	12-03-2023	Premature+	82	Y
Kelly (21P0887)	1450	F	20-12-2022	-36.3970	174.1279	25-12-2023	Mortality	5	N
Heidi (21P0919)	1450	F	20-12-2022	-36.3970	174.1279		No report		N
Sarah (21P0883)	1400	F	20-12-2022	-36.3970	174.1279	20-12-2022	Premature+	0	Y
Marie (21P0879)	1370	F	20-12-2022	-36.3968	174.1292	03-09-2023	Capture	257	Y
Caitlyn (21P0896)	1550*	F	20-12-2022	-36.3968	174.1292	30-08-2023	Premature+	253	N
Etoile (21P0880)	1480*	F	20-12-2022	-36.3968	174.1292	20-12-2023	Scheduled	365	N

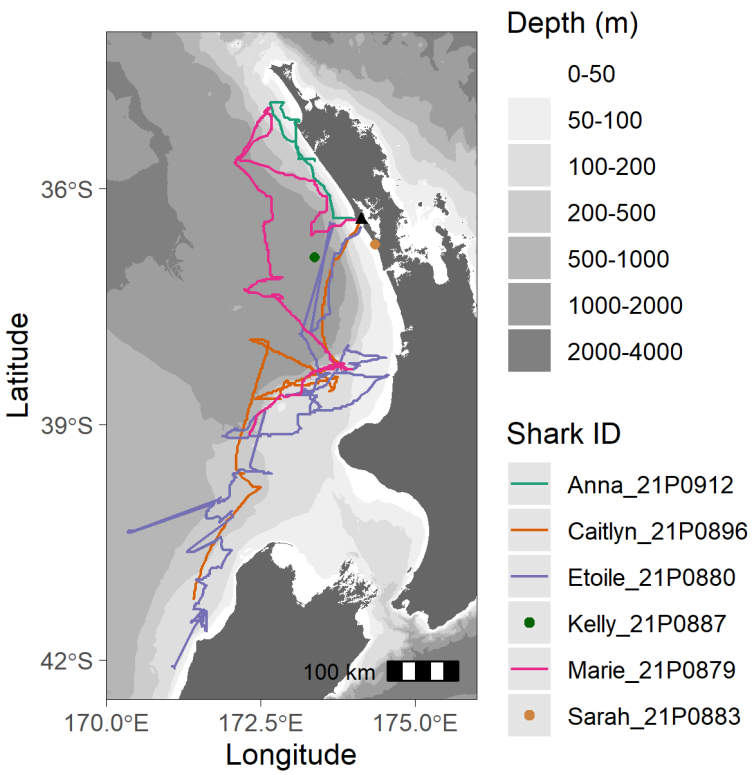
Of the data from the 11 tags that could be used, only four tags popped off on the scheduled release date (365 days after release, Table 5.1). The remaining tags either detached prematurely or were retrieved from captured sharks, ranging in deployment between 11 and 257 days (Table 5.1). Only two sharks tagged in March 2021 had tracks estimated. One migrated to the Cook Strait and the other rapidly migrated to the North Taranaki Bight (~300km in 11 days, Figures 5.2a, A4.4.1, and A4.4.2), the fastest movement of any of the tagged sharks. Individuals tagged in January 2022 showed the most variation in behaviour, with individuals migrating to the Three Kings Islands (n=1), Snares Islands (n=1), Cook Strait (n=1), and the North Taranaki Bight (n=2, Figure 5.2b and Figures A4.4.3-A4.4.7). Individuals tagged in December 2022 primarily migrated south towards Cape Egmont (n=1) and the West Coast of the South Island (n=2, Figure 5.2c and Figures A4.4.8-A4.4.10). Only one individual tagged in December 2022 migrated north to coastal areas near Ahipara and the Hokianga Harbour (Figure 5.2c and Figures A4.4.11).



a) March 2021



b) January 2022



c) December 2022

Figure 5.2: *Maximum likelihood tracks and capture/tag pop-up locations of female school sharks tagged with satellite tags by deployment period. The black triangle is the release location for the tagged sharks. The lines are the maximum likelihood tracks estimated for sharks that moved more than 120km from the release location. The filled circles are capture/pop-up locations for sharks that moved less than 120km from the release site that had tags report or recovered.*

During migrations, the majority of the tagged school sharks temporarily resided in specific areas for extended periods before continuing with their migrations (Figure 5.2 and Appendix 4.4 and 4.5). Maximum probabilities of modelled residency ranged from 0.05 to 0.74 (highest probability = 1), with most sharks ranging from 0.3 to 0.74 (Appendix 4.5). Temporary residency behaviour occurred in many areas throughout New Zealand, such as Ahipara, the Three Kings Islands, and Westport, but was most concentrated in three temporary residency "hot spots" (Figure 5.3). These were located on the west coast of Northland near the Hokianga Harbour mouth (Tutamoe), North Taranaki Bight shelf break (North Taranaki Bight), and between d'Urville Island and the Cook Strait Narrows (Outer Cook Strait). All three temporary residency hot spots were located on narrow sections of the continental shelf and/or included the continental shelf break (~200m) and slope (Figure 5.3). Each hot spot was predominantly used at different times of the year; however, school sharks used the North Taranaki Bight year-round (Figure 5.3). In some cases, temporary residency hot spots were used one after another; for example, some school sharks temporarily resided in the Tutamoe hot spot after leaving the Kaipara Harbour and then in the North Taranaki Bight before carrying on with their migration (Appendix 4.4 and 4.5).

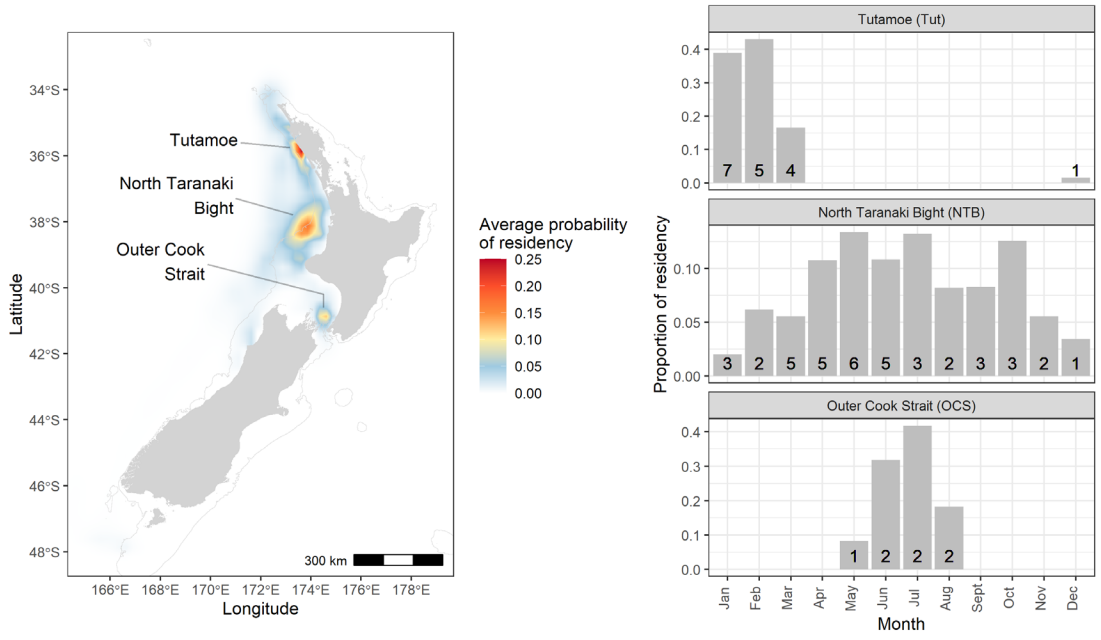


Figure 5.3: *Left: Locations of the three 'temporary residency hot spots' for school sharks tagged in the Kaipara Harbour, based on averaged probabilities of modelled residency states for sharks that travelled >120km from the release location. Areas with probabilities greater than 0.08 were deemed temporary residency hot spots for all included sharks. The grey contour symbolises 200m, which coincides with the continental shelf break. Right: Portion of time spent in each temporary residency hot spot by month. Values inside each column represent how many tagged school sharks were present in each hot spot during a given month.*

Individuals in both migrating and residing states typically used waters less than 160m (Figure 5.4 and Appendix 4.6), though many school sharks spent time along or near the continental shelf break or in deeper waters (≥200m, Figures 5.2 and 5.3). Depth use varied between 0 and 546m; however, except for some of the vertical migrations in the North Taranaki Bight and Outer Cook Strait temporary residency hot spots, use of waters deeper than 200m was generally restricted to sharks in a migrating state (Figure 5.4 and Appendix 4.6). At the Tutamoe temporary residency site, depth use was typically limited to less than 100m. Temperatures ranged from 8.2°C to 22.5°C (Figure 5.4), though sharks in migrating and residing states typically remained in waters between 12°C and 22°C (Figure 5.4). Waters cooler than 12°C were only recorded during migrating behaviour in deep water (Appendix 4.6).

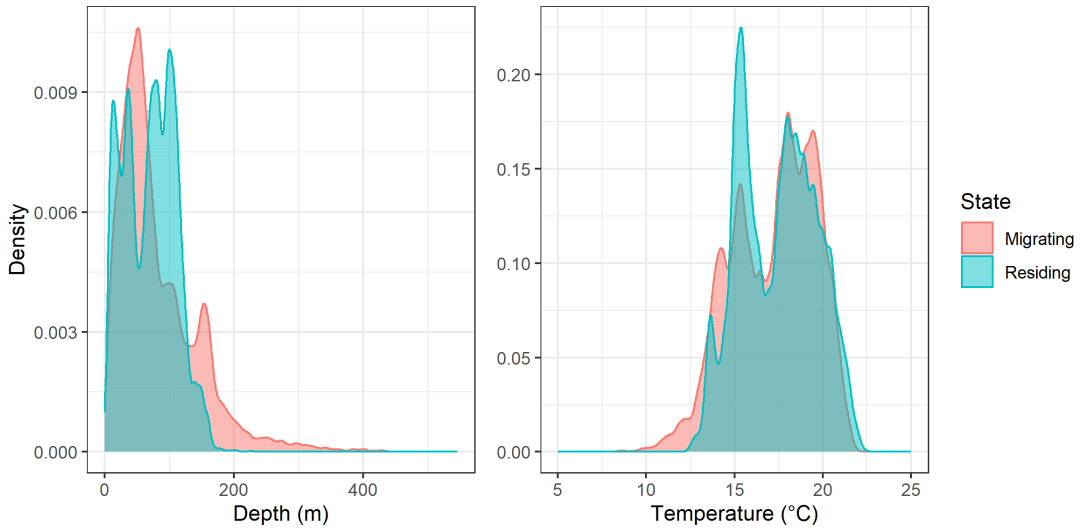
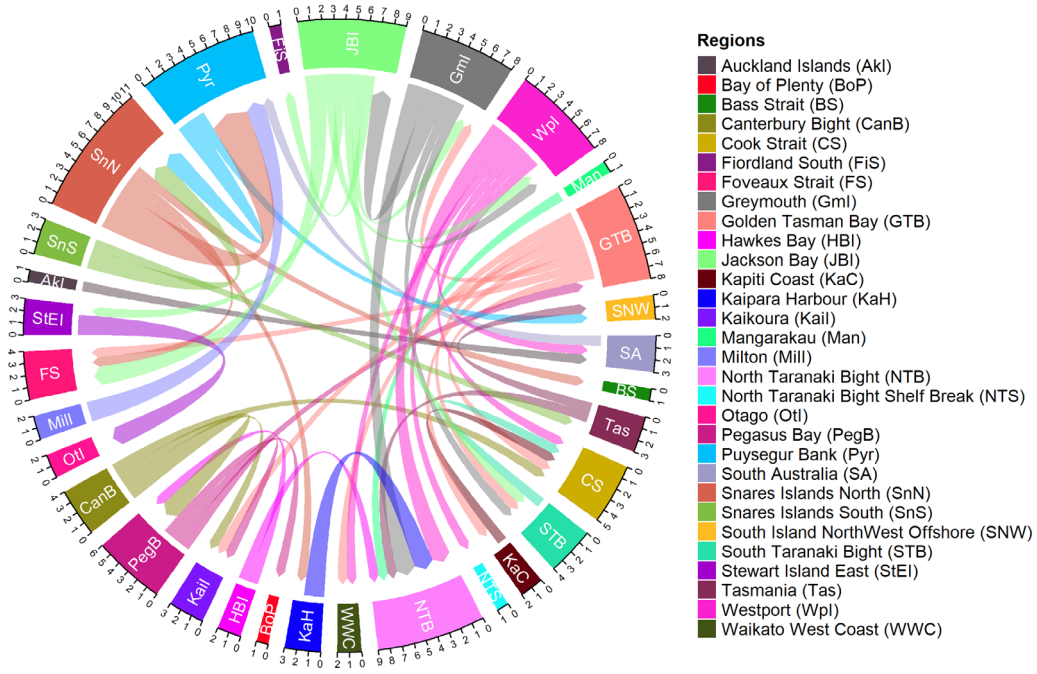
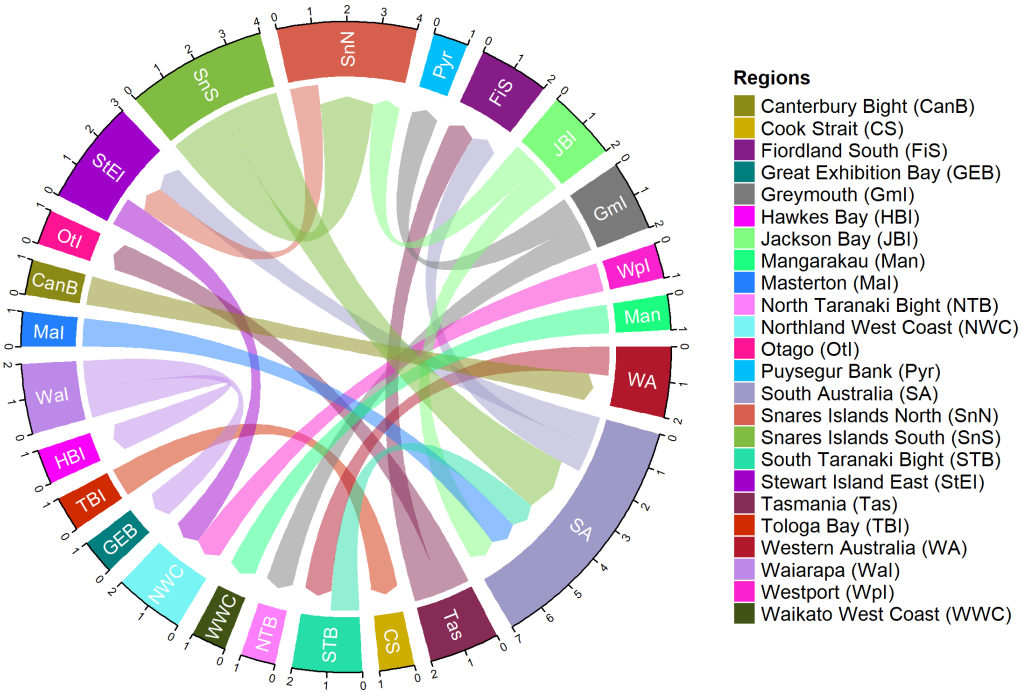


Figure 5.4: *Densities of the time spent at depth (left) and temperature (right) for sharks in residing vs migrating states.*

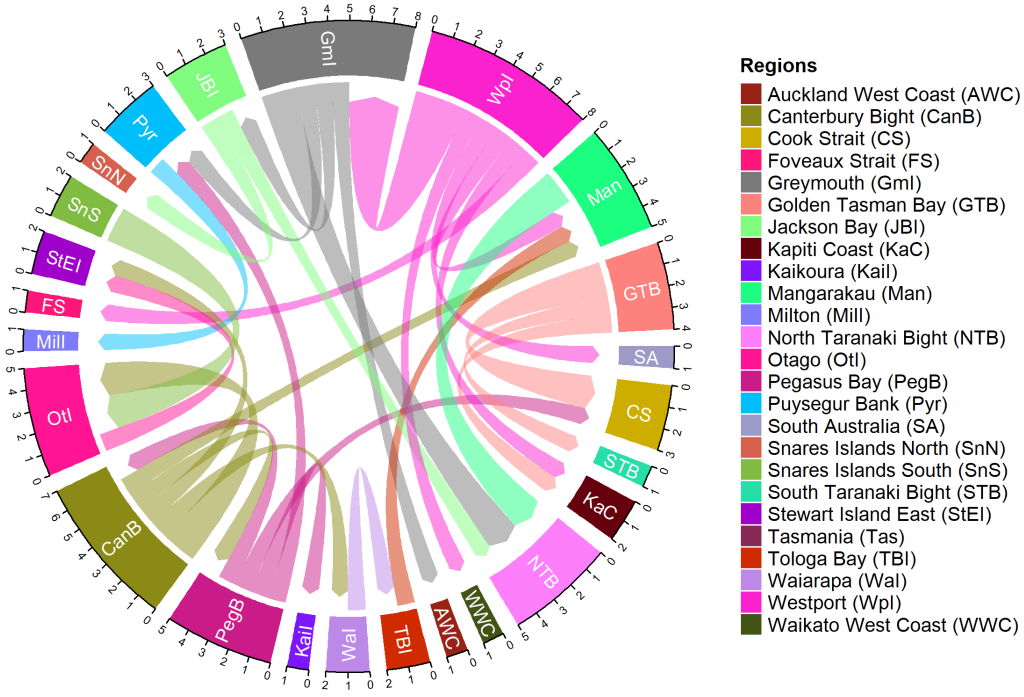
From mark-recapture data, connections between the Kaipara Harbour and the Snares Islands and North Taranaki Bight were observed in at least two juvenile female school sharks (Figure 5.5a). All life stages and both sexes of school sharks from around New Zealand were observed in the North Taranaki Bight and Outer Cook Strait temporary residency hot spots, with some individuals originally tagged in southern Australia recaptured in the North Taranaki Bight or near the Outer Cook Strait hot spots, at similar times as when the satellite tagged school sharks were temporarily residing there (Figure 5.5a-d and Appendix 4.7). Adult females from Westport and Stewart Island were recaptured in the Tutamoe temporary residency hot spot; however, their recaptures did not coincide with the periods when satellite tagged females were temporarily residing there (Figure 5.5b and Appendix 4.7). For individual temporary residency areas, a juvenile female from Australia was recaptured in the Three Kings Shelf temporary residency area, but not at the same time that a satellite tagged female was temporarily residing there (Appendix 4.7). School sharks tagged or recaptured near the Cook Strait, Snares Islands, Stewart Island, as well as the west (including Westport) and east coasts of the South Island also migrated to and from Australia (Figure 5.5a-d). School shark migrations from Australia to New Zealand also included the recapture of a late-term pregnant female off the Otago Peninsula 11.8 years after it was released.



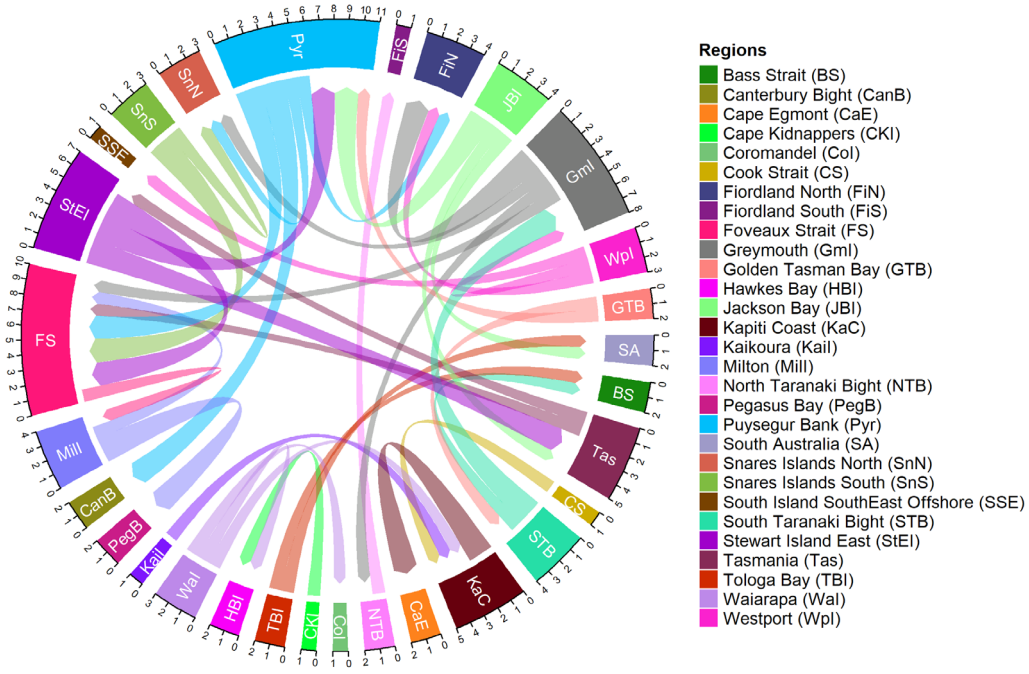
a) Juvenile females



b) Adult females



c) Juvenile males



d) Adult males

Figure 5.5: *Connectivity of different stages and sexes of school sharks between regions given by direction and number of individuals moving between regions. See Appendix 4.3 for region definitions.*

5.5: Discussion

School sharks that frequent the Kaipara Harbour migrate to and from locations widely dispersed within and beyond the latitudinal extent of mainland New Zealand, suggesting that the Kaipara Harbour is connected to a variety of habitats used by the wider New Zealand school shark population. While data on movements into the Kaipara Harbour is limited to mark recapture data from a few individuals (Figure 5.5), large female school sharks observed in the Kaipara Harbour utilize a variety of habitats throughout New Zealand that are also frequented by other school shark life-history stages from around New Zealand (Figures 5.2, 5.3, and 5.5; Appendix 4.6; McMillan et al., 2019). As seen in at least three other school shark populations, the larger scale migrations to and from the Kaipara Harbour may reflect partial migrations, with philopatry and/or site fidelity being among the motivators involved (Chapman et al., 2012; McMillan et al., 2019; Nosal et al., 2021; Thorburn et al., 2019). Although not directly observed in this study, school sharks may exhibit philopatry, reproductive site fidelity, and/or feeding site fidelity to the Kaipara Harbour as it is likely being used as gestation, pupping, nursery, and feeding grounds for school sharks (Hernández et al., 2014; Morrison, Lowe, et al., 2014; A. Burton unpublished data; C. Duffy unpublished data). Similar patterns of feeding and reproductive site fidelity have been observed over various spatio-temporal scales in other elasmobranch species (e.g., Acuña-Marrero et al., 2017; Madigan et al., 2015; Pratt et al., 2022), including in New Zealand (e.g., Duffy et al., 2012). However, our limited knowledge on the biology of school sharks in New Zealand, such as reproductive behaviours, makes it difficult to evaluate the factors driving the use and relative importance of the Kaipara Harbour to the New Zealand school shark population.

In addition to the Kaipara Harbour, three areas predominantly used by satellite tagged females may also serve as important feeding and reproductive habitats for New Zealand school sharks, with some evidence of use by a small number of school sharks tagged in Australian waters. The Tutamoe, North Taranaki Bight, and Outer Cook Strait temporary residency hot spots encompassed the continental shelf break and/or warm coastal waters (Figure 5.3; Jones et al., 2018) which are supplied with nutrients from harbours, upwellings, and/or water mixing (Allen & Madron, 2009; Bowman et al., 1983; Chiswell et al., 2017; Ridgway, 1980; Roberts & Paul, 1978; Stevens et al., 2021; Sutton & Bowen, 2011). A combination of the conditions and nutrients present allow each area to support a large abundance and diversity of species including not only prey (Table A4.8.1) and predators of school sharks but also all life-history stages of school sharks at the same time that satellite tagged females were temporarily residing there (Appendix 4.7; Duffy et al., 2012; Fisheries New Zealand, 2024; Jones et al., 2016; Morrison, Jones, et al., 2014; Paul & Sanders, 2001; Tremblay-Boyer, 2021; York, 1970; C. Duffy unpublished data; A. Burton personal observations). To mitigate the cost of migrations, especially migrations through prey-scarce areas, sharks will reside in prey-rich areas to gather sufficient energy prior to carrying on with their migration (Chapman et al., 2011; Gleiss et al., 2022; Del Raye et al., 2013). School sharks of all life-history stages from around New Zealand and Australia migrated to and from these temporary residency areas, including to and from areas known or suspected to be important to school shark life-history (Figure 5.5a-d; Table A4.9.1). When temporarily residing in these temporary residency areas, school sharks were also regularly vertically migrating within 250m. Given the high prey abundance and variety, it is possible that school sharks were selectively targeting abundant, vertically migrating prey to rebuild energy stores to sustain activities such as continued migration. Another possible driver for use of these three temporary residency areas is reproduction based on

the presence of adult males and females at the same time (Appendix 4.7; Tremblay-Boyer, 2021; York, 1970; A. Burton personal observations from donated individuals). However, given the presence of all life-history stages of school sharks in the same general area and time, the use of temporary residency areas for other activities, such as social interactions, cannot be ruled out, as motivations driving the use of an area can co-exist and interact (Lubitz et al., 2022; McInturf et al., 2023). Moreover, vertical migration patterns as a result of predator or con-specific avoidance strategies (Braun et al., 2022) also cannot be ruled out. Given the national importance of the three temporary residency areas for New Zealand school sharks, as well as evidence that some Australian school sharks also use them, further research is needed to determine why and how these areas are used by school sharks.

Despite temporarily residing in important habitats for extended periods, some school sharks chose to continue migrating to other areas. If these important habitats were able to continually provide ample resources, why would school sharks not remain there? The North Taranaki Bight temporary residency area was used by school sharks and able to support abundances of prey year-round (Figure 5.3; Table A4.8.1; Fisheries New Zealand, 2024). The Kaipara Harbour and the North Taranaki Bight likely provide the resources required for school sharks to complete their life cycle (e.g., feeding, mating, and pupping grounds); yet, after extended temporary residency in the North Taranaki Bight, some individuals continued to migrate and spend time near Westport or the Snares Islands before the tags detached. Both Westport and the Snares Islands are also likely important feeding and reproductive habitats based on the presence of school sharks and prey as well as the connectivity with habitats throughout New Zealand and southern Australia (Figure 5.5a-d; Fisheries New Zealand, 2024; McMillan et al., 2019; Morrison, Jones, et al., 2014; Paul & Bradford, 2000). Even though it may be more energetically costly to the individual to migrate to Westport or the Snares Islands, school sharks would possibly migrate to these areas if it minimised the overall costs, for example rebuilding energy reserves in prey-rich areas closer to a destination would allow for sustained large-scale migrations, such as migrations to Australia, or individuals were showing individual preference or site fidelity to specific areas (Chapman et al., 2011; Chapman et al., 2015; Shaw, 2020). However, more information is required to better understand why school sharks only temporarily use regions that appear to provide ample resources throughout the year.

The movement patterns and habitat use described here were limited to year-long tracks of 11 large female school sharks, where data was often incomplete due to premature detachment and patchiness in transmitted data. Length and spatio-temporal gear selectivity also affected the mark-recapture data, particularly for New Zealand, where most school sharks were initially tagged during NIWA trawl surveys. Additionally, the lack of reproductive data meant that the life-history stage assignments for satellite-tagged and many dart-tagged individuals relied on length-at-maturity estimates, introducing uncertainty in the true stage of individuals. As a result, these factors limited the modelling of tracks, inferences and interpretations of the data, and generalisation to only a fraction of the New Zealand school shark population. To better understand the spatio-temporal complexity of New Zealand school sharks and extent of exchange between the Australian and New Zealand populations, it is recommended that school sharks of various life-history stages and sexes are tagged around Australia and New Zealand with satellite and acoustic tags at different times of the year to look at movement and habitat use over various spatio-temporal scales. Tagging should involve methods that minimise post tagging recovery time and impact to the shark as well as

biofouling of the tag to maximise the amount of data collected during a deployment. Moreover, efforts to non-lethally assess the reproductive stage of sharks at the time of release (and if recaptured and re-released) should also be considered. Future work should also investigate improving upon the modelling of school shark migration routes and spatial state (migrating vs residing) by incorporating different types of data (e.g., time series depth, temperature, and tri-axial acceleration data) to improve estimates. As mentioned by Lubitz et al. (2022), dedicated studies are required to better understand the drivers behind school shark movements and habitat use. This would include utilizing developing techniques, such as animal-borne cameras, baited remote underwater videos, remotely operated vehicles, cloacal swabs, and accelerometers, to better observe behaviours. However, extensive investigations into the diet and reproduction of New Zealand school sharks are required prior to such a study being undertaken, as current knowledge is limited.

This study presents the first in-depth look into the movement and habitat use of school sharks in New Zealand, re-affirming the spatio-temporal complexity of the population's dynamics inferred from mark-recaptured data. The Kaipara Harbour was found to be one of many interconnect habitats important to the life-history of the New Zealand school shark population. Temporary residency patterns of satellite-tagged female school sharks revealed multiple areas of likely significance to the New Zealand school shark population, which are also used to some extent by school sharks migrating from Australia. Located off the west coast of Northland, in the North Taranaki Bight, and in the Outer Cook Strait, these areas are likely used for feeding and, potentially, reproduction. Despite further research being required to determine the drivers of the migrations as well as the habitat use in the Kaipara Harbour and other areas of likely significance, these results provide fundamental knowledge on the movements and habitat use of school sharks in New Zealand. Such information enhances our understanding of stock structure and key habitats, aiding in improving the management of the New Zealand school shark population and the sustainability of the fishery it supports.

Chapter 6: Is it my burden to bear: The maternal transfer potential of school sharks (*Galeorhinus galeus*)

6.1: Abstract

Maternal transfer, defined here as the process where inorganic or organic contaminants that are stored in a mother's tissues are mobilised during vitellogenesis, gestation, and/or lactation and passed onto the developing follicles, embryos, and young, respectively, is often thought to be the process responsible for the initial exposure of contaminants to developing elasmobranchs. Yet, there is a lack of mechanistic evidence to support maternal transfer being the process responsible. By examining how and when school sharks (*Galeorhinus galeus*) provide their young with nutrients and associations of several essential and non-essential elements between maternal and embryonic tissues, this study evaluates the extent to which school sharks from the New Zealand population transfer elements to their young. It is likely that developing school sharks are provided with the majority of their nutrients by those assimilated from the mother's diet during vitellogenesis. Coupled with the lack of evidence of associations between maternal and embryonic element tissue concentrations, there was no evidence to support maternal transfer being the process responsible for the initial exposure of selected elements in school sharks from the New Zealand population. Instead, elements assimilated from the mother's diet at the time of vitellogenesis is the more likely process. However, further work under controlled conditions is needed to confirm the patterns observed in this study.

6.2: Introduction

The term "maternal transfer" has been used to describe the transfer of nutrients as well as inorganic contaminants (i.e., essential and non-essential elements) or organic contaminants (e.g., persistent organic pollutants) from mother to young across a wide range of taxa. In contrast, the term "maternal offloading" refers specifically to the transfer of contaminants. While maternal transfer and maternal offloading have been used to describe different processes, the consensus among researchers is that, for all vertebrate classes, the contaminants in an animal's young originate from the mother's accumulated stores (e.g., Addison & Brodie, 1977; Guirlet et al., 2008; Hopkins et al., 2006; Lyons & Lowe, 2013a; Niimi, 1983; Peterson & Ellarson, 1976). Here, maternal transfer/offloading (herein referred to as maternal transfer) is defined as the process where inorganic or organic contaminants that are stored in a mother's tissues are mobilised during vitellogenesis, gestation, and/or lactation and passed onto the developing follicles, embryos, and young, respectively. More specifically, when maternal reserves of lipids and other metabolites are catabolised to supplement their developing follicles or young, contaminants that are associated with or stored in the same tissue as the metabolites will be transported with the metabolites to the developing young. Importantly, this definition assumes the contaminants in young are solely derived from the mother's accumulated reserves and not what she is assimilating from her diet at the time of reproductive events that provide nutrients to young such as oogenesis (follicle development, including vitellogenesis for non-mammalian taxa), gestation, and lactation. It is

important to distinguish the sources of contaminants in young, as contaminants transferred from maternal reserves will have multi-generational impacts, whereas contaminants assimilated from a mother's diet at the time of reproductive events will only affect a single generation.

Over the past 48 years, literature on maternal transfer of contaminants has been steadily increasing, covering a wide array of species and taxa. This is because maternal transfer creates a pathway for significant accumulation of contaminants in animals over multiple generations (Lyons et al., 2013; Martins et al., 2022). For many species, mechanistic ("direct") evidence of maternal transfer, as defined here, remains limited (Guiney et al., 1979), with most studies relying on comparisons between contaminant concentrations in maternal and young tissues, timing of reproductive events, and mass/metabolite concentrations of tissues suspected of being involved in the provisioning of young ("in-direct" evidence; e.g., Borrell et al., 1995; Guirlet et al., 2008; Hopkins et al., 2006; Lyons & Lowe, 2013a; Niimi, 1983; Peterson & Ellarson, 1976). While maternal transfer could be occurring, particularly during fasting periods (e.g., Addison & Brodie, 1987; Findlay & Defreitas, 1971; Kelly et al., 2011; Miller, 1993), other potential origins of contaminants in the young also need to be considered, such as contaminants assimilated by the mother during key reproductive events (e.g., Addison & Brodie, 1987; Giesy et al., 2002; Hammerschmidt & Sandheinrich, 2005; Jeffree et al., 2015; Lahaye et al., 2007).

For elasmobranchs, maternal transfer is often assumed because sharks are primarily capital breeders; that is, they build up energy reserves in the liver prior to oogenesis and gestation which are then used to supplement developing follicles and young (Bonnet et al., 1998; Houston et al., 2007; Jönsson, 1997; King, 1984; Lyons & Lowe, 2013a; Rossouw, 1987). It is theorised that, as these reserves are being catabolised for nutrient production, contaminants stored in the liver are transported with or "expected to passively follow" the catabolised molecules and subsequent nutrients to developing follicles or embryos during vitellogenesis or gestation (Lyons & Lowe, 2013a, 2013b). However, while the liver is a major site for contaminant detoxification and subsequent accumulation in elasmobranchs (Hauser-Davis et al., 2021; Storelli & Marcotrigiano, 2002; Wosnick et al., 2021), co-occurrence of detoxification and nutrient mobilisation in the liver does not necessarily imply that fully sequestered contaminants are mobilised with the nutrients. To the best of our knowledge, there is no direct evidence to support this mechanism. Moreover, there is some recent evidence to suggest that some shark species can use the income (rather than capital) breeding strategy, meaning that young are provisioned primarily from what the mother consumes during breeding rather than from reserves (Bonnet et al., 1998; Houston et al., 2007; Jönsson, 1997), and may actively switch between income and capital breeding strategies (Hammerschlag et al., 2018; Lawson et al., 2022; Rangel et al., 2021). Furthermore, radionuclide spiked feeding experiments showed that contaminants ingested at the time of vitellogenesis and oviposition appeared in deposited eggs of *Scyliorhinus canicula* within four days, consistent with known timeframes for digestion, yolk production, and oviposition in this species (Craik, 1978; Jeffree et al., 2015, 2024; Mellinger, 1983; Sims et al., 1996). Although this information is lacking for many species, these results highlight the potential importance of maternal diet during reproduction being the primary or a major source of contaminants and nutrients for developing elasmobranchs.

The school shark (*Galeorhinus galeus*) is a migratory species that has low biological productivity and occupies a high trophic position (Domi et al., 2005; Dureuil & Worm, 2015; Hurst et al., 1999; Nosal et al., 2021; Torres et al., 2014; Walker, 2005). Like many other elasmobranchs, these

characteristics make school sharks particularly susceptible to accumulating high levels of contaminants. Maternal transfer has been proposed as a possible driver of sex related differences in the bioaccumulation of mercury for school sharks (Walker, 1976). Yet, little is known about whether school sharks can transfer contaminants to their young, the mechanisms by which contaminants could be transferred, and potential detrimental effects to the young.

Knowledge of the extent of the maternal transfer of contaminants to the young of a species is crucial for understanding pathways of contaminant exposure. The aim of the current study was to measure the concentrations of three essential (Cu, Se, Zn) and five non-essential elements (Ag, As, Hg (total, THg), Pb, U) in the tissues of school sharks caught in New Zealand to evaluate evidence for maternal transfer of these elements to their pups.

We propose that, if maternal transfer is indeed occurring, one would expect to see changes in maternal mass at the time young are provisioned with nutrients and positive associations in the concentration of contaminants between embryonic tissues and the mother's tissue from which the contaminants are sourced. Therefore, the specific objectives of this study were to examine

1) when school sharks' supplement/provision their young with nutrients,
2) if school sharks use maternal derived mass to provide these nutrients, and
3) the extent to which school sharks could transfer elements if maternal transfer occurs.

6.3: Methods

6.3.1: Specimen collection and sampling

Between November 2021 and October 2023, seven pregnant females were obtained from around New Zealand via donations by fishers (Figure 6.1).

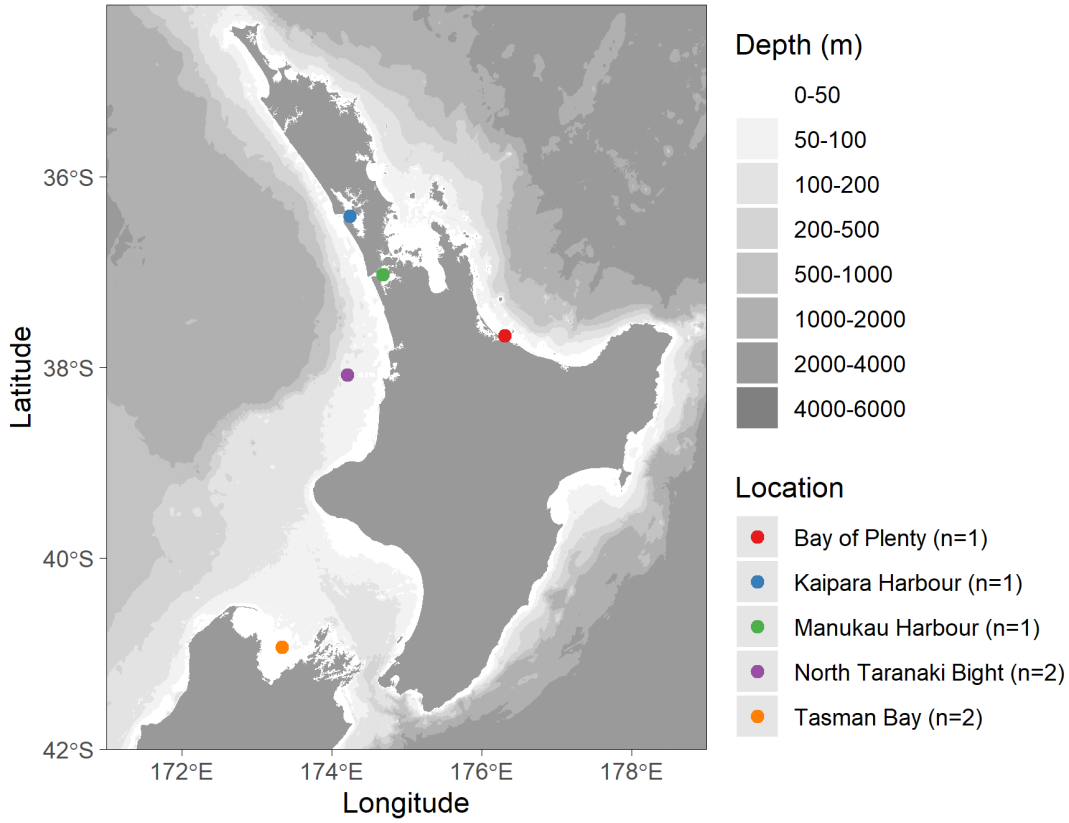
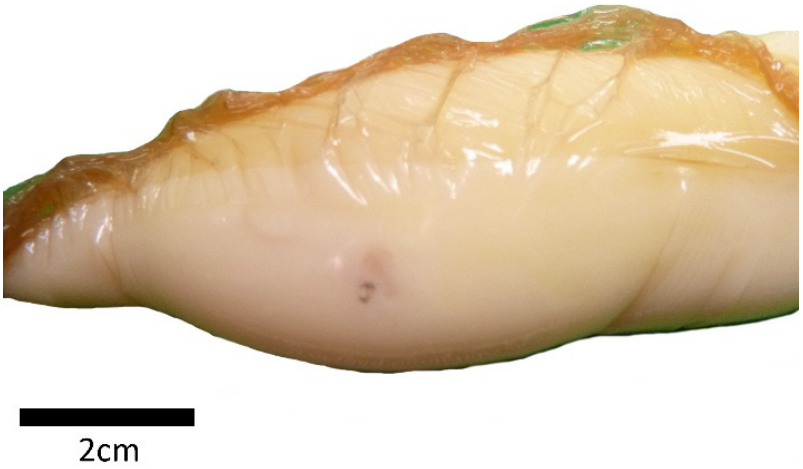


Figure 6.1: *Sample locations of the pregnant females.*

Two of these specimens were dissected fresh, and five were frozen at -20°C within two days of capture and then dissected at a later date. During dissections, full and partial body lengths (described in Chapter 2 and Appendix 1.1), girth, stages of reproductive tissues (as described in Table A2.2.1), and total body and organ weights were recorded for mothers. For embryos, total length, weight, yolk-sac weight, and sex were taken where applicable, whereas in-utero ova only had total weight recorded. The gestation stage was assessed by the appearance and size of in utero ova and embryos (i.e., “early-term”: in utero egg with embryo tissue differentiation, Figure 6.2a; “late-term 1”: large embryos that still had a proportionally large, external yolk sac, Figure 6.2b; “late-term 2”: embryos with nearly depleted, external yolk sacs, Figure 6.2c). A sample of two eggs per uterus (one from anterior and posterior of the uterus) and four embryos per uterus (one male and female from the anterior and posterior of the uterus) was taken from each mother. In two of the mothers, both eggs and late-term embryos were present in the uterus. Given that eggs were primarily found in the anterior part of the uterus, one egg and two embryos were sampled per uterus following the sampling procedure mentioned above.



(a) Early-term

(b) Late-term 1

(c) Late-term 2

Figure 6.2: *The gestation stages of embryos that were present in mothers used for this study. a) early-term, b) late-term 1, c) late-term 2. See section '6.3.1: Specimen collection and sampling' for gestation stage definitions.*

Samples of muscle and liver were collected from each mother and embryo. Yolk was also extracted from sampled yolk sacs and in-utero eggs. Yolk from eggs also included early-stage embryos. While

noted in all late-term embryos that were dissected, internal yolk stores were not sampled due to limited quantity of the yolk. Muscle samples were taken from the dorsal trunk muscle anterior to the first dorsal fin. Liver samples were extracted from the anterior section of the right liver lobe. Samples were placed in low density polyethylene bags and kept on ice until samples could be frozen to -22°C for further analysis. Extracted yolk was further processed by homogenizing samples with an acid-washed glass rod and storing samples in 50ml polypropylene centrifuge tubes (NEST Biotechnology) at -20°C until further analysis. Samples of all other tissues were also extracted and frozen in an archive for further study.

6.3.2: Chemical analysis

6.3.2.1: Sampling - dry vs wet weight

Prior to digesting samples, trials were conducted to assess whether tissue samples were going to be digested wet or dry. Sub-samples of 1g of muscle and liver were collected via acid washed stainless steel tools on silicon baking paper (beta-Bake, Dragonfire). Sub-samples were dried at 80-100°C in a convection oven (Heratherm OMS180, Thermofisher) until the samples reached a stable weight, $\pm$ 0.001g (~36hrs). Muscle sub-samples were successfully dried to a stable weight with minimal seepage of any fluid from within. Unfortunately, sub-samples of liver did not successfully dry, as, even though tissue samples had reached a stable weight, they continued to seep lipids. Given that not all samples could be dried without freeze drying, all samples were digested as wet tissue.

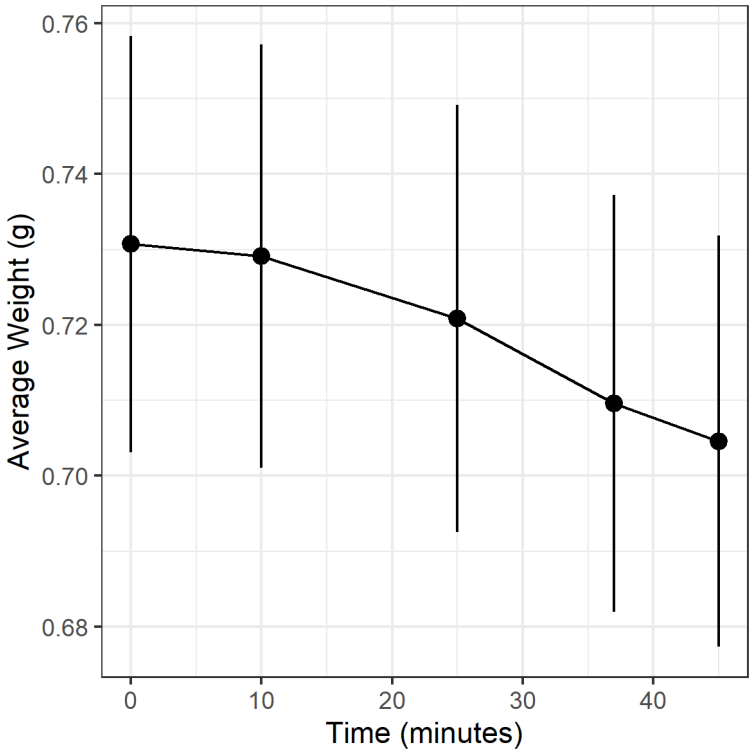


Figure 6.3: *Thawing effect on tissue sample weight. Average weight is based on the thawing of four sub-samples of muscle tissue. Time is the time after sub-samples were extracted from the frozen bulk tissue sample. The vertical lines are the 95% confidence intervals of the mean.*

When sub-sampling wet tissues, cryo-pumping (i.e., water condensing on the tissue surface) was found to increase the weight of samples in the first couple of minutes after being removed from the freezer. To overcome this issue, sub-samples would be extracted once tissues had thawed and warmed to room temperature. This process usually took fewer than 10 minutes which was when the lowest rate of change in the weight of sub-samples was observed (Figure 6.3).

6.3.2.2: Digestions

All digestions were carried out using a Multiwave Pro Microwave Reaction System (Anton Parr) with Teflon lined pressure vessels (HF100 Pressure Vessels, Anton Parr).

Sub-samples of 0.80g $\pm$ 0.02g of wet tissue were weighed (Mettler-Toledo Analytical balance, model: ME204) for all digestions. Prior to the main analysis digestions, tests were carried out to determine what acid digestion mixture and microwave digestion programme were required to completely digest samples across the different tissues. Samples for analysis were digested using 3.5ml of 68% HNO_3 (PrimarPlus Trace Analysis Grade, Fisher Scientific) and 3ml Milli-Q ultra-pure water (Milli-Q EQ 7000, Millipore Corporation). Digestions were temperature controlled via the following three steps: (1) ramp to 190˚C over 15 minutes, (2) hold at 190˚C for 45 minutes, and (3) cooling to 70˚C over 20 minutes. If the pressure in the internal temperature and pressure probe monitored vessel reached 35 bar, the temperature was adjusted to ensure that the vessel was $\leq$ 35 bar. Only one cycle using this method was required to completely digest samples.

Digested samples were then diluted to 25ml with Milli-Q water, quantitatively transferred to polypropylene centrifuge tubes (NEST Biotechnology), and stored at 4˚C until chemical analysis.

Prior to analysis by Microwave Plasma Atomic Emission Spectroscopy (MP-AES) or Inductively Coupled Plasma Mass Spectrometry (ICP-MS), titrations of diluted samples were undertaken to make sure that samples did not exceed acid concentration thresholds (i.e., 8%). Samples were titrated against known concentrations of NaOH (made from NaOH pellets (NaOH pellets, Analytical Reagent Grade, LabServ) dissolved in Milli-Q water), with bromothyol blue indicator (0.1% in EtOH, Scharlau).

6.3.2.3: Element analysis

6.3.2.3.1: Element selection

Elements examined in this study were selected for the following reasons. Cu and Zn are key to numerous biological processes and have previously been analysed in New Zealand school sharks (e.g., Vlieg et al., 1991). Moreover, both Cu and Zn can become toxic in excess concentrations and have been found above safe thresholds in several waterways in New Zealand (e.g., Griffiths, 2014). Due to increasing concentrations in aquatic environments (Blaser et al., 2008), Ag has been analysed in embryos of multiple shark species (e.g., Baró-Camarasa et al., 2023; Dutton et al., 2019), but has yet to be analysed in school sharks. Similarly, the radioactive element U has been detected in embryos of several shark species (e.g., Baró-Camarasa et al., 2023; de Souza-Araujo et al., 2020), yet has not been analysed in school sharks. As, Pb, and Hg are among the most studied non-essential elements in sharks due to their toxicity. Although Pb concentrations have decreased since the use of non-leaded fuel, high concentrations may persist in sharks if maternal transfer occurs. In New Zealand, As concentrations have exceeded safe thresholds in several waterways (e.g., Allen, 2023). Previous studies have also analysed As, Pb, and Hg in New Zealand school sharks (e.g., Mitchell et al., 1982; Vlieg et al., 1991). Finally, Se is frequently analysed with Hg due

to the apparent protective effects of Se against the toxic effects of Hg and has also been previously analysed in New Zealand school sharks (e.g., Vlieg, 1990).

6.3.2.3.2: Element measurements

Initial measurements of element concentrations were carried out using MP-AES (MP-AES 4200, Agilent Technologies). Concentrations of some elements, for example Ag, were too low to be accurately quantified with this method, even with the use of standard addition methods. Trials to concentrate elements via evaporating digested samples were also unsuccessful due to resulting sample acid concentrations being too high. As a result, MP-AES was used to help determine approximate concentrations of the target elements, which guided analysis via ICP-MS.

Concentrations of Ag, As, Cu, THg, Pb, Se, U, Zn were determined via ICP-MS (ICP-MS 7700, Agilent Technologies) undertaken by the Mass Spectrometry Centre, The University of Auckland, Auckland, New Zealand. Calibration standards were prepared in a 5% HNO_3 solution (made from 69% HNO_3; Tracepur, Merck) from 1000ppm single element standards (CPI International, USA). The analysis was run in He mode (He flow rate: 4 mL/min; see Appendix 5.1 for other tuning parameters) to reduce the effects of poly-atomic interferents. To make sure there were no effects of the sample matrix or chemical drift, a 20ppb solution of Y and Tb were mixed online during the analysis. Initial results were measured in mg L^{-1} and then converted to mg kg^{-1} wet weight (ww).

6.3.2.3.3: Limits of detection and quantification

Limits of detection and quantification for each element measured by ICP-MS were calculated using the following equation.

$$X_L = \frac{k.\sigma_{bi} \times C}{(S - B)}$$

where X_L is the Limit of Detection (LOD) or Limit of Quantification (LOQ) in mg L^{-1}; k is the numerical factor applied for a given limit; LOD: k = 3, LOQ: k = 10; σ_{bi} is the standard deviation in counts per second of a blank solution; C is the factor to convert 10ppb to standard units, for this study C=0.01 to convert to mg L^{-1}; S is the counts per second of a 10ppb solution; B is the counts per second of the blank background (blank from calibration).

Limits of Detection and Quantification are available in Table 6.1. Concentrations of measurements below limits of quantification, before being converted to mg kg^{-1}, are listed as <LOQ. The ICP-MS was re-calibrated after half of the samples were analysed to ensure the accuracy of the measurements. Hence, there are separate Limits of Detection and Quantification for before and after the re-calibration as different blanks were used in each calibration.

Table 6.1: *Limits of Detection (LOD) and Quantification (LOQ) for each element by calibration.*

Element	Calibration	Limit of Detection (mg L^{-1})	Limit of Quantification (mg L^{-1})
Ag	1	2.83e-06	9.44e-06
As	1	1.06e-05	3.53e-05
Cu	1	1.14e-05	3.82e-05
Hg	1	3.63e-05	1.21e-04

Element	Calibration	Limit of Detection (mg L^{-1})	Limit of Quantification (mg L^{-1})
Pb	1	3.60e-06	1.20e-05
Se	1	2.04e-05	6.81e-05
U	1	2.67e-07	8.89e-07
Zn	1	3.89e-05	1.30e-04
Ag	2	2.86e-06	9.54e-06
As	2	2.05e-05	6.85e-05
Cu	2	3.04e-05	1.01e-04
Hg	2	8.40e-06	2.80e-05
Pb	2	5.04e-06	1.68e-05
Se	2	2.25e-05	7.49e-05
U	2	3.73e-07	1.24e-06
Zn	2	5.14e-05	1.71e-04

6.3.2.3.4: Quality control

Multiple measures were used to ensure quality control of the analysis. Certified reference material DOLT-5 (Dogfish Liver Certified Reference Material for Trace Metals and other Constituents, National Research Council Canada) was prepared following recommended procedures, that is, drying to a stable weight ($\pm$ 0.001g) before analysis (Yang et al., 2014). To reduce the amount of moisture resorption by the dried sample, it was stored and transported in a desiccator. A subsample of 0.18g of DOLT-5 was digested with the other tissue subsamples and also stored in polypropylene centrifuge tubes (NEST Biotechnology) at 4°C until analysis.

Table 6.2: *Measured and certified concentrations of elements from the certified reference material DOLT-5. * represents expected concentrations where there was insufficient data to provide any estimate of uncertainty (Yang et al., 2014). Error for measured concentrations is the relative standard deviation of the measurement expressed as a proportion. Error for expected concentrations is the expanded uncertainty of the expected concentration (Yang et al., 2014). Error for recovery values is the propagated error based on the standard deviations of the measured and expected concentrations.*

Element	Measured (mg kg^{-1})	Expected (mg kg^{-1})	Recovery (%)
Ag	1.7257±0.0039	2.05±0.08	84.2±1.7
As	30.992±0.013	34.6±2.4	89.6±3.3
Cu	26.997±0.012	35.0±2.4	77.1±2.8
Hg	0.190±0.038	0.44±0.18	43.1±9.0
Pb	0.155±0.015	0.162±0.032	95.9±9.6
Se	5.981±0.016	8.3±1.8	72.1±7.9
U	0.074±0.024	0.082*	90.5
Zn	79.998±0.014	105.3±5.4	76.0±2.2

Recoveries for each element were calculated as $r = \frac{m}{e} \times 100$ and the error of the recovery as

$\sigma_r = r \times \sqrt{\left(\frac{\sigma_m}{m}\right)^2 + \left(\frac{\sigma_e}{e}\right)^2}$ where r is the calculated recovery, m is the measured concentration of the reference sample, e is the expected concentration of the reference sample, σ_r is the error of the recovery, σ_m is the standard deviation of the measured concentration, and σ_e is the standard deviation of the expected concentration.

Recoveries of most elements were within acceptable ranges (~80-110%, Table 6.2). Unfortunately, mercury (Hg) had a recovery of 43%. As such, mercury measurements could be underestimated by more than a factor of 2. A low recovery of Hg could possibly be due to the loss of mercury during the handling of samples of the reference material, including the time between digestion and analysis (Heiden & Aikens, 1983; Parker & Bloom, 2005; Yu & Yan, 2003).

To check for potential contamination of samples during digestion, one vessel from each digestion run contained a blank (only HNO_3 and Milli-Q water added). These blanks were diluted to 25ml with Milli-Q and stored in polypropylene centrifuge tubes (NEST Biotechnology) at 4°C until analysis.

The HNO_3 used for digestions was different to that used to create the calibration standards. To check for differences in element concentrations between standards and samples due to potential matrix effects, sample blanks of 5% HNO_3, made from the same acid used in the digestions and Milli-Q water, were prepped and stored in polypropylene centrifuge tubes (NEST Biotechnology) at 4°C until analysis.

6.3.3: Data analysis

All statistical analyses were undertaken using R and R Studio (Posit team, 2024; R Core Team, 2024). Models were constructed and compared using the brms and rstan packages (Bürkner, 2017; Stan Development Team, 2024).

In addition to the seven pregnant females collected from around New Zealand, data from 28 non-pregnant female school sharks captured around New Zealand between 2020 and 2023 were used to assess whether maternal mass was used to supplement developing young. However, because data from New Zealand school sharks were limited, data collected from Australian school sharks by Walker (2005) were also used in analyses to evaluate when school sharks provision their young with nutrients and whether maternal mass is used to supplement. The data comprised of the total length, weight, liver weight, and ovary weight as well as the stages of ovaries and uteri of individuals. Additionally, for the Australian data, total length and weight of embryos and eggs were recorded. The models described in Chapter 2 were used to convert the total length measured in the Australian data (as described in Chapter 2; Table 3.2) to the total length measurement used in this study, that is, fresh total length, measured in a straight line, with the tail in a natural position. These models were also used to convert defrosted lengths and weights recorded from the New Zealand population, where necessary, to fresh to allow for unbiased comparisons. As the Australian and New Zealand populations have some degree of connectivity (Brown et al., 2000; Devloo-Delva et al., 2019; Hurst et al., 1999) and because weight data recorded from New Zealand school sharks generally fell within the ranges of the Australian data (e.g., Figure 6.4), it is assumed that data were comparable between the two populations.

6.3.3.1: Objective 1: School shark embryo provision mode

The timing of when a shark embryo is provided with nutrients depends on the provision mode. In live-bearing species (viviparity), young are provisioned by yolk sac only (lecithotrophy) or by yolk sac and additional nutrients throughout gestation (matrotrophy) (Hamlett et al., 2005). To establish which provision mode is used by school sharks, the following Bayesian Analysis of Variance (ANOVA) model was used to see if there was a difference between the total wet weights of in-utero eggs vs embryos. If school sharks are lecithotrophs, one would expect to see little to no evidence of a difference in the total weight of both stages, whereas there would be evidence of a difference if they were matrotrophs. Considering that in-utero eggs and embryos were not independent from one another, the mother was included as a random effect.

$$\begin{aligned}
\text{Wgt}_i &\sim \text{Normal}(\mu_i, \sigma_i) \\
\mu_i &= \text{Mother}_{j[i]} + \text{Stage}_i \\
\sigma_i &\sim \text{Exponential}(1) \\
\text{Stage}_i &\sim \text{Normal}(0{,}25) \\
\text{Mother}_j &\sim \text{Normal}(0, \sigma_{Mother}), \text{for } j = 1, \ldots, 42 \\
\sigma_{Mother} &\sim \text{Exponential}(1)
\end{aligned}$$

A variant of this model that included a parameter for mother's total length L_T was also developed to test whether the difference between the total weights of eggs and embryos varied with the total length of the mother.

$$\begin{aligned}
\text{Wgt}_i &\sim \text{Normal}(\mu_i, \sigma_i) \\
\mu_i &= \text{Mother}_{j[i]} + \text{Stage}_i + L_T \\
\sigma_i &\sim \text{Exponential}(1) \\
\text{Stage}_i &\sim \text{Normal}(0{,}25) \\
\text{Mother}_j &\sim \text{Normal}(0, \sigma_{Mother}), \text{for } j = 1, \ldots, 42 \\
\sigma_{Mother} &\sim \text{Exponential}(1)
\end{aligned}$$

6.3.3.2: Objective 2: Source of mass for developing young

A natural log-normal model (see Chapter 2 for details) of liver mass L_{wgt} against ovary mass O_{wgt} (defined below) was used to visualise whether school sharks can use maternal mass, in the form of liver lipid reserves, to supplement their young. Ovarian mass was used as it is a metric for the progression of vitellogenesis, which is when school sharks are expected to initially get supplemented by liver derived nutrients if maternal transfer is occurring. The total length of the mother L_T was also included in the model to account for changes in liver and ovarian mass with the size of the mother. Stage of the ovary and uteri were also included in the visualisation of the model to show changes in the relationship not only over the stages of vitellogenesis but pregnancy as well. If maternal transfer did occur in school sharks, one would expect that the liver mass would decrease with the progression of vitellogenesis, that is heavier ovaries would have lighter livers.

$$\begin{aligned}
L_{wgt} &\sim \text{Log-Normal}(\mu_i, \sigma_i) \\
\log(\mu_i) &= \beta_0 + \beta_1 \log\left(O_{wgt}\right) + \log(L_T) \\
\log(\sigma_i) &= \zeta_0 + \zeta_1 \log\left(O_{wgt}\right)
\end{aligned}$$

6.3.3.3: Objective 3: Ability and scope of maternal transfer

If school sharks did maternally transfer elements to their young, then the correlations and differences in the concentrations of each element between maternal and embryonic tissues could highlight the extent of the transfer. Therefore, tissue partitioning ratios, as well as Pearson correlation coefficients and visuals of the concentrations of each element among maternal and embryonic tissues, were examined to evaluate the possibility that school sharks maternally transferred elements to their young.

Ratios of element concentrations between liver and muscle samples from both mothers and embryos were examined to evaluate which tissues elements were most concentrated in. Ratios between maternal liver and embryonic tissues were also calculated. Ratios that included concentrations of elements from embryonic tissues used the median concentration due to the variation in element concentrations within a litter.

Pearson correlation coefficients and plots of element concentrations between maternal and embryonic tissues were used to evaluate differences in the concentration of elements between tissues, as well as associations of element concentrations between maternal tissues and embryonic tissues. If maternal transfer does occur, then the mother's liver is the likely source of elements transferred to their young. Accordingly, the analysis focused on the associations of element concentrations between maternal liver and embryonic tissues. For plots visualising the correlations between the maternal liver and embryonic tissues, the element label was coloured by the maternal tissue where the element was most concentrated.

6.4: Results

6.4.1: Objective 1: School shark embryo provision mode

Pregnant school sharks sampled from New Zealand ranged in size from 1434mm to 1654mm total length (TL, Table 6.3). One shark was depredated by a great white shark (*Carcharodon carcharias*, Sc. Tindale personal observation) upon capture and was estimated to be ~1678mm TL based on partial body length conversions using the models from Chapter 2. Three of the sharks were in the early stages of pregnancy with 14-27 in-utero eggs. The other four sharks were in the later stages of pregnancy, that is, the embryos had developed to late-stage (see section *'6.3.1: Specimen collection and sampling'* for stage definitions). These sharks were carrying between 5 and 29 embryos, all still with external yolk sacs. Additionally, all embryos were encased in a transparent-brown membrane, surrounded by a colourless fluid. ES3 was an exception, carrying only five late-stage embryos and 15 eggs. Upon examination, there were no obvious signs of tissue differentiation in these eggs. However, the ovary was still in a state of vitellogenesis, like the early-stage pregnant females (Table 6.3). Whereas the other late-stage pregnant females had ovaries in a resting state.

Table 6.3: *Biological information related to mothers and their litters sampled from New Zealand. Total length is the total length of the mother measured in a straight line, with the tail in a natural position. Embryo length range is the range of total lengths for embryos in a litter, taken in a straight line, with the tail in a natural position. Total weight is the total body weight of the mother. Embryo weight range is the range of the total body weights (including the weight of the yolk sac) of embryos in a litter. Egg weight range is the range of the weights of eggs in a litter. Ovary state is whether the ovary was undergoing vitellogenesis (1) or not (0). No. embryos and No. eggs are the total number of embryos and eggs found in a mother's uteri, respectively. * Yolk sac ruptured, incomplete total weight. ** Depredated individual, incomplete weight and egg count, estimated total length. Mother ID's in* ***bold*** *represent the mothers and litters that needed lengths and weights converted from defrosted to fresh using models from Chapter 2.*

Mother ID	Total length (mm)	Total weight (g)	Ovary state	No. embryos	No. eggs	Embryo length range (mm)	Embryos weight range (g)	Egg weight range (g)
ES3	1570	21297	1	5	15	264-285	75.6*-175.9	77.9-91.18
ES4	1654	23732	0	29	1	259-285	82.8*-129.7	88.1
ET1	1451	19944	1	-	14	-	-	49.3-65.2
MK1	1568	22023	1	-	27	-	-	63.2-80.0
RK1	1434	18226	0	20	-	267-284	89.5*-102.0	-
RK2	1452	17122	0	23	-	272-293	94.0*-104.2	-
ST1**	1678	-	1	-	13	-	-	75.2-96.83

Combined with the data sampled from Australian school sharks, the range of weights for eggs and embryos was 42.0-99.0g and 67.9-175.9g, respectively (Figure 6.4). Within a litter, there was a large degree of variation in the total weights of eggs and embryos (Figure 6.4). There was evidence of a difference in total weight between eggs and embryos between litters (Figure 6.4, parameter estimate: 35.65 ± 1.20g, non-zero 95% credible interval). Furthermore, there was evidence of an effect of a mother's total length on the weights of eggs and embryos (Figure 6.5, parameter estimate: 0.14 ± 0.02g, non-zero 95% credible interval).

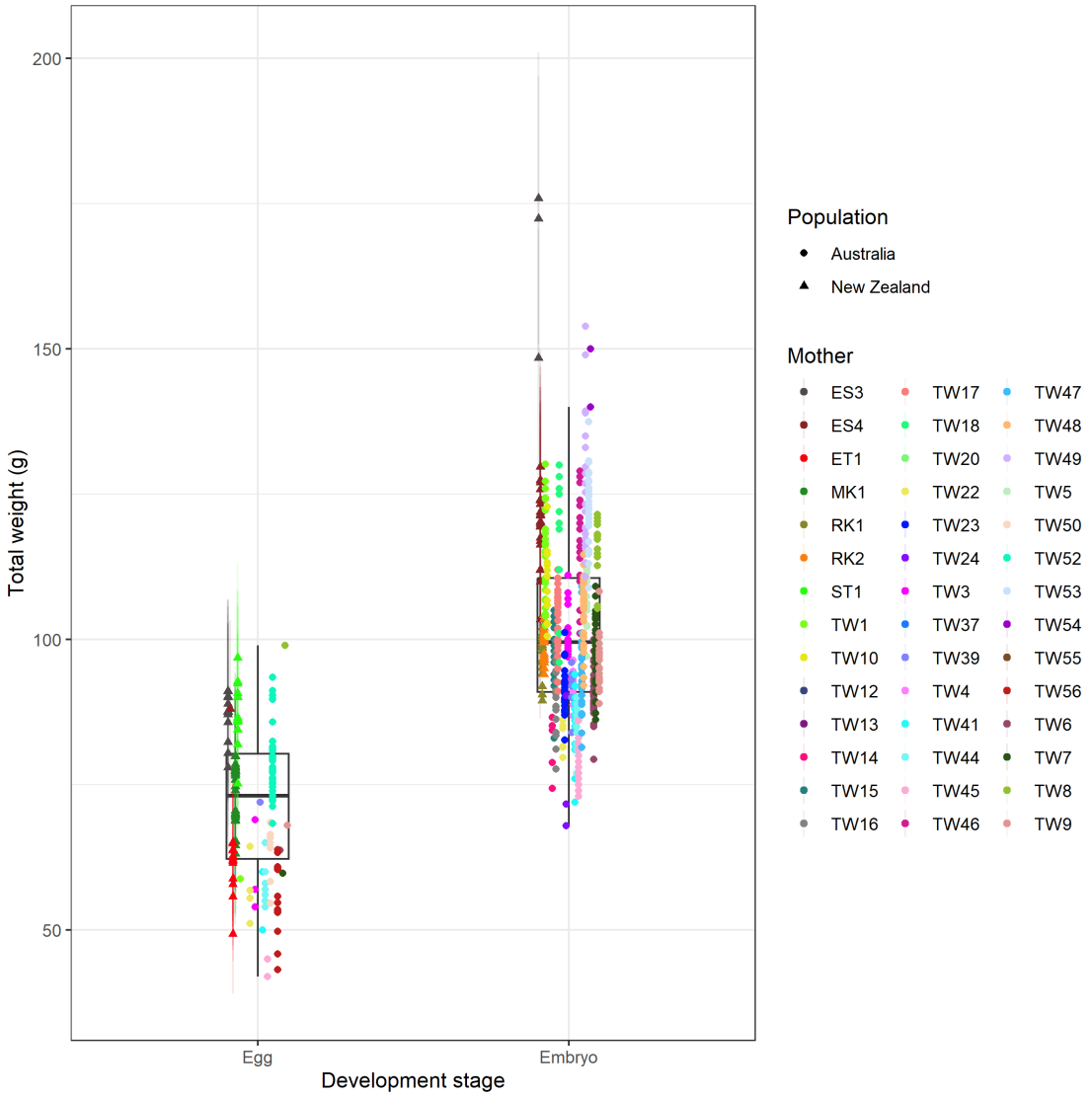


Figure 6.4: *Wet weight comparisons of in-utero eggs and embryos between different litters. Mother represents the litter an egg or embryo was a part of. The vertical lines are the standard deviations of defrosted total weights converted to fresh.*

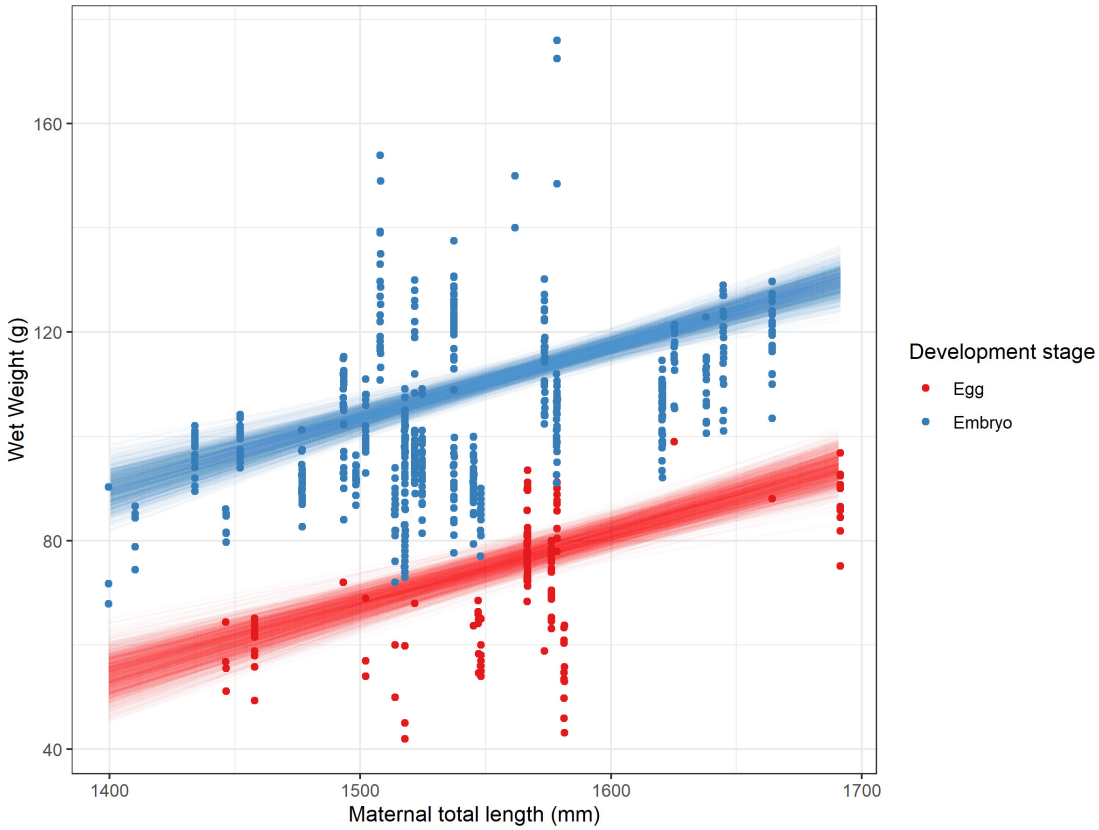


Figure 6.5: *Effect of maternal total length on the wet weight of in-utero eggs and embryos. The lines represent draws from the posterior distribution of the fitted model, coloured by development stage.*

6.4.2: Objective 2: Source of mass for developing young

For New Zealand and Australian school sharks, there was evidence of a positive allometric relationship between liver weight and ovary weight (Figure 6.6, parameter estimate log scale: 0.14 ± 0.06, non-zero 95% credible interval). There was also evidence of an effect of an individual's total length on liver weight (parameter estimate log scale: 2.21 ± 0.43, non-zero 95% credible interval). When including the ovary and pregnancy stage in the visualisations of the model, liver and ovary weights appear to be the highest in individuals that are in the process of vitellogenesis and either non-pregnant or in the early stages of pregnancy (Figure 6.6). On the other hand, liver and ovary weight is the lowest in individuals that have ovaries in a non-vitellogenic state or are in the mid to late stages of pregnancy (Figure 6.6).

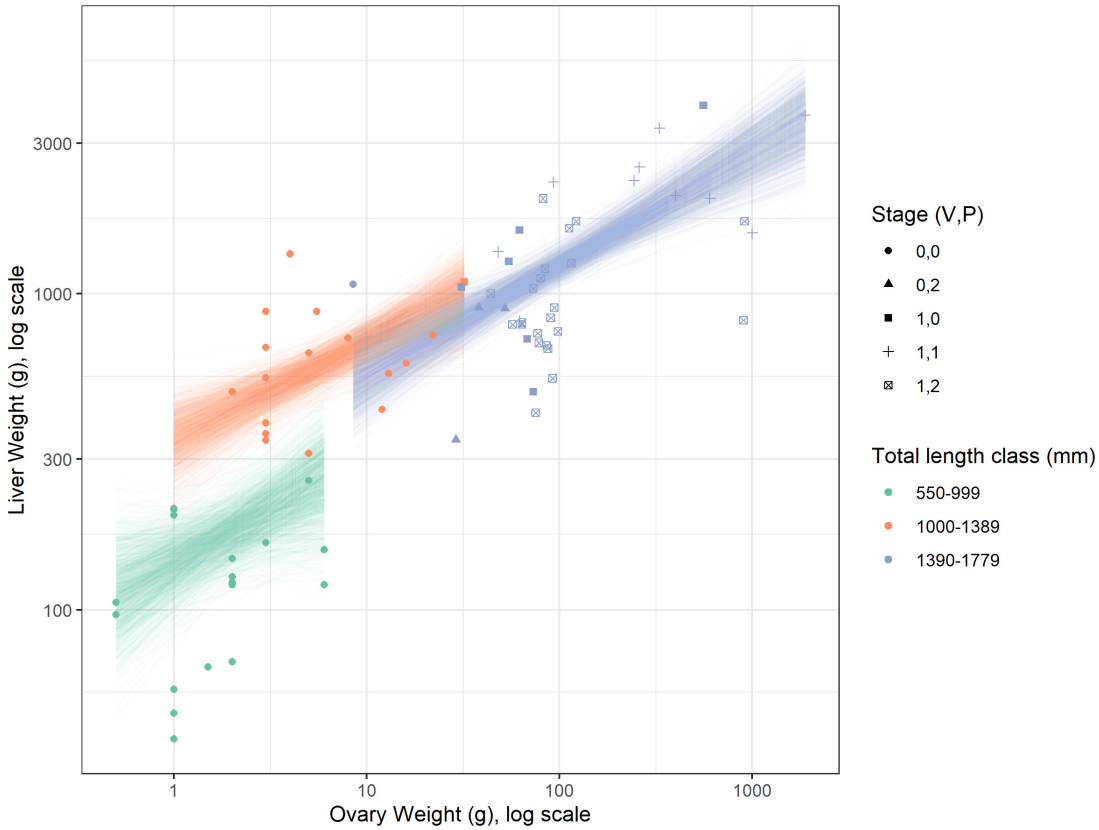


Figure 6.6: *Liver weight compared to ovary weight. Stage is whether an ovary was undergoing vitellogenesis (1) or not (0) and the stage of pregnancy a female was in: 0 = not pregnant, 1 = pregnant, in-utero ova, 2 = pregnant: in-utero embryos. The lines represent draws from the posterior distribution of the fitted model, coloured by total length class.*

6.4.3: Objective 3: Ability and scope of maternal transfer

Concentrations of all elements in all tissues were above the Limit of Quantification, except for Ag, Pb, and U in maternal and embryo muscle and liver as well as egg yolk for some individuals (Tables A5.2.1, A5.2.2, A5.2.3). 58% of the 19 samples with element concentrations below the Limit of Quantification were above the Limit of Detection. Unfortunately, yolk sac yolk could only be analysed in two litters as they had sufficient yolk remaining to sample. For each maternal and embryonic tissue, there was a large degree of variation in the concentration of elements within and/or between mothers, their litters, and capture location (Figures 6.7, A5.3.1, A5.3.2, A5.3.3). Ag, As, Cu, Se, and Zn were more concentrated in the liver and then the muscle for both mothers and embryos (Figure 6.7, Tables A5.4.1 and A5.4.2). Furthermore, U and Cu were more concentrated in the liver than the muscle tissue of mothers and embryos, respectively (Figure 6.7, Tables A5.4.1 and A5.4.2). Overall, maternal liver typically had higher concentrations of Hg and U compared to all embryonic tissues (Figure 6.7, Table A5.5.1). However, Ag, Cu, and Pb were more concentrated in several embryonic tissues compared to maternal liver (Figure 6.7, Table A5.5.1). For individual mothers, there was a large amount of variation in the element concentration ratios between the maternal liver and embryonic tissues (Figure 6.7, Table A5.5.2). However, As, Hg, and U were typically more concentrated in a mother's liver compared to the tissues of her young.

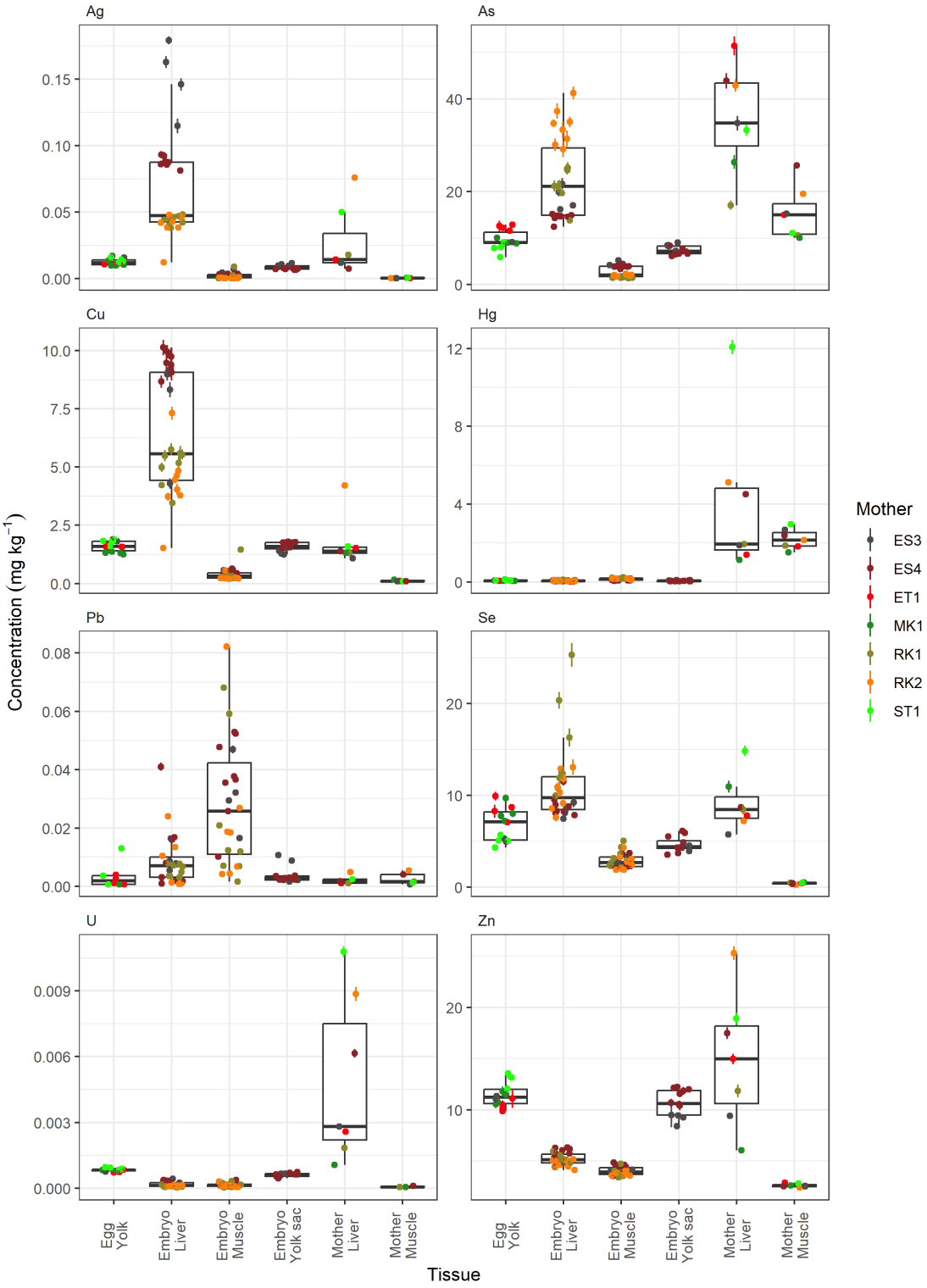


Figure 6.7: *Concentrations of elements analysed in maternal and embryonic tissues sampled from New Zealand school sharks. The vertical lines are the relative standard deviations of the measurements. Mother is the mother maternal or litter tissues were sampled from.*

Across all elements, there were no clear trends in the correlations between maternal and embryonic tissue concentrations (Figure 6.8, Figure A5.6.1). Most of the correlations between maternal and embryonic tissues were weak to moderate and were a mixture of positive and negative associations. The strong correlations between embryonic and maternal tissues tend to be restricted to associations between the yolk sac yolk and maternal tissues, which could only be measured for two mothers and their litters (Figure 6.8, Figure A5.6.1). There were also no clear trends in the variation of element concentrations in embryonic tissue with increasing maternal liver concentrations (Figure 6.8).

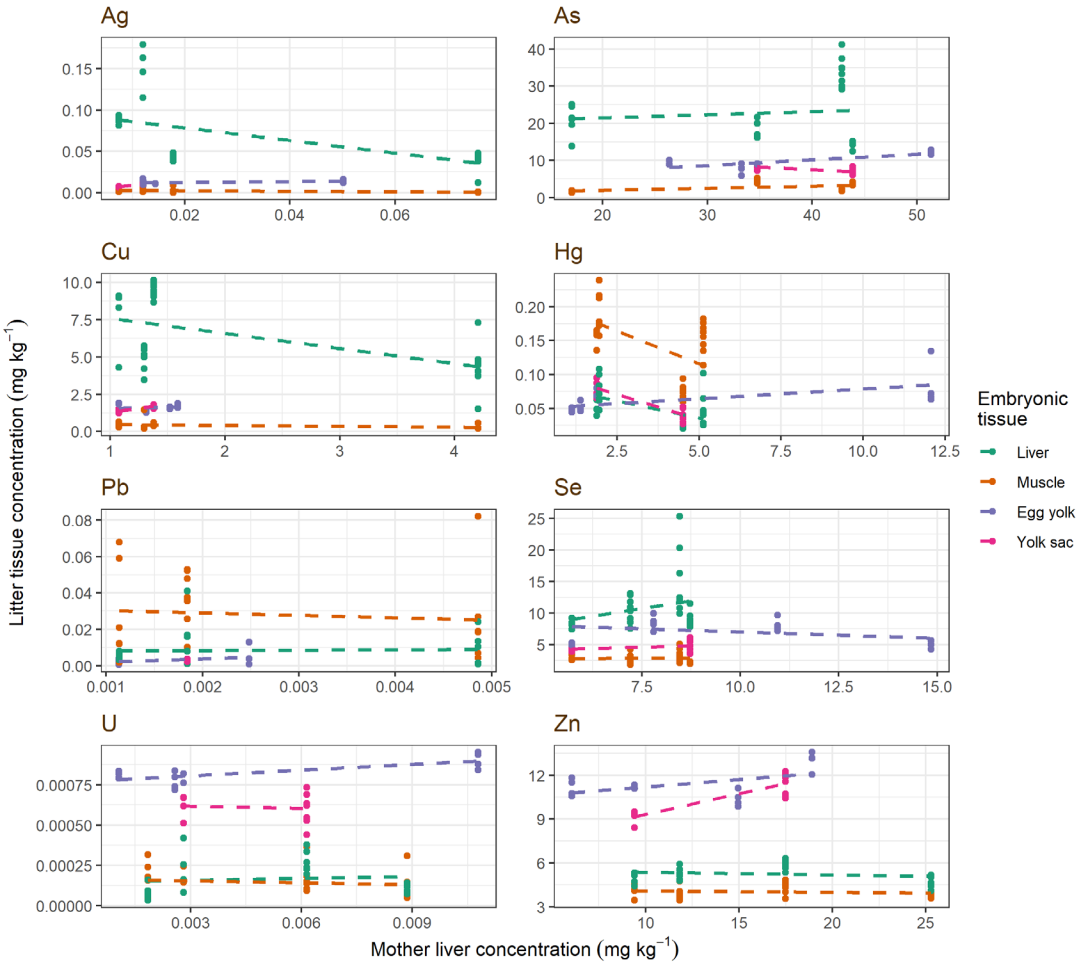


Figure 6.8: *Concentrations of essential and non-essential elements in the mother's liver vs the litter's tissues from New Zealand school sharks. Titles of each element are coloured by the maternal tissue that they concentrated in the most, based on the average maternal tissue partitioning ratio (Table A5.4.1). Titles for all elements were coloured brown as they were more concentrated in maternal liver than maternal muscle.*

6.5: Discussion

Knowledge on a species ability to transfer contaminants to their young provides key information on a species exposure and accumulation pathways as well as reproductive biology, such as the source of nutrition for developing young. Controlled experiments can be used to evaluate a species ability to transfer contaminants to their young (e.g., Jeffree et al., 2015, 2024); however, this may be difficult for many larger, highly mobile species that cannot be housed in controlled environments. Though difficult, it is possible to evaluate the maternal transfer potential of a species via in-direct methods, such as examining contaminant concentrations between mothers and their young. However, it is crucial that accurate knowledge of a species biology, which can impact how young are exposed to contamination, such as when embryos are provided with nutrition, is known before evaluating if a species transfers contaminants to their young. Here, we provide evidence of how and when school sharks provide their young with nutrients, as well as patterns in concentrations between mothers and their pups, to evaluate whether school sharks transfer several elements to their pups from their own accumulated reserves.

Knowing when a species supplements their young with nutrients is key to determining whether a species transfers contaminants to their young. Species of the Triakidae family supply nutrients to their young solely by yolk-sac (lecithotrophy) or provision of additional nutrients throughout gestation (matrotrophy) (Winn et al., 2024). Previous studies have suggested that school sharks use matrotrophy, in the form of minimal/incipient histotrophy, based on comparisons of the dry weight of eggs and embryos (Capapé et al., 2005; Ranzi, 1936). However, the lack of obvious weight gain observed in these two studies (weight ratio approximately 1:1) suggests that school sharks gain most of their nutrition from the yolk. In the present study, comparisons of wet weight between eggs and embryos sampled from litters of New Zealand and Australian school sharks showed evidence of a difference in weight between eggs and embryos (Figure 6.4). This difference in wet mass is likely attributed to hydration (e.g., Ranzi, 1936). Given that school sharks are encapsulated with a colourless fluid until birth (Walker, 2005), a process similar to embryotrophy, proposed by Castro et al. (2016), could be occurring if school sharks did provide additional nutrition during gestation. While further analysis is required to determine if additional nutrients are provided to young during gestation, it is likely that school sharks acquire the majority, if not all, of their nutrients from yolk deposited during vitellogenesis.

It is widely thought that female sharks use reserved mass stored in the liver to provide their young with nutrients (Bonnet et al., 1998; King, 1984; Lucifora et al., 2005; Rossouw, 1987). If this is indeed the case, one would expect the mass of the mother to decrease throughout the period in which nutrients are provided to the young. In particular, one would expect the liver mass to decrease over the vitellogenesis period in school sharks, given that the young likely acquire most of their nutrients during vitellogenesis. In our study, an opposite pattern was observed, with liver mass generally being larger in mothers in the later stages of vitellogenesis (after accounting for the overall size of the mother, Figure 6.6). Furthermore, non-pregnant and early-stage pregnant females with ovaries in a vitellogenic state had higher liver and ovarian mass compared to mid-late stage gravid (in-utero embryos) and non-vitellogenic non-pregnant individuals. While associating changes in liver mass with reproductive events needs to be done with care, given that liver reserves are also used for other biological processes (e.g., migrations; Del Raye et al., 2013; Hammerschlag et al., 2018), it is nevertheless more energetically favourable to provision young from dietary sources than

liver lipid reserves if mothers are actively feeding when nutrients are being provided. Taken together with the preliminary results from this study, it is likely that school sharks provision their young from sources other than their own mass, while liver stores are accumulated for later use, perhaps during reproduction-driven migrations in the later stages of gestation.

Once nutrients are assimilated by the intestines, they are transported to the liver for processing and, in the case of excess lipids, storage for later use (Ballantyne, 1997; Sargent et al., 1972; Sheridan, 1988). The liver is also the site where important nutrients and metabolites are synthesised, including vitellogenin, the yolk precursor supplied to developing follicles during vitellogenesis (Ballantyne, 1997; Ohishi et al., 2023; Speers-Roesch & Treberg, 2010; Tosti et al., 2006; Wourms, 1977). Even though lipid storage and nutrient synthesis co-occur in the liver, reserves of lipids in the liver are not necessarily the source of metabolites for vitellogenesis. The energetic cost of mobilising lipids already stored in the liver to fuel these syntheses would be greater than utilising metabolites that are readily available from recently ingested food (Bonnet et al., 1998; Jönsson, 1997). If a shark can provide ample metabolites from their immediate diet to synthesise nutrients for their young, then excess metabolites can be stored in the liver for other energy intensive tasks where food may be scarce, such as migrations, thereby increasing the liver mass of that individual. In recent years, income or a mixture of the income and capital breeding strategies has been proposed for many elasmobranch species (Hammerschlag et al., 2018; Lawson et al., 2022; Rangel et al., 2021). Furthermore, tiger sharks may change their diet during reproductive periods to account for the energetic demand associated with reproduction (Rangel et al., 2021). School sharks also selectively target higher energy prey, such as squid, when available (Lucifora et al., 2006). In New Zealand, all stages of adult female school sharks have been observed in areas of high prey abundance and diversity for extended periods (Chapter 5). Thus, school sharks may select high-energy prey, such as squid, in these areas to meet the demands of vitellogenesis. Although whether income, capital, or a mixture of the two strategies is used depends on many factors, such as food availability (Bonnet et al., 1998; Stephens et al., 2014), the observed changes in maternal mass during nutrient provision (Figure 6.6), together with their likely prey selection, suggest that school sharks in New Zealand may rely primarily on an income breeding strategy. If so, developing young could possibly be exposed to and accumulate higher concentrations of contaminants compared to the mother (Boldrocchi et al., 2021).

To determine the ability and scope elasmobranchs maternally transfer contaminants to their young, many have compared contaminant concentrations between maternal and embryonic tissues (Dutton & Venuti, 2019; Lyons & Lowe, 2013a; Martins et al., 2022; van Hees & Ebert, 2017; Weijs et al., 2015; Zvekic et al., 2024). If maternal transfer did occur, one would expect positive associations between maternal liver and embryonic tissue concentrations of a given contaminant. In New Zealand school sharks, concentrations of several elements in embryonic tissue were found to be similar to or, in the case of Cu, higher than the maternal liver (Figure 6.7, Tables A5.5.1 and A5.5.2). However, there were no clear associations between maternal liver and embryonic tissue concentrations for any element (Figures 6.7 and 6.8; Appendix 5.5 and 5.6). Admittedly, this study had a relatively small sample size of mothers (n=7). However, these preliminary results, along with evidence that school sharks likely provision their young from sources other their own mass, suggest no evidence to support maternal transfer as the process of initial exposure to contaminants.

Diet is the main source of contaminants in the tissues of elasmobranchs (Mathews & Fisher, 2009), yet maternal diet is often ignored as a source of contaminants in developing young. Essential and non-essential elements assimilated from the diet typically end up in the liver for processing via complexing with nutrients, association with metabolites or other molecules, or being sequestered by detoxification mechanisms, such as metallo-thioneins or -selenoneins (Ballatori et al., 2010; Oikawa et al., 1991; Palmisano et al., 1995; Roesijadi, 1992; Tjalve & Gottofrey, 1991). Similar to nutrients in the liver, it is unlikely that elements that have been sequestered by detoxification mechanisms and/or already stored in the liver will form complexes or be associated with nutrients synthesised in the liver due to the energetic cost of mobilisation. Limited mobilisation assumes that the interactions and binding affinities holding the sequestered elements are sufficient to prevent other interactions from occurring. Instead, readily available elements complexed with metabolites or molecular mimics, such as arsenate (which mimics phosphate; Bridges & Zalups, 2010), from the diet are likely to be used in the synthesis and subsequent transport of molecules used to provision young, such as vitellogenin. It is also possible for "free" cations to be directly deposited into developing young by either binding to vitellogenin in the blood stream, due to ion-binding properties of vitellogenin (Arukwe & Goksøyr, 2003), or passing through membranes via molecular or ionic mimicry (Bridges & Zalups, 2010). Evidence from radionuclide spiked feeding experiments supports that the primary or a major source of essential and non-essential elements comes from the diet of mothers at the time of vitellogenesis (Jeffree et al., 2015, 2024). Dietary contaminants are also the likely initial source of contaminants for New Zealand school sharks and could partly explain differences in element concentrations between maternal and embryonic tissues where there was no evidence of associations between these tissues (Figures 6.7 and 6.8). Moreover, dietary contaminants could also partly explain the observed variation within and/or between mothers, their litters, and capture location (Figures 6.7, A5.3.1, A5.3.2, A5.3.3) as school sharks can feed in various geographically separated habitats and on different prey sources throughout their life-history (e.g., Lucifora et al., 2006; Chapter 5), including during vitellogenesis.

Here, maternal transfer is defined as the process where inorganic or organic contaminants that are stored in a mother's tissues are mobilised during vitellogenesis, gestation, and/or lactation and passed onto the developing follicles, embryos, and young, respectively. Maternal transfer may occur in elasmobranchs, but there is little to no direct evidence of this process being the initial source of contaminants in developing young. While being limited to small samples sizes, the preliminary results and evidence from literature suggest no evidence in support of maternal transfer being the process responsible for the initial exposure of selected elements in school sharks from the New Zealand population. Instead, it seems more likely that elements assimilated from the mother's diet at the time of vitellogenesis is the more likely source. Future studies might look for more direct evidence of the strategies elasmobranchs use to provision their young, including the sources of nutrients and contaminants, through feeding experiments with tagged molecules or elements of interest. However, controlled experiments may not be feasible for many species, especially highly migratory megafauna. Researchers relying on indirect evidence to assess the maternal transfer potential should interpret the results with caution. Additionally, understanding key aspects of a species' biology is crucial before inferring possible processes from concentrations of contaminants in maternal and embryonic tissues. Such aspects would include factors that could affect how, when, and the scope of transfer, such as how and when young are provisioned with nutrients.

Chapter 7: General Discussion

Our ability to effectively manage and recover elasmobranch populations is dependent on having accurate information on the biology of species' (Frisk et al., 2001; Petersma et al., 2024; Simpfendorfer et al., 2011). Although substantial information on the biology for some species exists, including school sharks, important gaps and methodological limitations remain, potentially introducing bias into estimates needed to inform management. To assist with the effective recovery of the collapsed school shark populations and management of the New Zealand population, this thesis uses novel techniques to provide refined estimates and new insights into the biology of school sharks. The purpose of this general discussion is to 1) synthesise the findings of each of the data chapters, 2) describe how the thesis contributes to the management of school sharks, and 3) provide recommendations for future work.

7.1. Contribution to knowledge

7.1.1. Length-length measurement conversion

Studying the life-history of a species, particularly a wide-range species, often requires compiling data from multiple sources. However, a commonly encountered problem when compiling datasets from various sources is that researchers tend to measure the same biological trait, such as body length, using different methods, resulting in multiple variants of the same trait (De Wysiecki & Braccini, 2017; Francis, 2006; Natanson et al., 2022). In such cases, statistical models are needed to convert between the various length variants and obtain standardised datasets. Many existing models do not explicitly account for conversions between distinct length variants (e.g., fresh, natural, total length vs. stretched, total length) or how measurements deviate from the modelled relationship (error structure). Failure to consider these factors can lead to bias in converted lengths and parameters that subsequently rely on length data, such as length-at-maturity (Francis, 2006).

In Chapter 2, the performance of various statistical models (including linear and natural log-linear (log-linear) models with different error structures) was assessed when converting between different methods of measuring full and partial body length of school sharks. Additionally, since obtaining sufficient data on multiple length variants from live animals can be difficult, models constructed using length variants measured from defrosted individuals were tested for their ability to convert length variants of fresh animals where data were lacking. By comparing the out-of-sample predictive performance of the linear and log-linear models, the log-linear model, with an explicit heteroscedastic error structure (i.e., deviation of the data from the modelled relationship increased with increasing values of the predictor) was the best model to convert between length measurement variants of school sharks. Comparisons between estimated and actual values of fresh length variants found that models built from length variants measured from defrosted animals can be used to convert between length variants measured from fresh animals.

7.1.2. Extent of inter-population variation in length at life-history stage

Life-history parameters, such as attainment-at-maturity, often vary among populations of the same species (e.g., Bradley et al., 2017; Neer & Thompson, 2005). However, much of the observed variation may stem from artefacts of the sampling design, different methods of measuring biological traits, and/or statistical methods. Due to the spatial and temporal (spatio-temporal) complexity of populations and selectivity of sampling gear, datasets often poorly represent the population (Rufener et al., 2021; Walker et al., 1998; Walker, 2007). As a result, some life-history stages and/or length classes tend to be collected more than others, resulting in unbalanced datasets. As seen in Chapter 2, biological traits can be measured in multiple ways, and inappropriate methods or lack of standardisation can introduce bias into estimates of important biological parameters (Francis, 2006). Given that datasets are often non-representative of the population, commonly adopted models, such as logistic regression, are often inappropriate to model life-history stage transitions, as estimates tend to be biased towards the over-represented life-history stage (Cramer, 1999; Oommen et al., 2011). To accurately assess the variation in attainment at life-history stage among populations, methods need to be developed to mitigate the effects of these common methodological artefacts.

In Chapter 3, length and life-history data from six school shark populations around the world were compiled to examine the extent of inter-population variation in length at life-history stage transition for school sharks. To mitigate the effects of common methodological artefacts, novel techniques to standardise length and life-history data were applied. Additionally, a novel Bayesian generative classifier model that was designed to be less sensitive to data imbalance was used. While length-at-birth and female length-at-maturity could only be estimated for three populations, though not the same three for each parameter, there was sufficient data to examine the inter-population variation in male length-at-maturity among all six populations. Length-at-maturity for male school sharks varied among the six populations, with estimates ranging between 1238 and 1306 mm, total length (TL, fresh total length, measured in a straight line, with the tail in a natural position). Although the drivers of this variation could not be determined, population-specific estimates of length-at-maturity for male school sharks are necessary for ongoing management. Further work is required to determine the extent of variation of length-at-birth and female length-at-maturity among populations.

7.1.3. Degree of intra-population variation in somatic and hepatosomatic growth of juvenile school sharks

In many species, individuals may give birth in one of several areas within the geographical extent of a population (e.g., McMillan et al., 2018). Juveniles can remain in these areas for prolonged periods, depending on their dispersal abilities and habitat needs, exposing them to local conditions that can affect their somatic (growth in length with age) and hepatosomatic (increases of energy storage in the liver with age) growth rates (Dmitriew, 2011; Weideli et al., 2019). Differences in local conditions can result in intra-population variation in growth rates of juveniles. The influence that regional growth rates have on the broader population dynamics, such as growth and age- and length-at-maturity, depends on each region's contribution of juveniles to the population. The loss of juveniles from high-contribution regions could significantly impact population dynamics, highlighting the need to understand variation in juvenile growth rates and regional contributions within a population. Yet, few studies examine the intra-population variation in growth.

In Chapter 4, novel Bayesian growth models were developed to examine the extent of regional variation in the somatic and hepatosomatic growth of juvenile school sharks. There was little difference in somatic growth between three areas of likely importance to juvenile school sharks in New Zealand, namely, the Kaipara Harbour, Tasman and Golden Bays, and the Canterbury Bight. However, while the rate of hepatosomatic growth did not differ markedly among regions, individuals from the Canterbury Bight were in better condition compared to the other two areas. This study relied on opportunistically collected data, which resulted in sampling being restricted to certain months and gear types and small sample sizes from each region. As a result, the observed patterns may be influenced by sampling bias, and future work is required to confirm these findings.

7.1.4. Three-dimensional movement and habitat use of school sharks that disperse from the Kaipara Harbour

School sharks exhibit complex three-dimensional movements, including site fidelity to habitats that are important to their life-history, such as gestation grounds (e.g., McMillan et al., 2019; Nosal et al., 2021). In New Zealand, detailed knowledge on the movements and habitat use of school sharks remains limited, particularly regarding the connectivity of important areas, such as the Kaipara Harbour, to the wider population.

Chapter 5 provided the first in-depth study of the three-dimensional movements and habitat use of New Zealand school sharks by tracking the year-long movements of mature female school sharks that dispersed from the Kaipara Harbour. Satellite tagged females travelled to a range of locations and habitats throughout New Zealand, but predominantly temporarily resided in three regions: Tutamoe, North Taranaki Bight, and the Outer Cook Strait. While satellite tagged females temporarily resided in these areas, school sharks of all life-history stages, including individuals from around New Zealand and southern Australia, were also present alongside abundant prey. This suggests that the three temporary residency areas are potentially important feeding and reproductive grounds for the New Zealand school shark population, and they are also used by individuals who migrated to New Zealand from Australia. Further studies are required to determine the drivers of the migrations and the role of the Kaipara Harbour and other regions of likely importance in the broader dynamics of the New Zealand population.

7.1.5. Maternal transfer potential of school sharks

The term “maternal transfer” is broadly used in literature to describe the passing of nutrients and contaminants from a mother to her young. In this thesis, maternal transfer was defined as the process where inorganic or organic contaminants that are stored in a mother’s tissues are mobilised during vitellogenesis, gestation, and/or lactation and passed onto the developing follicles, embryos, and young, respectively. There is no direct evidence that contaminants in developing elasmobranchs result from maternal transfer by this definition, and few studies have considered alternative explanations, such as the passive transfer of contaminants in proportion to the energy and nutrients provided to the young from the mother’s diet.

Chapter 6 investigated how and when school sharks provide their young with nutrients and examined associations of concentrations of several elements between maternal and embryonic tissues to evaluate the process responsible for the initial exposure of contaminants in developing school sharks. Our findings suggest that developing school sharks receive most of their nutrients

during vitellogenesis, likely from sources other than the mother's liver. Although differences in the concentrations of several elements between maternal and embryonic tissues were observed, there were no clear associations between maternal and embryonic tissue concentrations. The lack of association between maternal and embryonic tissue concentrations and lack of evidence of nutrients being sourced from the maternal liver suggest that developing school sharks are unlikely to receive nutrients and contaminants from the mother's liver. Instead, other processes, such as assimilation from maternal diet at the time of nutrient provision, are a more likely source of several elements in developing school sharks.

7.2. Implications for management

This thesis provides new insights into the biology of school sharks. Robust statistical models that convert between specific length variants enable better standardisation of length data, reducing potential bias in the estimation of fundamental biological parameters, such as length-at-maturity and -age (Francis, 2006). By providing less biased and, for some populations, previously unknown estimates of length at life-history stage transitions, this research contributes to the improved estimation of broader population parameters such as population status and growth in length (Harry et al., 2022; Walker, 2005). Understanding variation in length at life-history stage transitions across populations informs whether population-specific parameters are necessary for management. Knowledge of the extent of intra-population variation in growth rates contributes to assessing a population's resilience to pressures such as fishing and habitat degradation (Benard & McCauley, 2008; Yates et al., 2012). Insights into school shark movements and habitat use help define population structure and spatial extent as well as identify key habitats used by a population (e.g., Braccini et al., 2016; Chapman et al., 2015; McMillan et al., 2019). Lastly, identifying how sharks are initially exposed to contaminants improves our understanding of their nutritional sources during gestation and the accumulation and effects of contaminants over ontogeny (e.g., Jeffree et al., 2024; Lyons et al., 2019).

Collectively, this thesis provides a substantial body of knowledge essential for the effective management and recovery efforts of school shark populations worldwide. Moreover, the techniques developed in this thesis can be applied to improve estimates of biological parameters for other elasmobranch populations, supporting broader management and recovery efforts.

7.3. General limitations and recommendations

7.3.1. General limitations

Like other elasmobranch studies, this thesis was limited by several challenges. Across the data chapters, limitations included knowledge gaps in the biology of the study population (chapters 3-5), lack of data (chapters 2 and 3), small sample sizes (chapters 3-6), non-representative data (chapters 3-5), and/or the subjectivity of the methods (chapters 3 and 4). While this thesis provides refined estimates and new insights into the biology of school sharks, these limitations mean that the results should be interpreted with caution, particularly where sample sizes were small. Beyond these limitations, important gaps in our knowledge of school shark biology remain, with implications on our ability to manage populations. The following recommendations outline approaches to help address these limitations and provide greater knowledge on the biology of species.

7.3.2. General recommendations

As observed in Chapters 2-4, there are multiple methods used to measure length and classify the life-history stage and age of individuals. Many of the commonly adopted methods to measure these biological traits, including those used in this thesis, are also lethal and/or subjective. With elasmobranch populations declining and the need for better knowledge on the biology of many species, there is a need to transition towards more standardised, deterministic, and non-lethal methods (Hammerschlag & Sulikowski, 2011; Heupel & Simpfendorfer, 2010). To allow for representative sampling throughout a population's spatio-temporal range, long-term monitoring, and deployment of the methods throughout the world, the methods would need to be fast, easy to deploy and follow, and cost-effective. Additionally, new methods should be comparable to existing methods, where possible, to allow for previously collected data to be used in future analyses. Because body morphology and structures used to classify age and life-history stage vary between species, species-specific methods will need to be developed. Furthermore, some non-lethal methods may still require validation using lethal methods. However, developing tissue archives from individuals that wash ashore (if in good, fresh condition) or are donated by fishers can reduce the need to lethally sample additional sharks for validation, minimising the impact on the study population.

Working with citizen scientists, fishers, and fish processors can help reduce the impact of the research on the populations while potentially increasing the representativeness of the data. Data and specimens obtained from citizen science and the fishing industry can cover a wider spatio-temporal and gear range than could be achieved during fieldwork. However, there are disadvantages to this sort of data. Their collection is usually unplanned and opportunistic rather than planned and systematic, so allowances must be made in cases where the data are non-representative of the population. Furthermore, validation of measurement data from citizen science is limited. However, developing methods to obtain morphometric measurements from photographs (e.g., Richardson et al., 2015) would help to validate measurement data as well as allow data to be retrieved from observations where an individual was not measured.

To improve the accuracy and reduce the bias of key biological parameters, future studies should develop models capable of accounting for complex error structures and influences of different factors, such as representativeness of the data. I generally recommend the use of Bayesian models that incorporate prior information and uncertainty around parameters, as this can improve the robustness of estimates (e.g., Smart & Grammer, 2021). Hierarchical Bayesian models, as used in Chapters 3 and 4, are especially useful when data includes data-poor categories, as they allow for estimates of these categories to borrow strength from the broader dataset, allowing for refined and informed estimates despite limited sample sizes.

7.4. Conclusion

This thesis provides new insights into the biology of school sharks. The development of models that convert between specific length variants and account for the error structure of the data provides methods to better standardise school shark length data, helping to mitigate potential biases in the estimation of biological parameters. Standardising length and life-history stage data collated from school shark populations around the globe, and applying a novel generative model that mitigates the influence of data imbalance, resulted in less biased and, for some populations, previously

unknown estimates of length-at-maturity and -birth. Moreover, the hierarchical modelling approach provided evidence that population-specific estimates of male length-at-maturity are necessary to inform ongoing management of school shark populations. While further work is needed, our application of novel Bayesian growth models offers preliminary insight into the intra-population variation in somatic and hepatosomatic growth of juvenile school sharks in New Zealand. Tracking the year-long movements of female school sharks that dispersed from the Kaipara Harbour offered the first detailed insight into the movements and habitat use of New Zealand school sharks, identifying at least three additional areas that are of likely importance to the New Zealand population. Finally, analysis of the nutrient provision of school sharks and concentrations of several elements in maternal and embryonic tissues suggest that nutrients and selected elements assimilated from the mother's diet at the time nutrients are provided are the initial source of contaminant exposure for school sharks. The techniques and knowledge contributed by this thesis deepen our understanding of school shark biology required to better inform the effective management and recovery of school shark populations worldwide. Moreover, the techniques developed in this thesis can help mitigate the bias in estimates of biological parameters required to guide recovery and management efforts of other elasmobranch populations. Given the ongoing decline and extinction risk faced by school sharks and many other elasmobranchs, future research should prioritise the development and application of standardised, deterministic, and non-lethal methods, alongside Bayesian models, to improve our understanding of the biology of the species while minimising the impact to the study populations.

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Appendices

Appendix 1 – Chapter 2: Length-length conversions

A1.1: Definitions of length variants

Concise subscript labels

First subscript takes one of these two options:

- `f__` = fresh
- `d__` = defrosted/thawed

Second subscript takes one of these 12 options:

- `_t_` = total (total length with tail in natural position)
- `_s_` = stretchtotal (total length with tail in stretched position)
- `_p_` = precaudal length
- `_f_` = fork length
- `_dp_` = dopcp length (dorsal origin to precaudal origin/pit)
- `_dt_` = doct length (dorsal origin to caudal tip)
- `_ds_` = stretchdoct length
- `_id_` = interdorsal length
- `_pl_` = preoral length
- `_pb_` = prebranchial length
- `_pp_` = prepectoral length
- `_hl_` = head length

Third subscript takes one of these two:

- `__o` = over-body
- `__s` = straight

Examples of length variants with concise subscript labels:

- `dts` = defrosted-total-straight
- `dss` = defrosted-stretchtotal-straight
- `ffo` = fresh-fork-overbody

Definitions

Table A1.1.1: *Definition of full body length measurements. Descriptions exclude shark state (fresh vs frozen) and position (lying on ventral abdomen or lateral abdomen). Visual examples of these full body length measurements are available in Figure 2.1.*

Length	Definition
Precaudal length, straight line	From the apex of the snout to the origin of the upper lobe of the caudal fin in a straight line.
Precaudal length, over-the-body	From the apex of the snout to the origin of the upper lobe of the caudal fin over the dorsomedial curve of the body.
Fork length, straight line	From the apex of the snout to the middle of the caudal fin (where the upper and lower lobes meet), with the tail in a natural position, in a straight line.
Fork length, over-the-body	From the apex of the snout to the middle of the caudal fin (where the upper and lower lobes meet), with the tail in a natural position, over the dorsomedial curve of the body.
Natural total length, straight line	From the apex of the snout to the apex of the upper lobe of the caudal fin, with the tail in a natural position, in a straight line.
Natural total length, over-the-body	From the apex of the snout to the apex of the upper lobe of the caudal fin, with the tail in a natural position, over the dorsomedial curve of the body.
Stretched total length, straight line	From the apex of the snout to the apex of the upper lobe of the caudal fin, with the tail stretched to be in line with the body axis/to its fullest extension, in a straight line.
Stretched total length, over-the-body	From the apex of the snout to the apex of the upper lobe of the caudal fin, with the tail in a stretched to be in line with the body axis/to fullest extension, over the dorsomedial curve of the body.

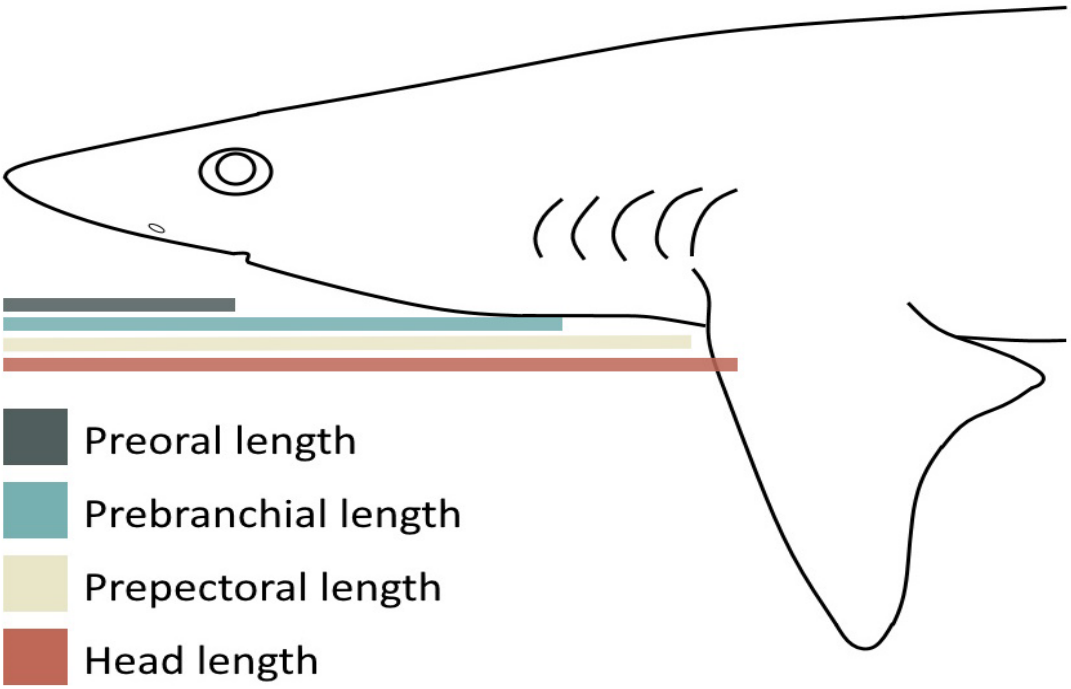


Figure A1.1.1: *Partial lengths of a shark, anterior of first dorsal fin. Definitions of the length variants are available in Table A1.1.2.*

Table A1.1.2: *Definition of partial body length measurements - head. Descriptions exclude shark state (fresh vs frozen) and position (lying on ventral abdomen or lateral abdomen).*

Length	Definition
Preoral length, straight line	From the apex of the snout to the apex of the upper jaw in a straight line.
Preoral length, over-the-body	From the apex of the snout to the apex of the upper jaw over the curvature of the body.
Prebranchial length, straight line	From the apex of the snout to the most distal edge of the first gill slit in a straight line.
Prebranchial length, over-the-body	From the apex of the snout to the most distal edge of the first gill slit over the curvature of the body.
Prepectoral length, straight line	From the apex of the snout to the origin of the pectoral fins in a straight line.
Prepectoral length, over-the-body	From the apex of the snout to the origin of the pectoral fins over the curvature of the body.
Head length, straight line	From the apex of the snout to the most distal edge of the fifth gill slit in a straight line.
Head length, over-the-body	From the apex of the snout to the most distal edge of the fifth gill slit over the curvature of the body.

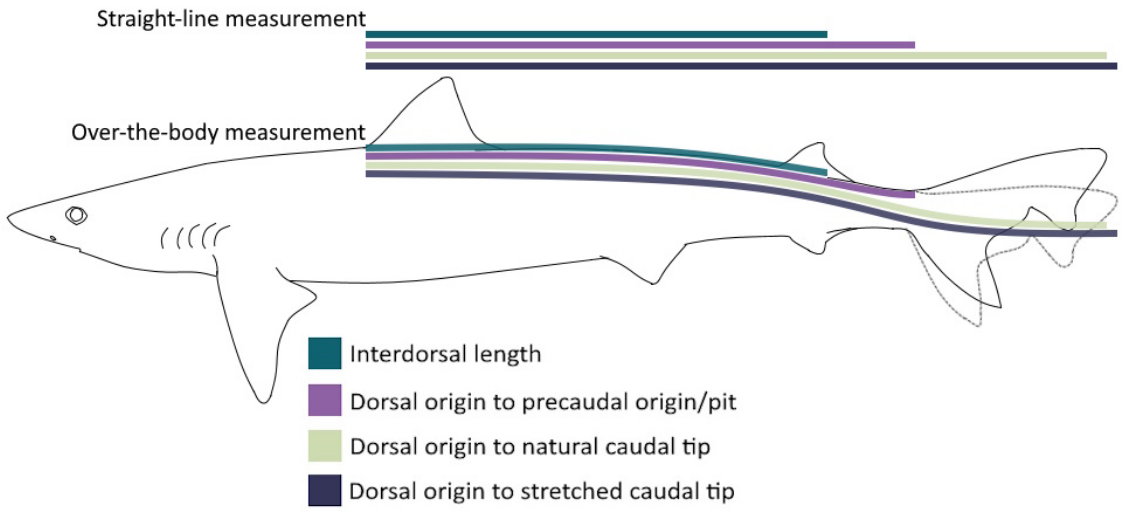


Figure A1.1.2: *Partial lengths of a shark, at and posterior to first dorsal fin. The grey outlined tail illustrates when the tail is in a stretched position. Definitions of the length variants are available in Table A1.1.3.*

Table A1.1.3: *Definition of partial body length measurements - fins and tail. Descriptions exclude shark state (fresh vs frozen) and position (lying on ventral abdomen or lateral abdomen).*

Length	Definition
Interdorsal length, straight line	From the origin of the first dorsal fin to the insertion of the second dorsal fin, in a straight line.
Interdorsal length, over-the-body	From the origin of the first dorsal fin to the insertion of the second dorsal fin, over the dorsomedial curve of the body.
Dorsal origin to precaudal origin/pit length, straight line	From the origin of the first dorsal fin to the origin of the upper lobe of the caudal fin, in a straight line.
Dorsal origin to precaudal origin/pit length, over-the-body	From the origin of the first dorsal fin to the origin of the upper lobe of the caudal fin, over the dorsomedial curve of the body.
Dorsal origin to natural caudal tip length, straight line	From the origin of the first dorsal fin to the apex of the upper lobe of the caudal fin, with the tail in a natural position, in a straight line.
Dorsal origin to natural caudal tip length, over-the-body	From the origin of the first dorsal fin to the apex of the upper lobe of the caudal fin, with the tail in a natural position, over the dorsomedial curve of the body.
Dorsal origin to stretched caudal tip length, straight line	From the origin of the first dorsal fin to the apex of the upper lobe of the caudal fin, with the tail in a stretched to be in line with the body axis/to fullest extension, in a straight line.
Dorsal origin to stretched caudal tip length, over-the-body	From the origin of the first dorsal fin to the apex of the upper lobe of the caudal fin, with the tail in a stretched to be in line with the body axis/to fullest extension, over the dorsomedial curve of the body.

A1.2: Fit and residual plots of the four models for each of the 17 conversions

A1.2.1: fts ~ dts - Fresh, natural, total length ~ defrosted, natural, total length

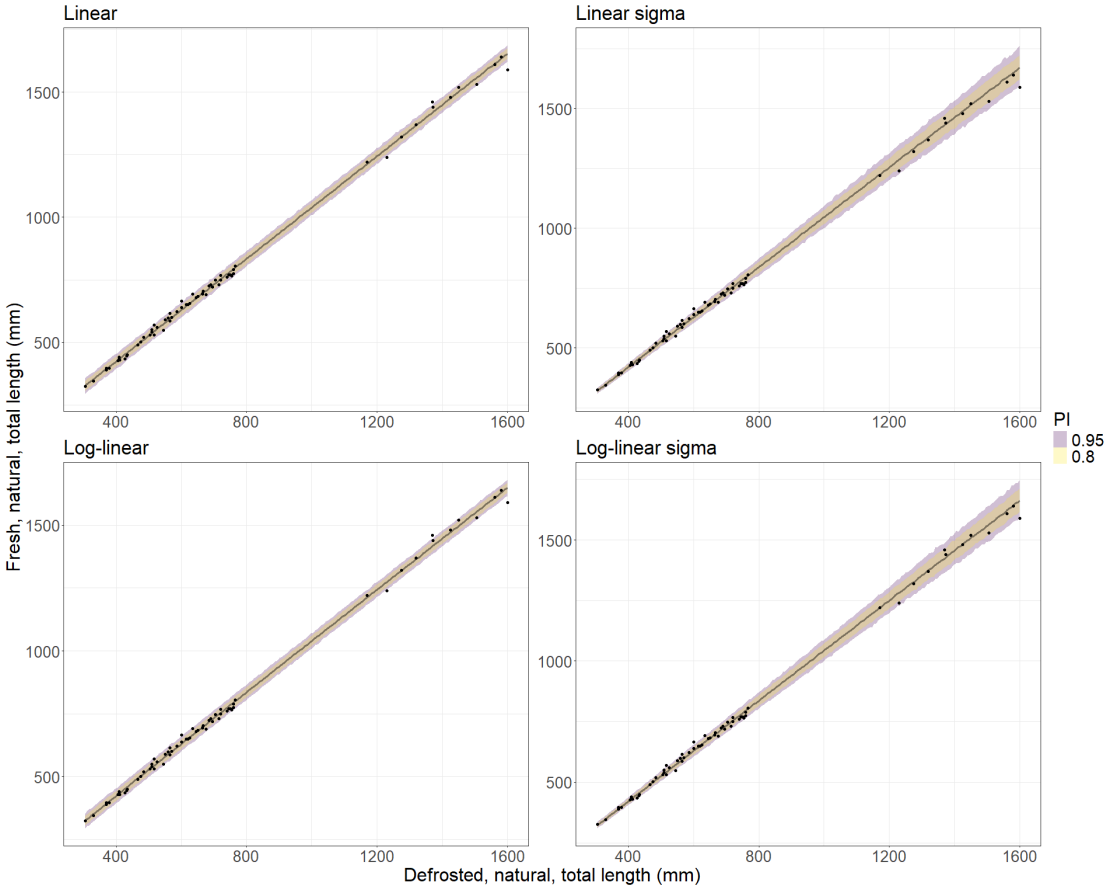


Figure A1.2.1.1: *Predicted fit of the linear and log-linear models (with different error structures) for converting defrosted, natural, total length to fresh, natural, total length. PI corresponds to 80% and 95% posterior prediction intervals. Fresh, natural, total length is the total length measured from a fresh shark, in a straight line, with the tail in a natural position. Defrosted, natural, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a natural position.*

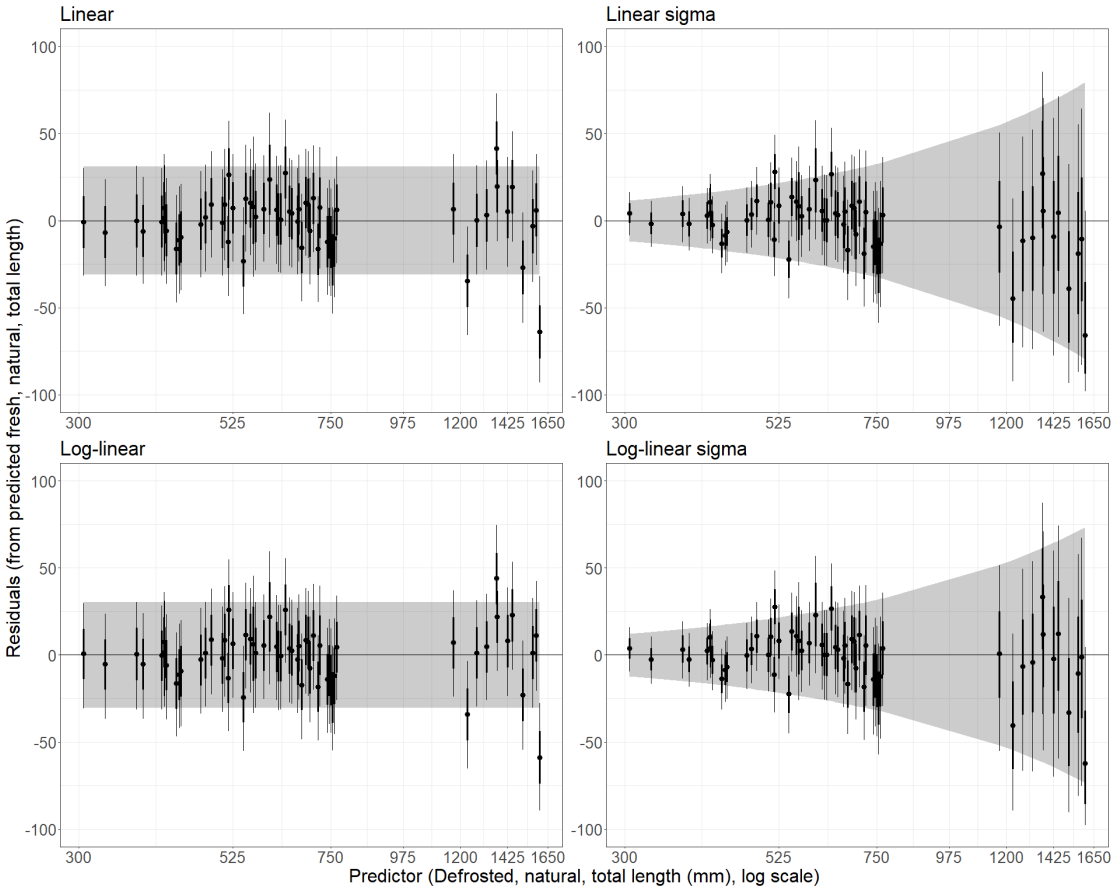


Figure A1.2.1.2: *Residual plots of the linear and log-linear models (with different error structures) for converting defrosted, natural, total length to fresh, natural, total length. Points represent the point estimates of the residual posterior distributions. Vertical lines indicate the 66% and 95% credible intervals of the residual posterior distributions. The shaded area is the 95% range of the residual variation, as determined by the model's error structure. Fresh, natural, total length is the total length measured from a fresh shark, in a straight line, with the tail in a natural position. Defrosted, natural, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a natural position.*

A1.2.2: fts ~ dhls - Fresh, natural, total length ~ defrosted head length

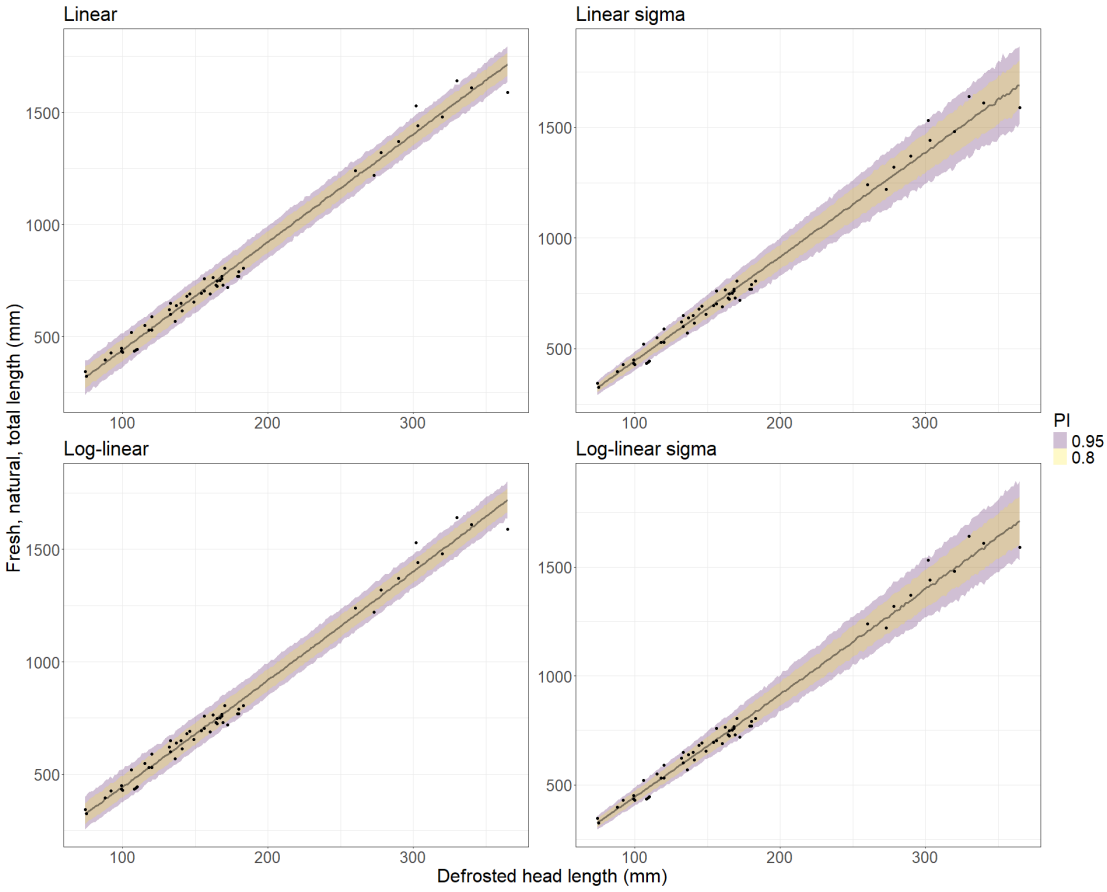


Figure A1.2.2.1: *Predicted fit of the linear and log-linear models (with different error structures) for converting defrosted head length to fresh, natural, total length. PI corresponds to 80% and 95% posterior prediction intervals. Defrosted head length is the head length measured from a defrosted shark, in a straight line. Defrosted, natural, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a natural position.*

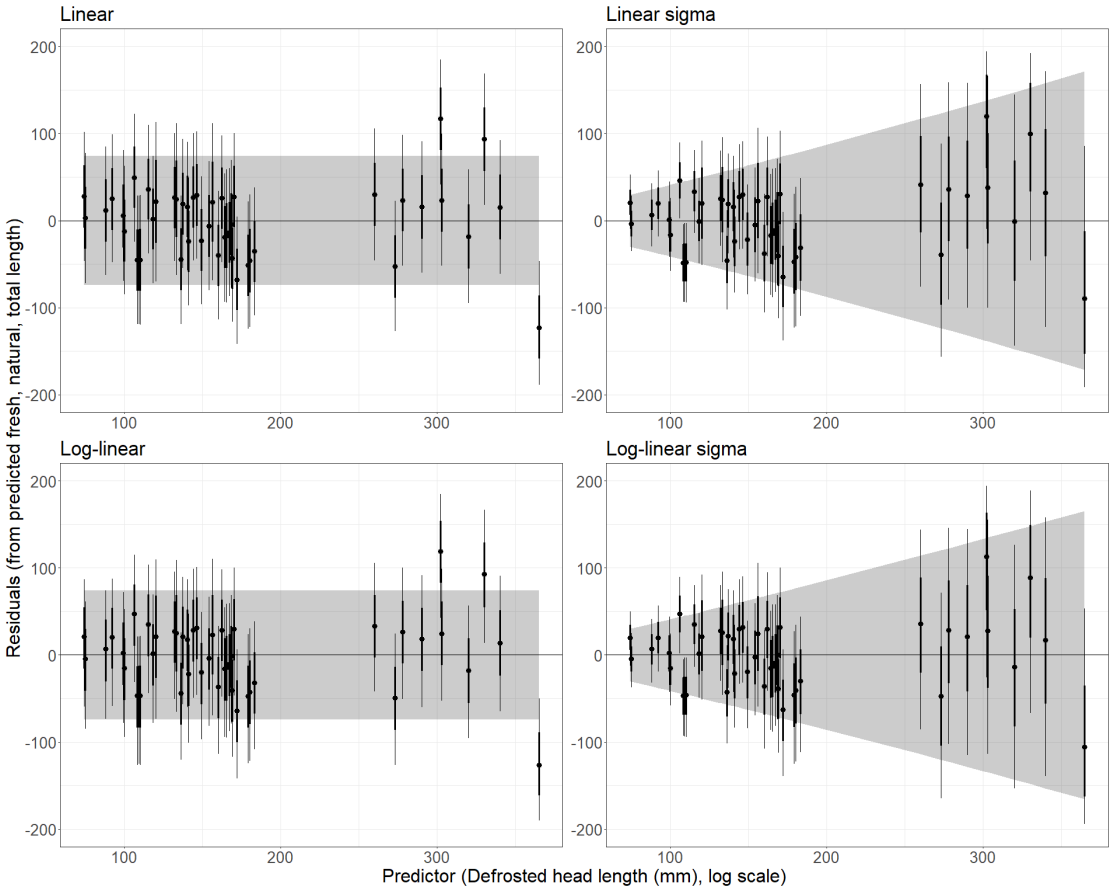


Figure A1.2.2 2: *Residual plots of the linear and log-linear models (with different error structures) for converting defrosted head length to fresh, natural, total length. Points represent the point estimates of the residual posterior distributions. Vertical lines indicate the 66% and 95% credible intervals of the residual posterior distributions. The shaded area is the 95% range of the residual variation, as determined by the model's error structure. Defrosted head length is the head length measured from a defrosted shark, in a straight line. Defrosted, natural, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a natural position.*

A1.2.3: fts ~ dpls - Fresh, natural, total length ~ defrosted preoral length

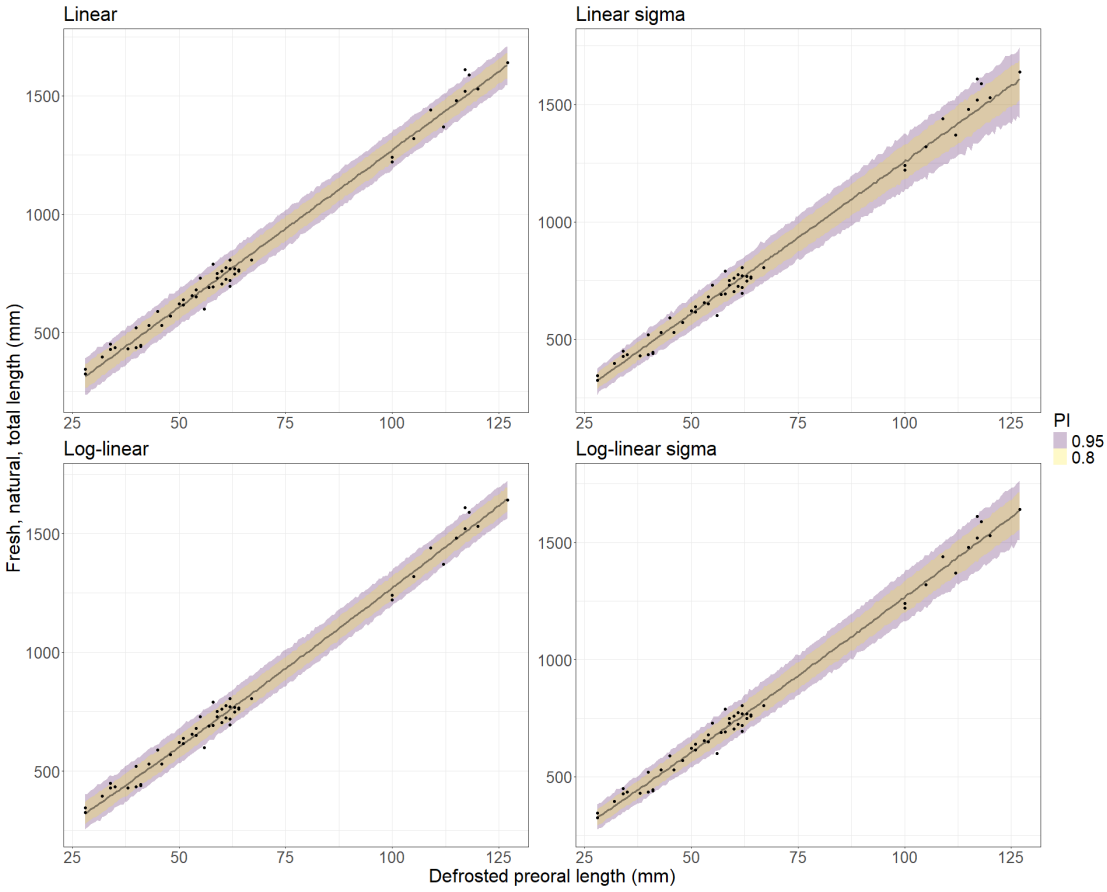


Figure A1.2.3.1: *Predicted fit of the linear and log-linear models (with different error structures) for converting defrosted preoral length to fresh, natural, total length. PI corresponds to 80% and 95% posterior prediction intervals. Defrosted preoral length is the preoral length measured from a defrosted shark, in a straight line. Fresh, natural, total length is the total length measured from a fresh shark, in a straight line, with the tail in a natural position.*

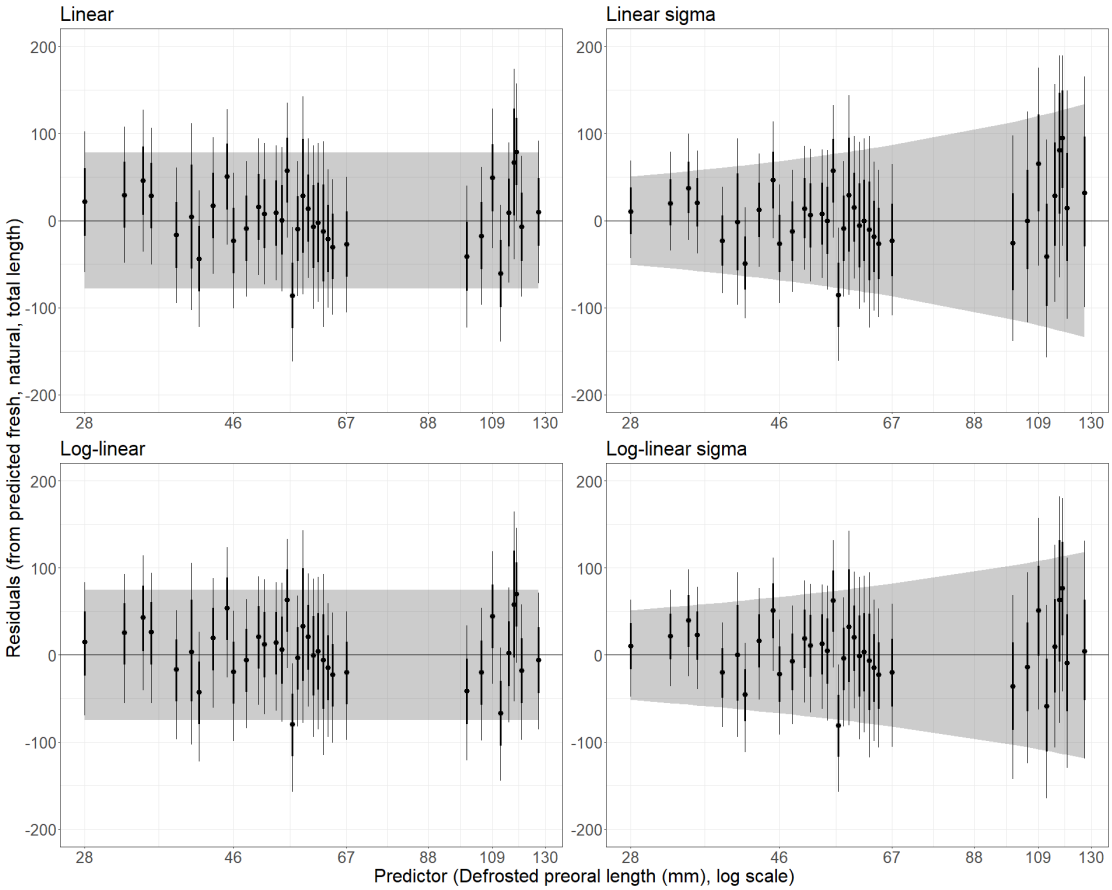


Figure A1.2.3.2: *Residual plots of the linear and log-linear models (with different error structures) for converting defrosted preoral length to fresh, natural, total length. Points represent the point estimates of the residual posterior distributions. Vertical lines indicate the 66% and 95% credible intervals of the residual posterior distributions. The shaded area is the 95% range of the residual variation, as determined by the model's error structure. Defrosted preoral length is the preoral length measured from a defrosted shark, in a straight line. Fresh, natural, total length is the total length measured from a fresh shark, in a straight line, with the tail in a natural position.*

A1.2.4: dts ~ dto - Defrosted, natural, total length ~ defrosted, natural, over-the-body total length

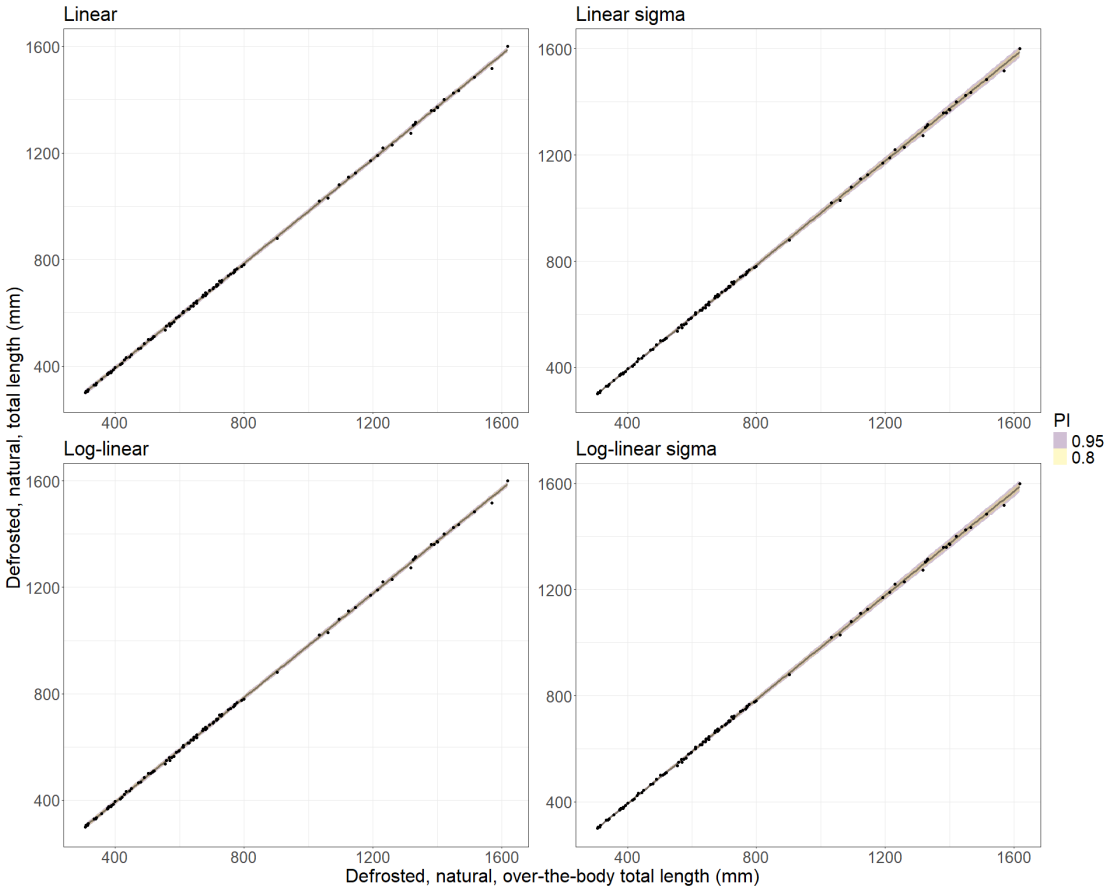


Figure A1.2.4.1: *Predicted fit of the linear and log-linear models (with different error structures) for converting defrosted, natural, over-the-body total length to defrosted, natural, total length. PI corresponds to 80% and 95% posterior prediction intervals. Defrosted, natural, over-the-body total length is the total length measured from a defrosted shark, over the curvature of the body, with the tail in a natural position. Defrosted, natural, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a natural position.*

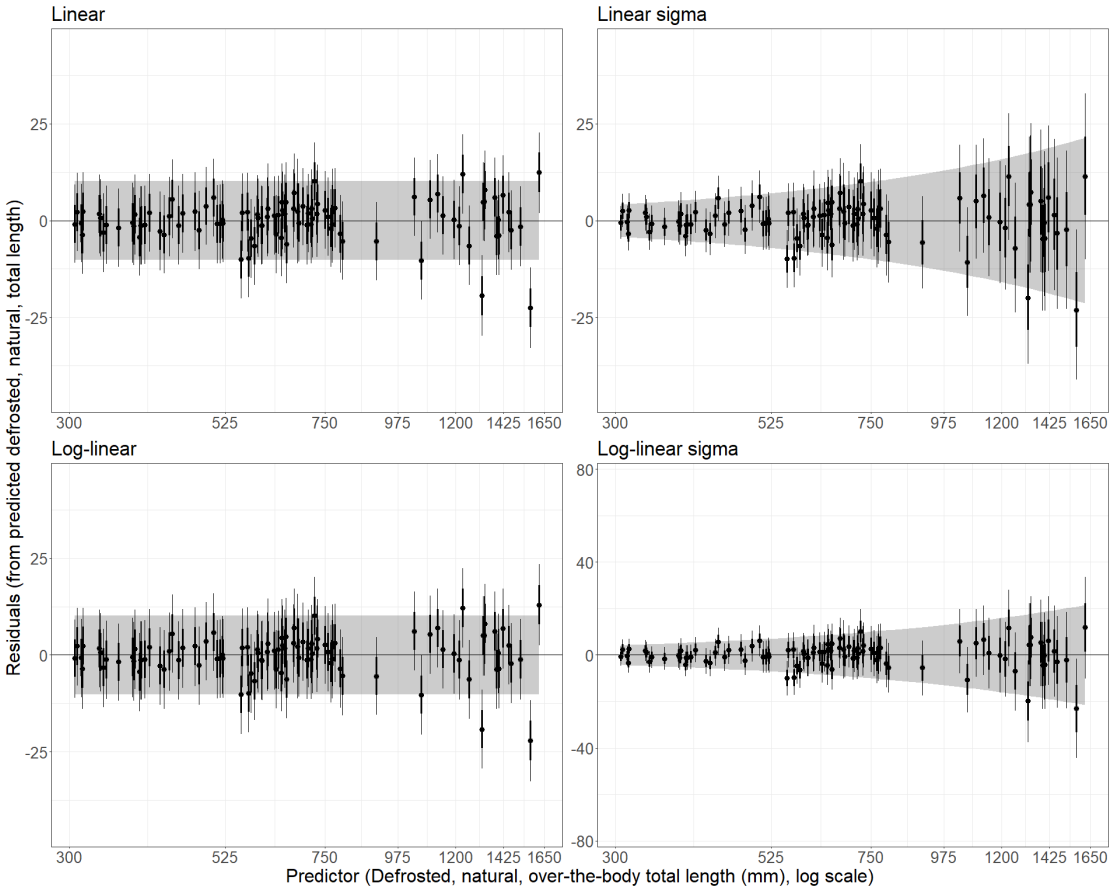


Figure A1.2.4.2: *Residual plots of the linear and log-linear models (with different error structures) for converting defrosted, natural, over-the-body total length to defrosted, natural, total length. Points represent the point estimates of the residual posterior distributions. Vertical lines indicate the 66% and 95% credible intervals of the residual posterior distributions. The shaded area is the 95% range of the residual variation, as determined by the model's error structure. Defrosted, natural, over-the-body total length is the total length measured from a defrosted shark, over the curvature of the body, with the tail in a natural position. Defrosted, natural, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a natural position.*

A1.2.5: dts ~ dso - Defrosted, natural, total length ~ defrosted, stretched, over-the-body total length

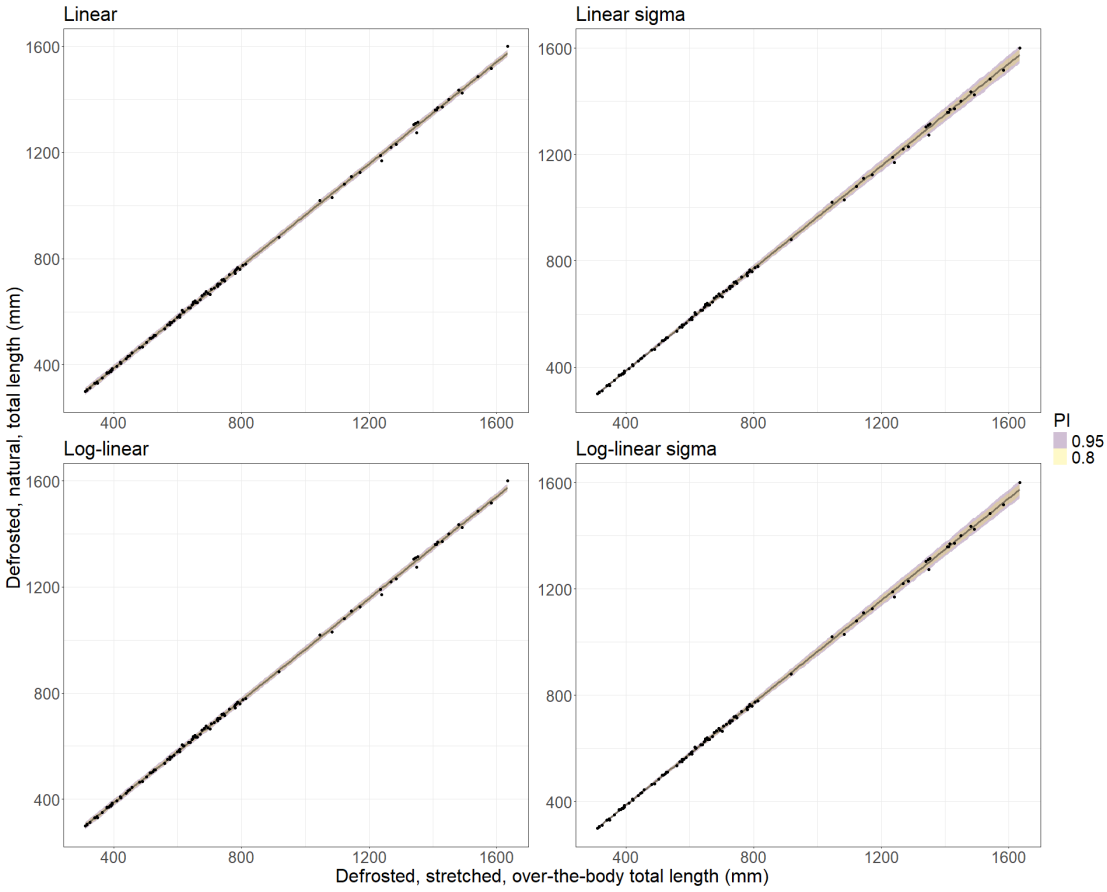


Figure A1.2.5.1: *Predicted fit of the linear and log-linear models (with different error structures) for converting defrosted, stretched, over-the-body total length to defrosted, natural, total length. PI corresponds to 80% and 95% posterior prediction intervals. Defrosted, stretched, over-the-body total length is the total length measured from a defrosted shark, over the curvature of the body, with the tail in a stretched position. Defrosted, natural, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a natural position.*

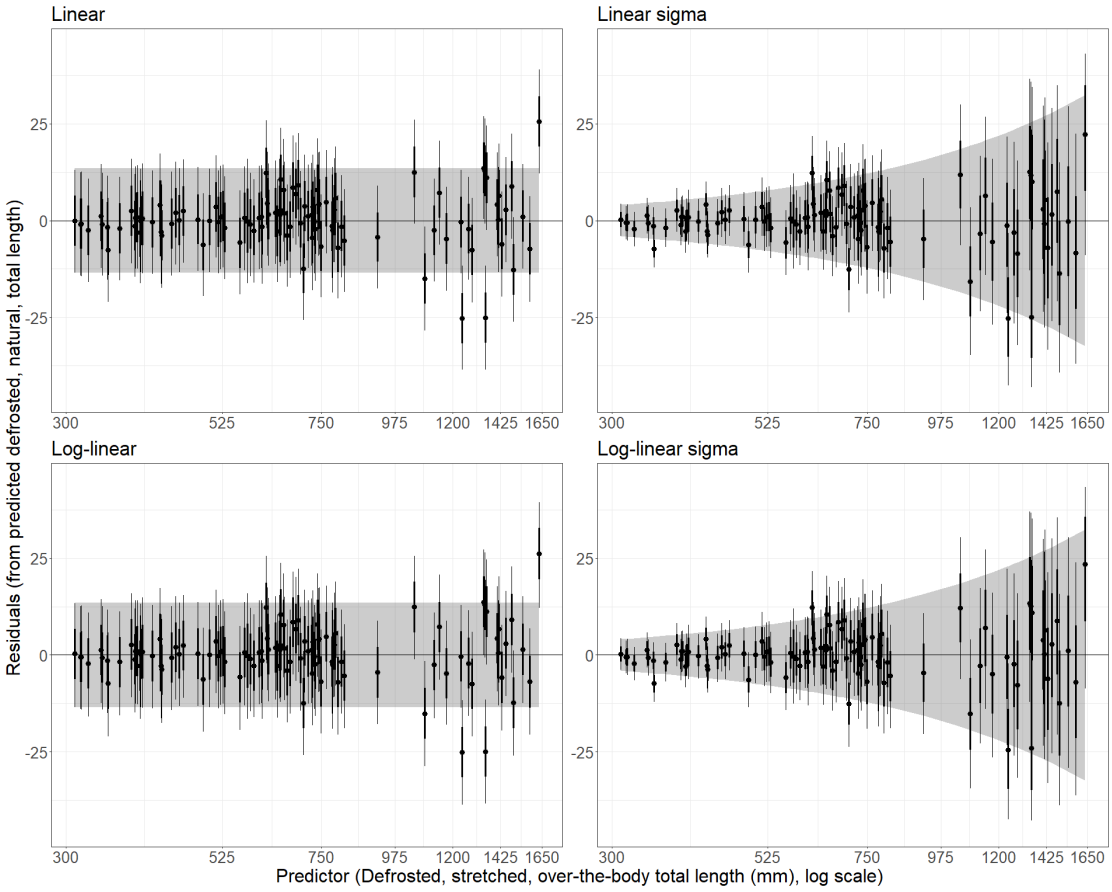


Figure A1.2.5.2: *Residual plots of the linear and log-linear models (with different error structures) for converting defrosted, stretched, over-the-body total length to defrosted, natural, total length. Points represent the point estimates of the residual posterior distributions. Vertical lines indicate the 66% and 95% credible intervals of the residual posterior distributions. The shaded area is the 95% range of the residual variation, as determined by the model's error structure. Defrosted, stretched, over-the-body total length is the total length measured from a defrosted shark, over the curvature of the body, with the tail in a stretched position. Defrosted, natural, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a natural position.*

A1.2.6: dts ~ dfs - Defrosted, natural, total length ~ defrosted, natural, fork length

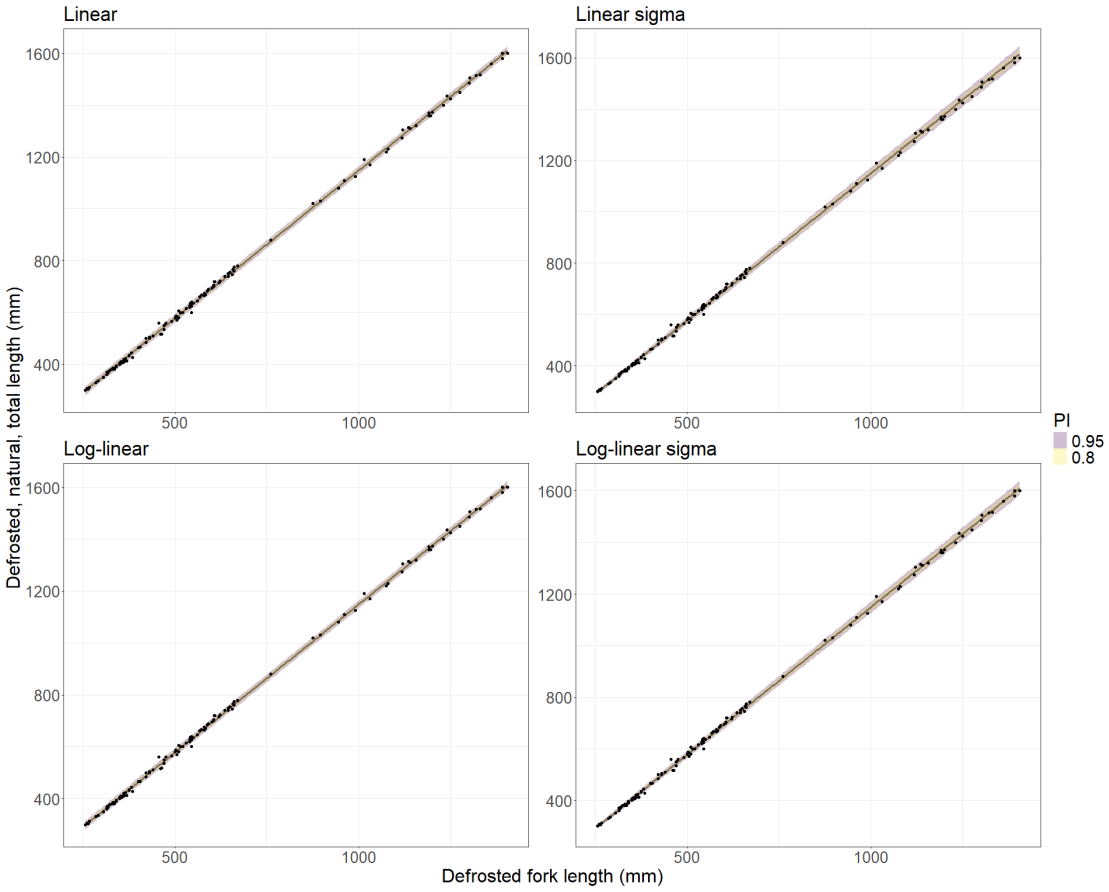


Figure A1.2.6.1: *Predicted fit of the linear and log-linear models (with different error structures) for converting defrosted fork length to defrosted, natural, total length. PI corresponds to 80% and 95% posterior prediction intervals. Defrosted fork length is the fork length measured from a defrosted shark, in a straight line, with the tail in a natural position. Defrosted, natural, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a natural position.*

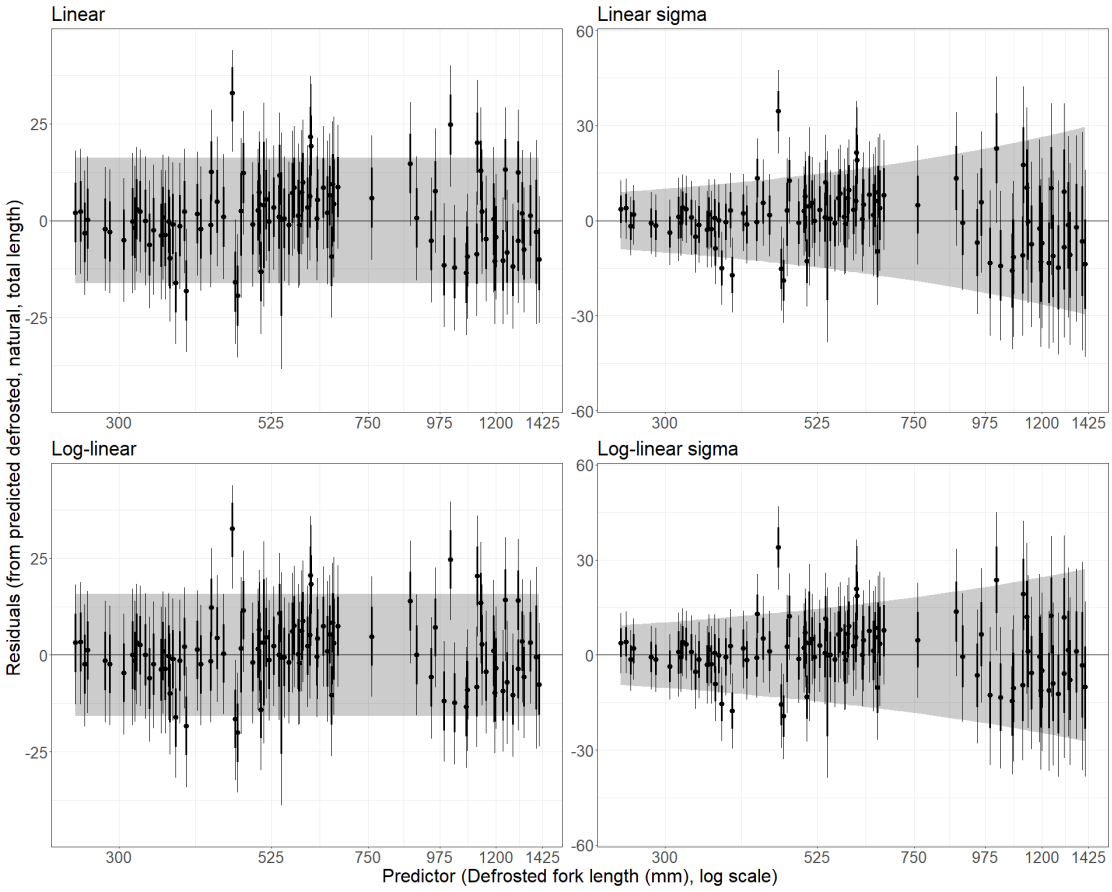


Figure A1.2.6.2: *Residual plots of the linear and log-linear models (with different error structures) for converting defrosted fork length to defrosted, natural, total length. Points represent the point estimates of the residual posterior distributions. Vertical lines indicate the 66% and 95% credible intervals of the residual posterior distributions. The shaded area is the 95% range of the residual variation, as determined by the model's error structure. Defrosted fork length is the fork length measured from a defrosted shark, in a straight line, with the tail in a natural position. Defrosted, natural, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a natural position.*

A1.2.7: dts ~ dps - Defrosted, natural, total length ~ defrosted precaudal length

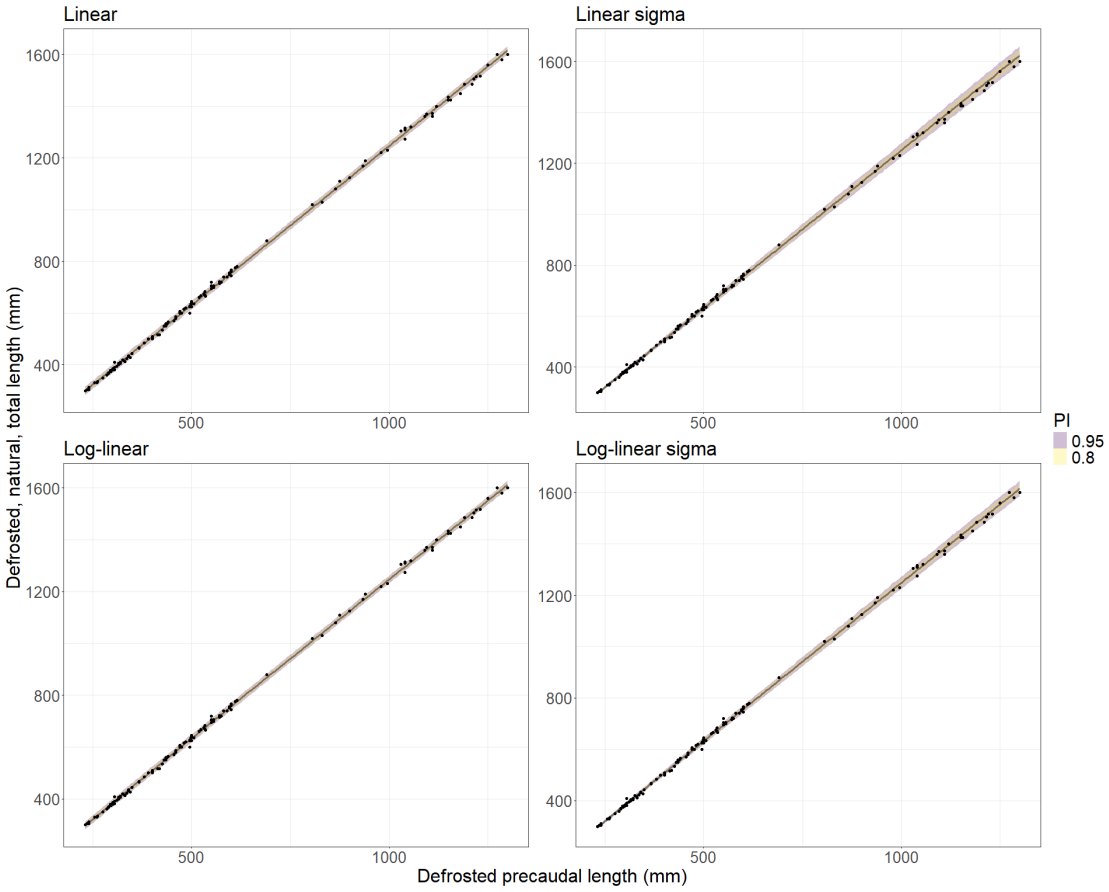


Figure A1.2.7.1: *Predicted fit of the linear and log-linear models (with different error structures) for converting defrosted precaudal length to defrosted, natural, total length. PI corresponds to 80% and 95% posterior prediction intervals. Defrosted precaudal length is the precaudal length measured from a defrosted shark, in a straight line. Defrosted, natural, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a natural position.*

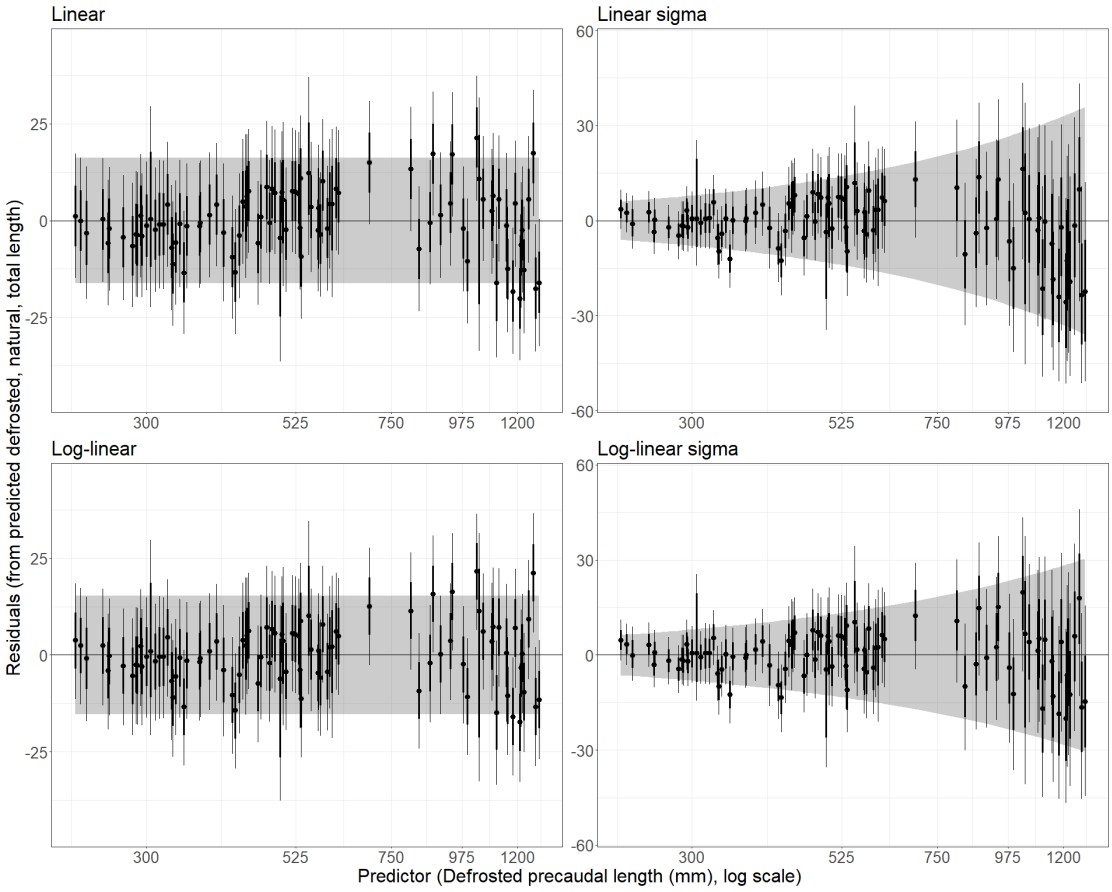


Figure A1.2.7.2: *Residual plots of the linear and log-linear models (with different error structures) for converting defrosted precaudal length to defrosted, natural, total length. Points represent the point estimates of the residual posterior distributions. Vertical lines indicate the 66% and 95% credible intervals of the residual posterior distributions. The shaded area is the 95% range of the residual variation, as determined by the model's error structure. Defrosted precaudal length is the precaudal length measured from a defrosted shark, in a straight line. Defrosted, natural, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a natural position.*

A1.2.8: dts ~ ddso - Defrosted, natural, total length ~ defrosted, stretched, over-the-body dorsal origin to caudal tip length

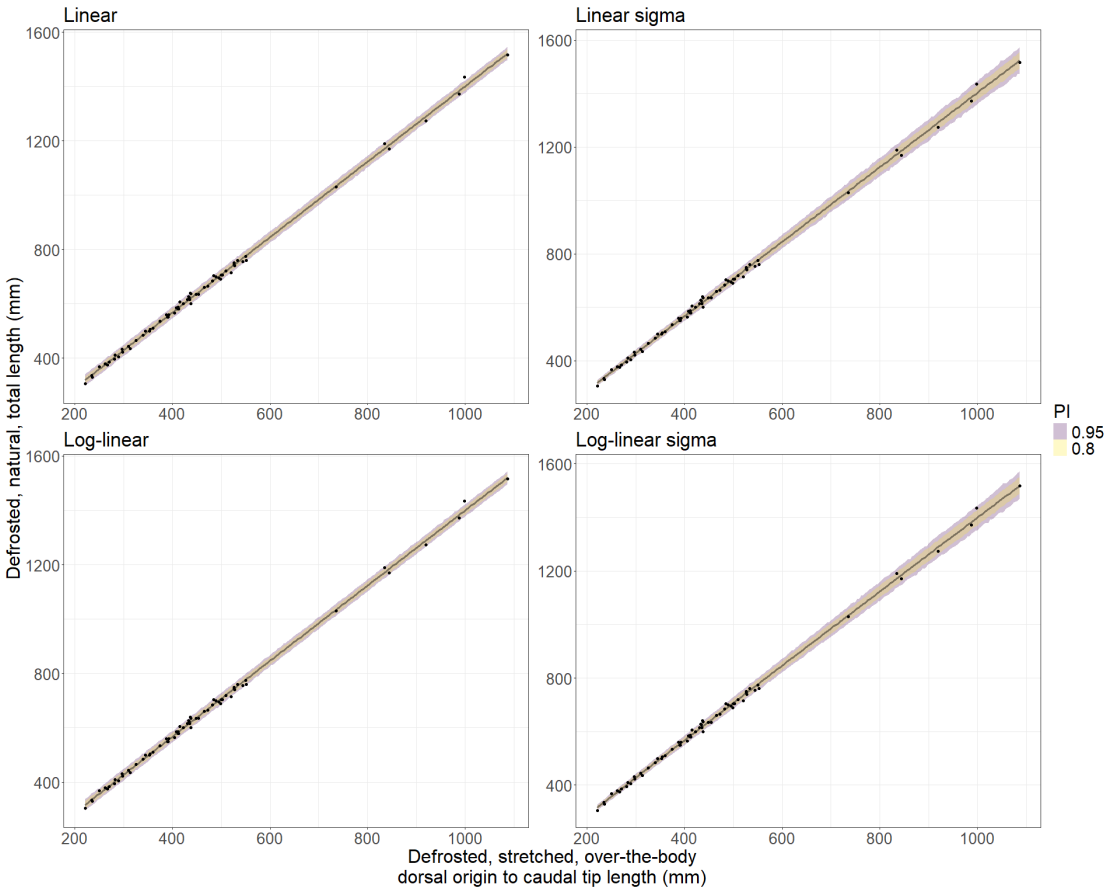


Figure A1.2.8.1: *Predicted fit of the linear and log-linear models (with different error structures) for converting defrosted, stretched, over-the-body dorsal origin to caudal tip length to defrosted, natural, total length. PI corresponds to 80% and 95% posterior prediction intervals. Defrosted, stretched, over-the-body dorsal origin to caudal tip length is the first dorsal fin origin to caudal tip length measured from a defrosted shark, over the curvature of the body, with the tail in a stretched position. Defrosted, natural, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a natural position.*

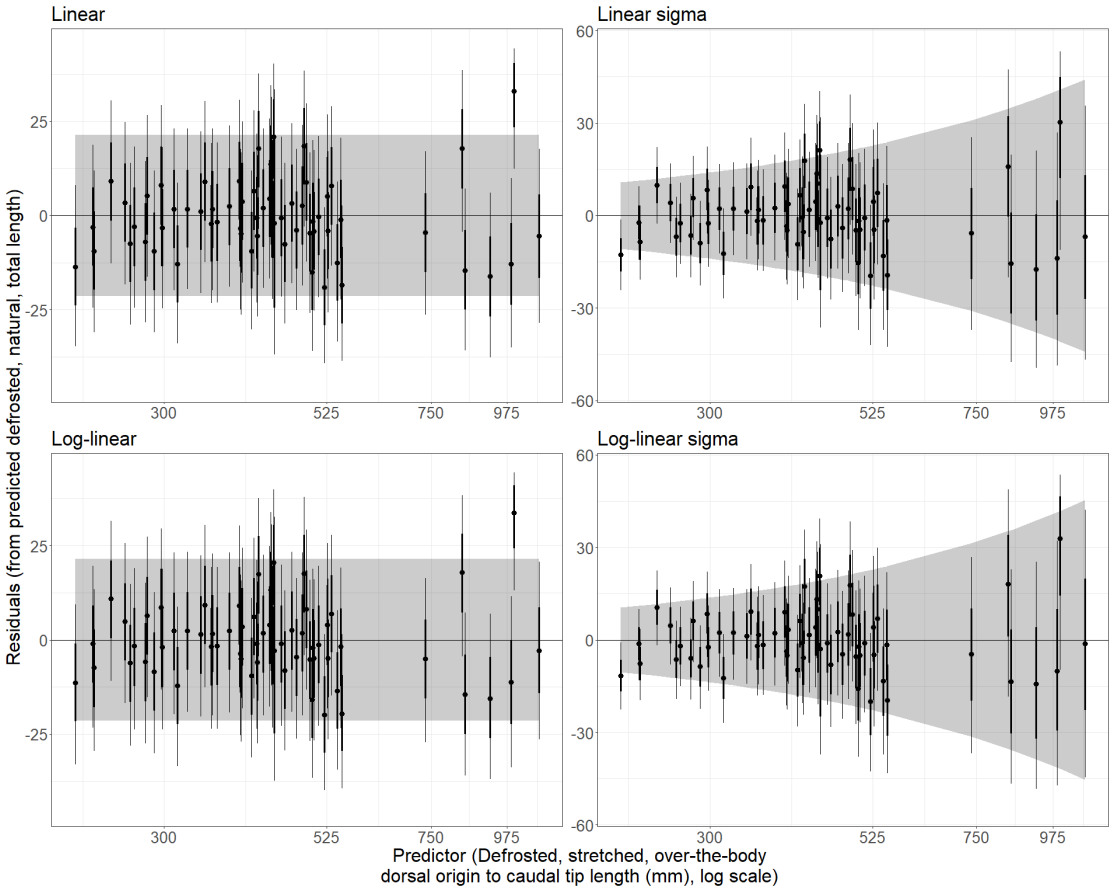


Figure A1.2.8.2: *Residual plots of the linear and log-linear models (with different error structures) for converting defrosted, stretched, over-the-body dorsal origin to caudal tip length to defrosted, natural, total length. Points represent the point estimates of the residual posterior distributions. Vertical lines indicate the 66% and 95% credible intervals of the residual posterior distributions. The shaded area is the 95% range of the residual variation, as determined by the model's error structure. Defrosted, stretched, over-the-body dorsal origin to caudal tip length is the first dorsal fin origin to caudal tip length measured from a defrosted shark, over the curvature of the body, with the tail in a stretched position. Defrosted, natural, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a natural position.*

A1.2.9: dss ~ dts - Defrosted, stretched, total length ~ defrosted, natural, total length

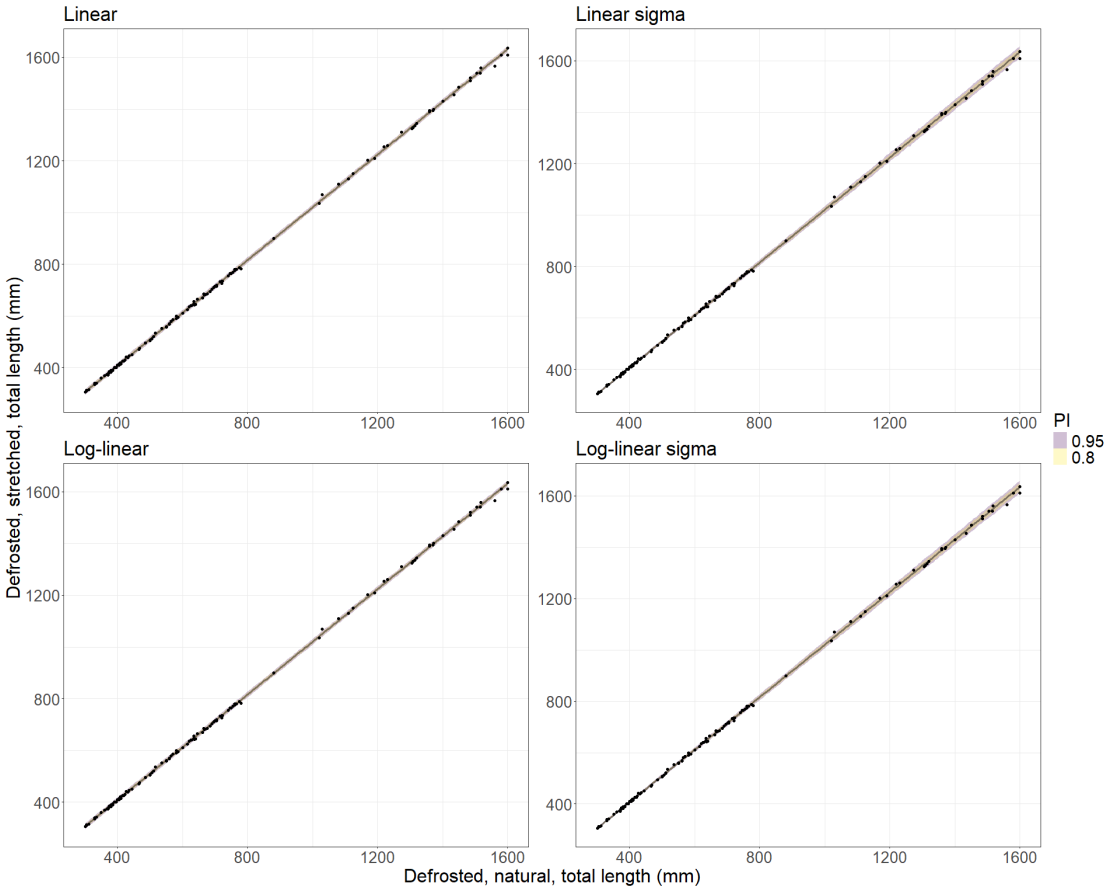


Figure A1.2.9.1: *Predicted fit of the linear and log-linear models (with different error structures) for converting defrosted, natural, total length to defrosted, stretched, total length. PI corresponds to 80% and 95% posterior prediction intervals. Defrosted, natural, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a natural position. Defrosted, stretched, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a stretched position.*

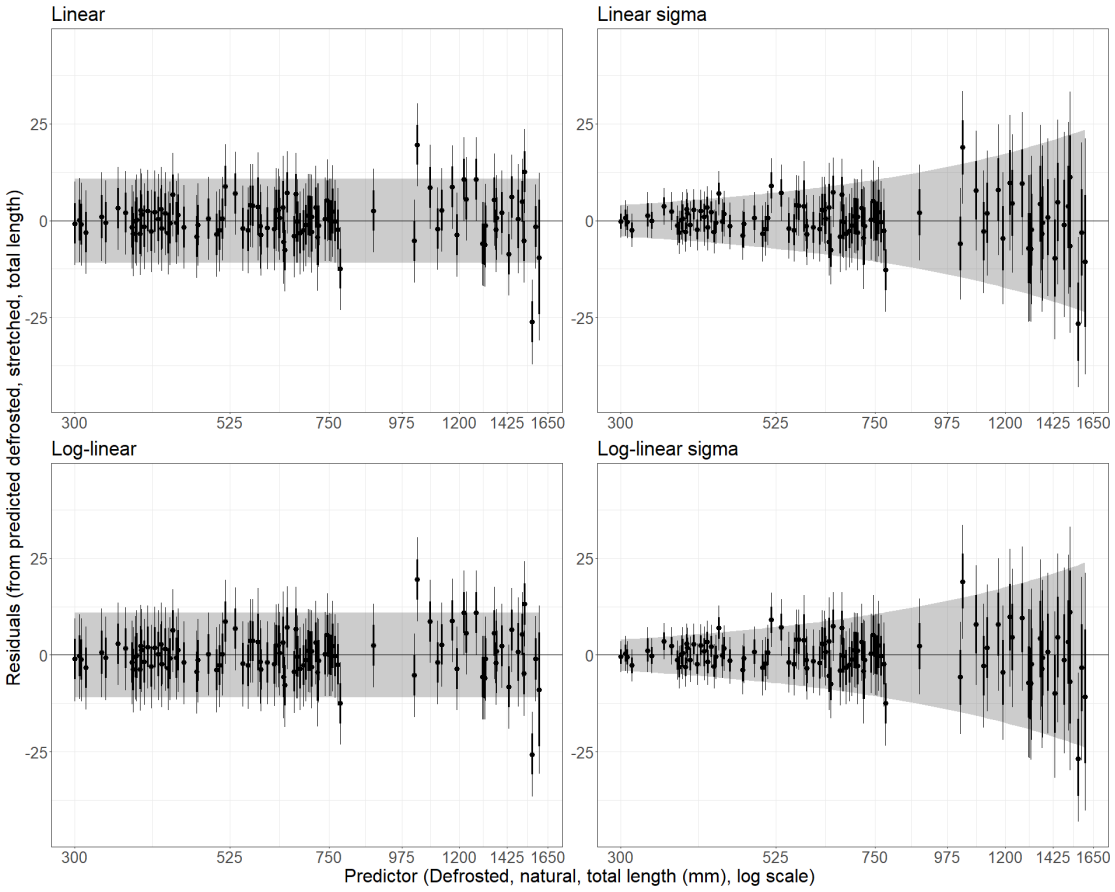


Figure A1.2.9.2: *Residual plots of the linear and log-linear models (with different error structures) for converting defrosted, natural, total length to defrosted, stretched, total length. Points represent the point estimates of the residual posterior distributions. Vertical lines indicate the 66% and 95% credible intervals of the residual posterior distributions. The shaded area is the 95% range of the residual variation, as determined by the model's error structure. Defrosted, natural, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a natural position. Defrosted, stretched, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a stretched position.*

A1.2.10: dss ~ dto - Defrosted, stretched, total length ~ defrosted, natural, over-the-body total length

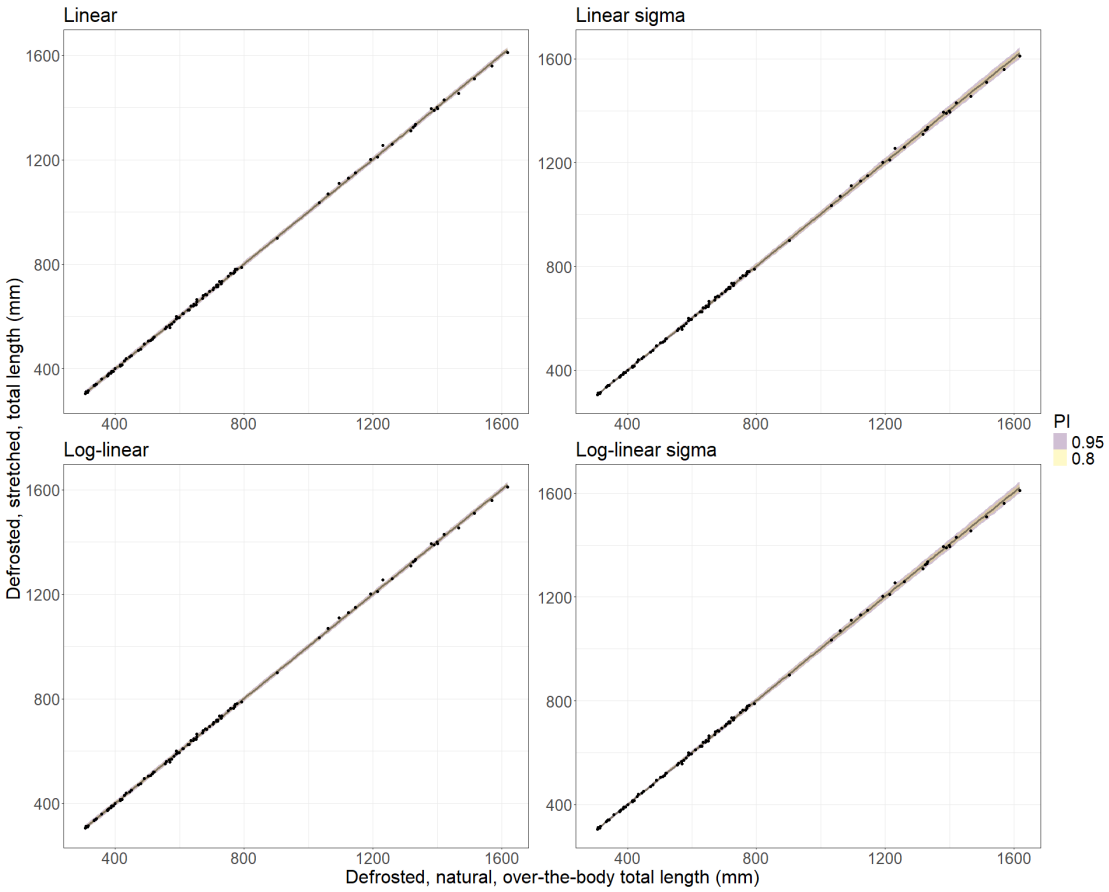


Figure A1.2.10.1: *Predicted fit of the linear and log-linear models (with different error structures) for converting defrosted, natural, over-the-body total length to defrosted, stretched, total length. PI corresponds to 80% and 95% posterior prediction intervals. Defrosted, natural, over-the-body total length is the total length measured from a defrosted shark, over the curvature of the body, with the tail in a natural position. Defrosted, stretched, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a stretched position.*

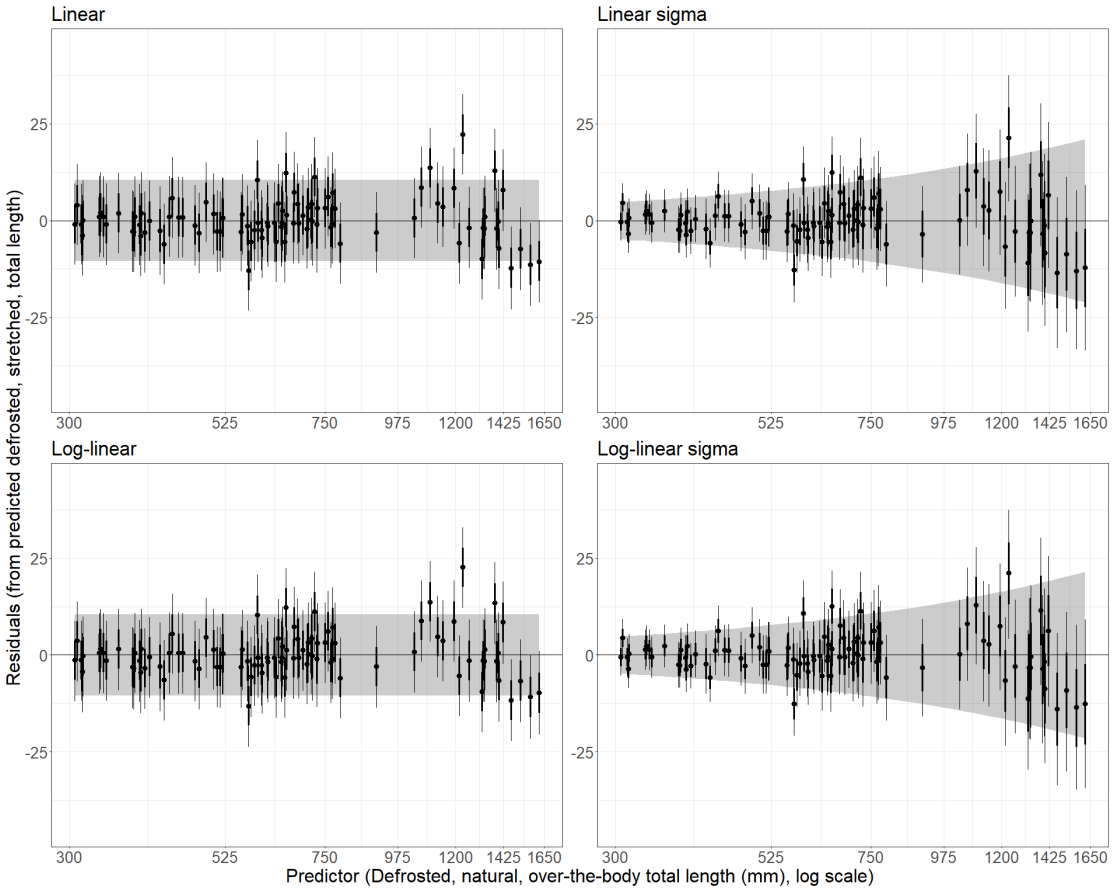


Figure A1.2.10.2: *Residual plots of the linear and log-linear models (with different error structures) for converting defrosted, natural, over-the-body total length to defrosted, stretched, total length. Points represent the point estimates of the residual posterior distributions. Vertical lines indicate the 66% and 95% credible intervals of the residual posterior distributions. The shaded area is the 95% range of the residual variation, as determined by the model's error structure. Defrosted, stretched, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a stretched position. Defrosted, natural, over-the-body total length is the total length measured from a defrosted shark, over the curvature of the body, with the tail in a natural position.*

A1.2.11: dss ~ dso - Defrosted, stretched, total length ~ defrosted, stretched, over-the-body total length

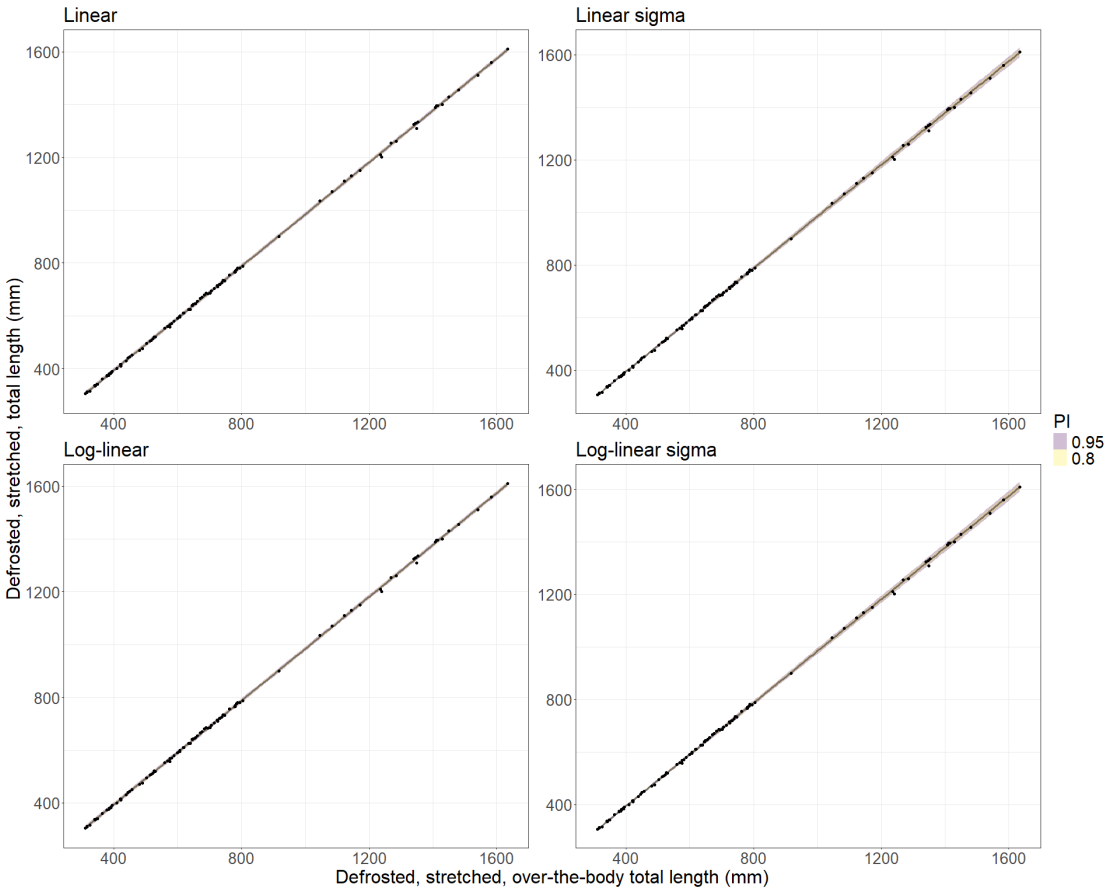


Figure A1.2.11.1: *Predicted fit of the linear and log-linear models (with different error structures) for converting defrosted, stretched, over-the-body total length to defrosted, stretched, total length. PI corresponds to 80% and 95% posterior prediction intervals. Defrosted, stretched, over-the-body total length is the total length measured from a defrosted shark, over the curvature of the body, with the tail in a stretched position. Defrosted, stretched, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a stretched position.*

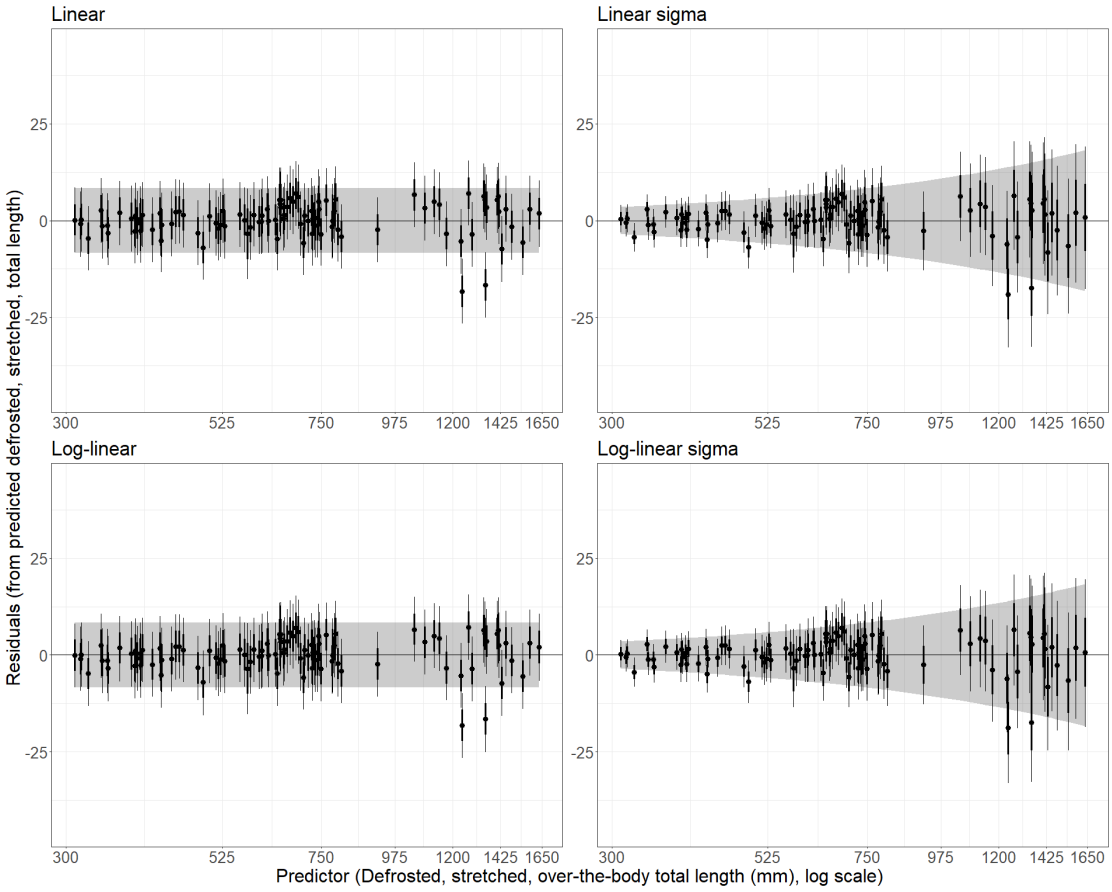


Figure A1.2.11.2: *Residual plots of the linear and log-linear models (with different error structures) for converting defrosted, stretched, over-the-body total length to defrosted, stretched, total length. Points represent the point estimates of the residual posterior distributions. Vertical lines indicate the 66% and 95% credible intervals of the residual posterior distributions. The shaded area is the 95% range of the residual variation, as determined by the model's error structure. Defrosted, stretched, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a stretched position. Defrosted, stretched, over-the-body total length is the total length measured from a defrosted shark, over the curvature of the body, with the tail in a stretched position.*

A1.2.12: dss ~ dfs - Defrosted, stretched, total length ~ defrosted, natural, fork length

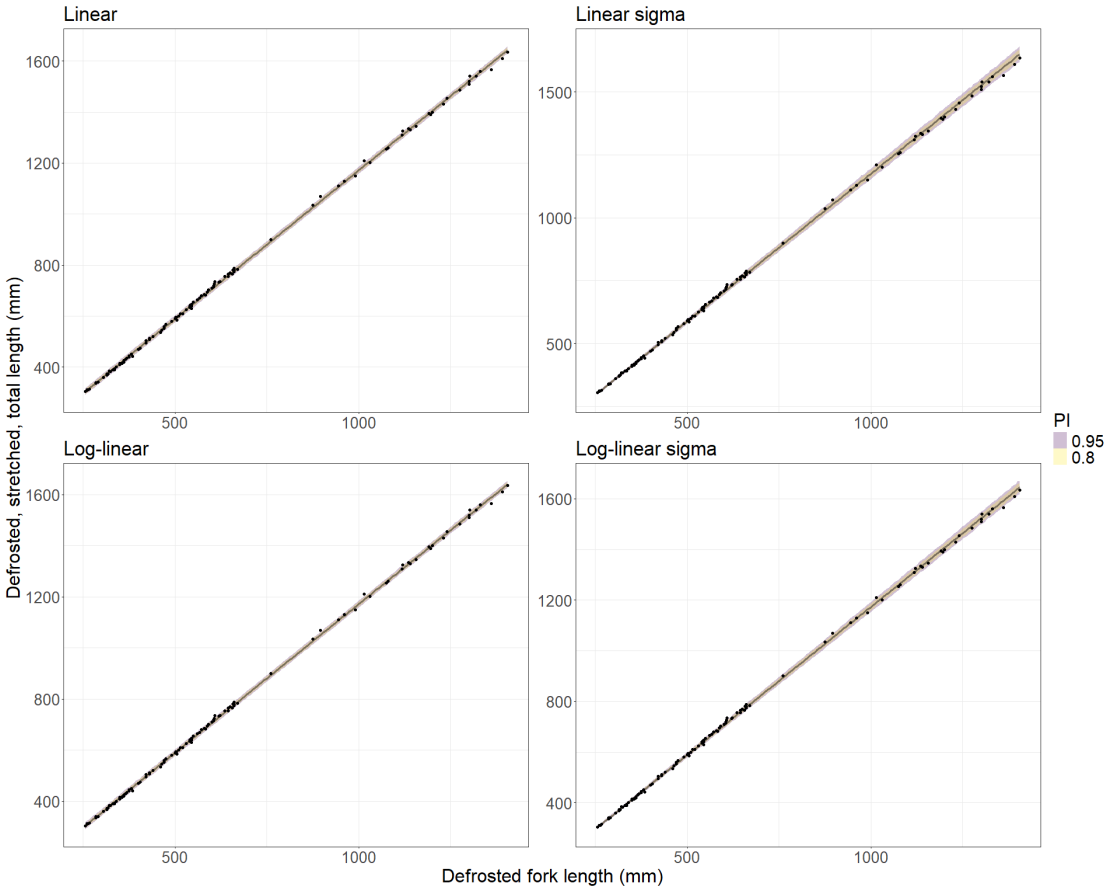


Figure A1.2.12.1: *Predicted fit of the linear and log-linear models (with different error structures) for converting defrosted fork length to defrosted, stretched, total length. PI corresponds to 80% and 95% posterior prediction intervals. Defrosted fork length is the fork length measured from a defrosted shark, in a straight line, with the tail in a natural position. Defrosted, stretched, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a stretched position.*

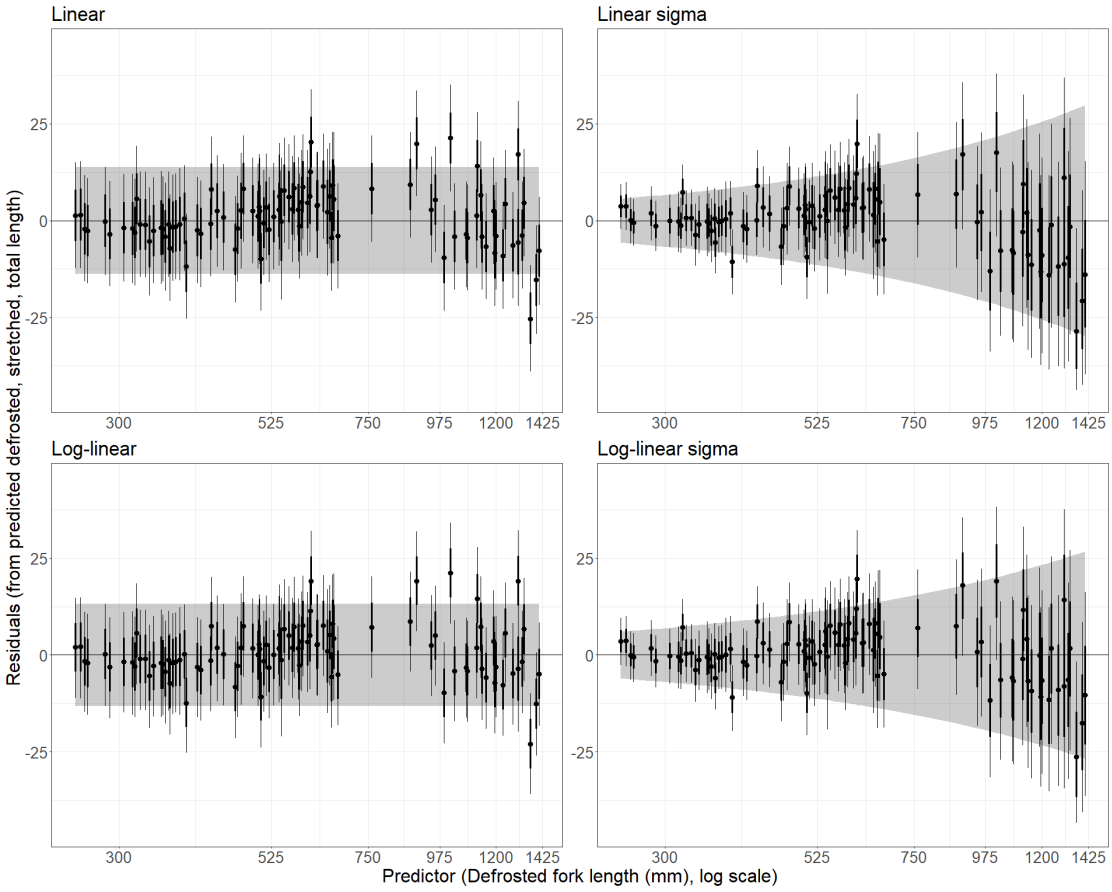


Figure A1.2.12 2: *Residual plots of the linear and log-linear models (with different error structures) for converting defrosted fork length to defrosted, stretched, total length. Points represent the point estimates of the residual posterior distributions. Vertical lines indicate the 66% and 95% credible intervals of the residual posterior distributions. The shaded area is the 95% range of the residual variation, as determined by the model's error structure. Defrosted fork length is the fork length measured from a defrosted shark, in a straight line, with the tail in a natural position. Defrosted, stretched, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a stretched position.*

A1.2.13: dss ~ dps - Defrosted, stretched, total length ~ defrosted precaudal length

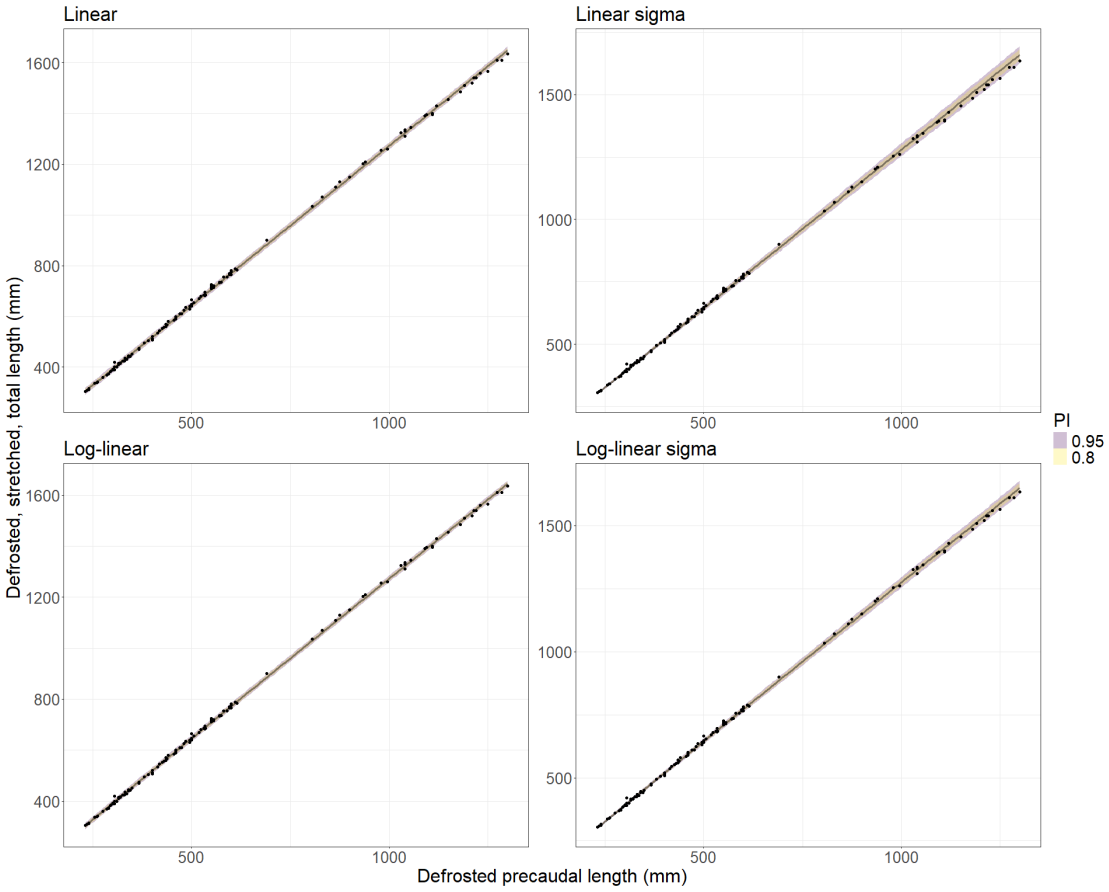


Figure A1.2.13.1: *Predicted fit of the linear and log-linear models (with different error structures) for converting defrosted precaudal length to defrosted, stretched, total length. PI corresponds to 80% and 95% posterior prediction intervals. Defrosted, stretched, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a stretched position. Defrosted precaudal length is the precaudal length measured from a defrosted shark, in a straight line.*

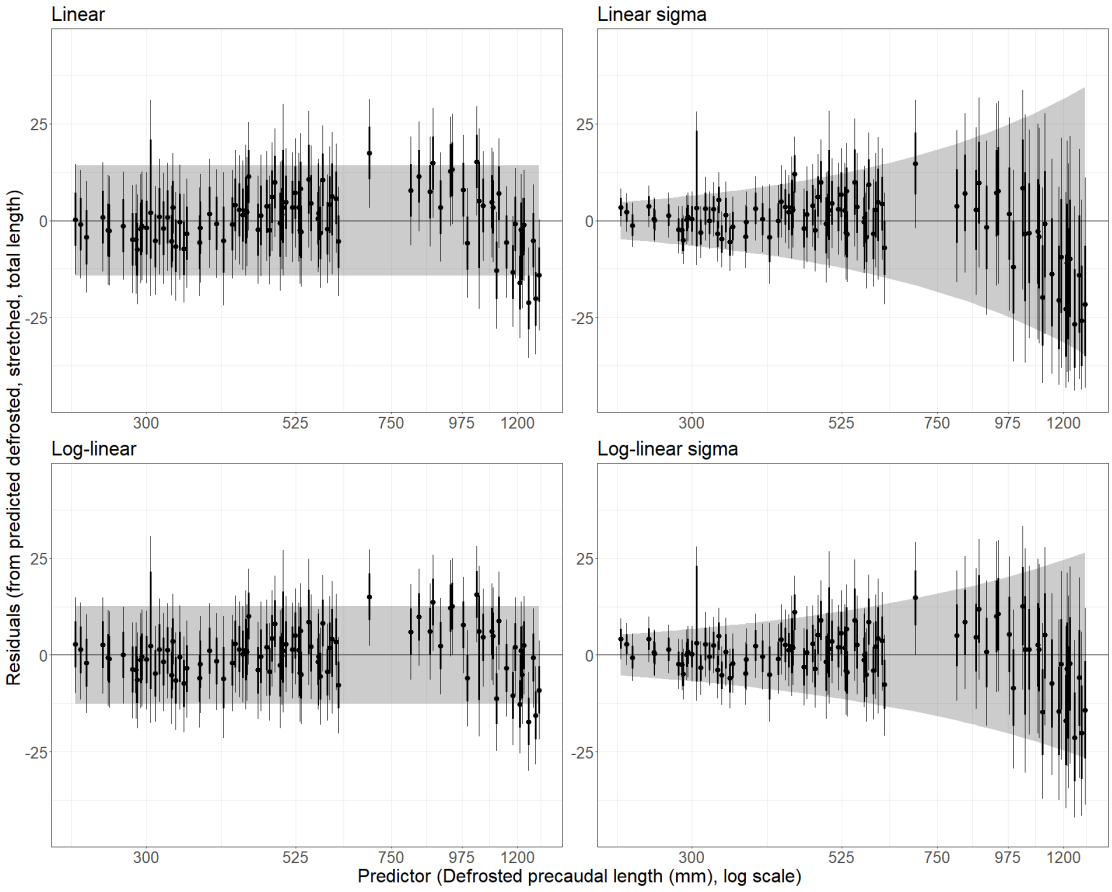


Figure A1.2.13.2: *Residual plots of the linear and log-linear models (with different error structures) for converting defrosted precaudal length to defrosted, stretched, total length. Points represent the point estimates of the residual posterior distributions. Vertical lines indicate the 66% and 95% credible intervals of the residual posterior distributions. The shaded area is the 95% range of the residual variation, as determined by the model's error structure. Defrosted, stretched, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a stretched position. Defrosted precaudal length is the precaudal length measured from a defrosted shark, in a straight line.*

A1.2.14: dss ~ dpls - Defrosted, stretched, total length ~ defrosted preoral length

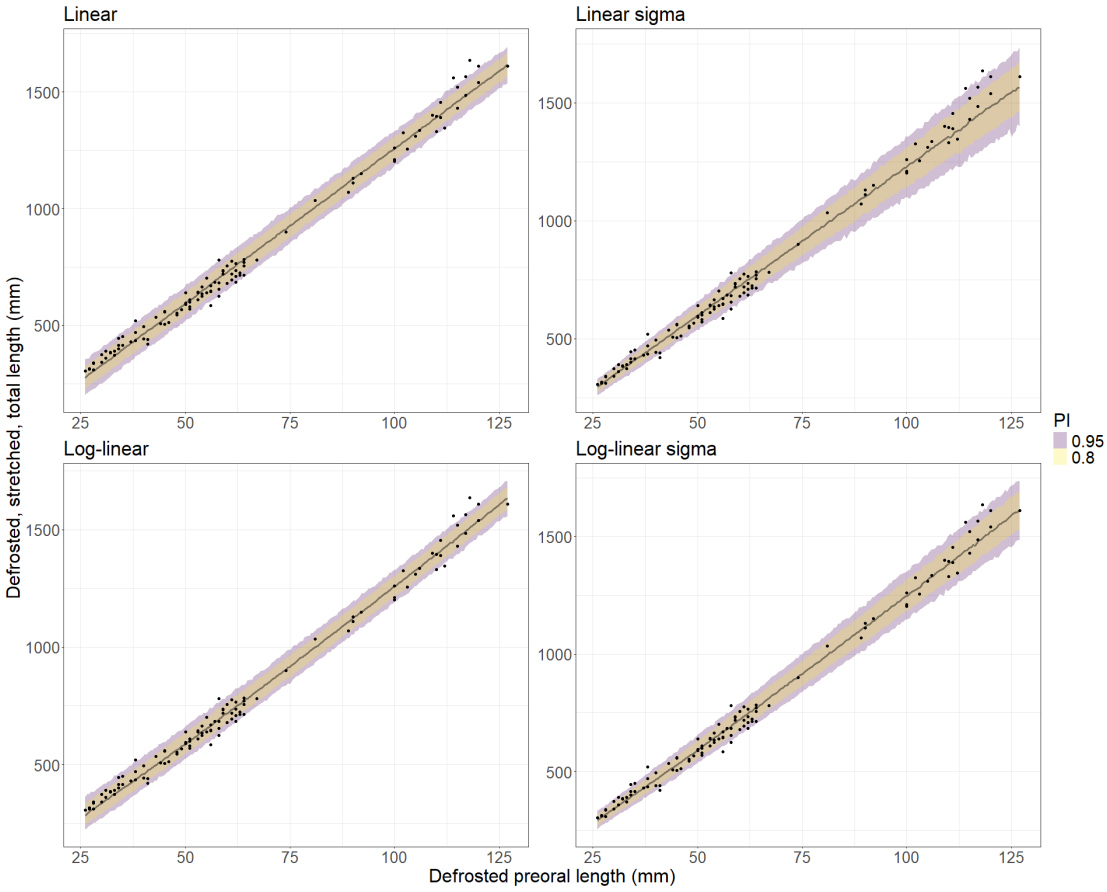


Figure A1.2.14.1: *Predicted fit of the linear and log-linear models (with different error structures) for converting defrosted preoral length to defrosted, stretched, total length. PI corresponds to 80% and 95% posterior prediction intervals. Defrosted, stretched, total length is the total length measured from a defrosted shark in a straight line with the tail in a stretched position. Defrosted preoral length is the preoral length measured from a defrosted shark in a straight line.*

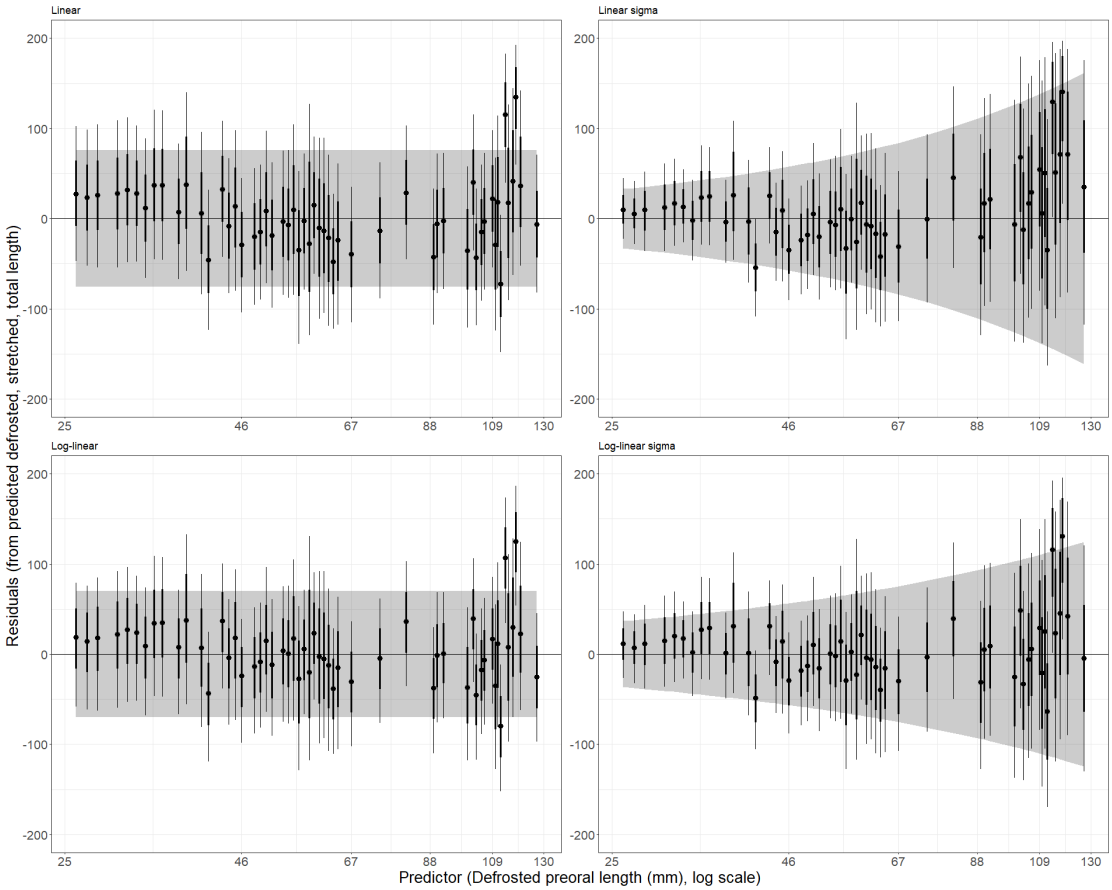


Figure A1.2.14.2: *Residual plots of the linear and log-linear models (with different error structures) for converting defrosted preoral length to defrosted, stretched, total length. Points represent the point estimates of the residual posterior distributions. Vertical lines indicate the 66% and 95% credible intervals of the residual posterior distributions. The shaded area is the 95% range of the residual variation, as determined by the model's error structure. Defrosted, stretched, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a stretched position. Defrosted preoral length is the preoral length measured from a defrosted shark in a straight line.*

A1.2.15: dss ~ dhls - Defrosted, stretched, total length ~ defrosted head length

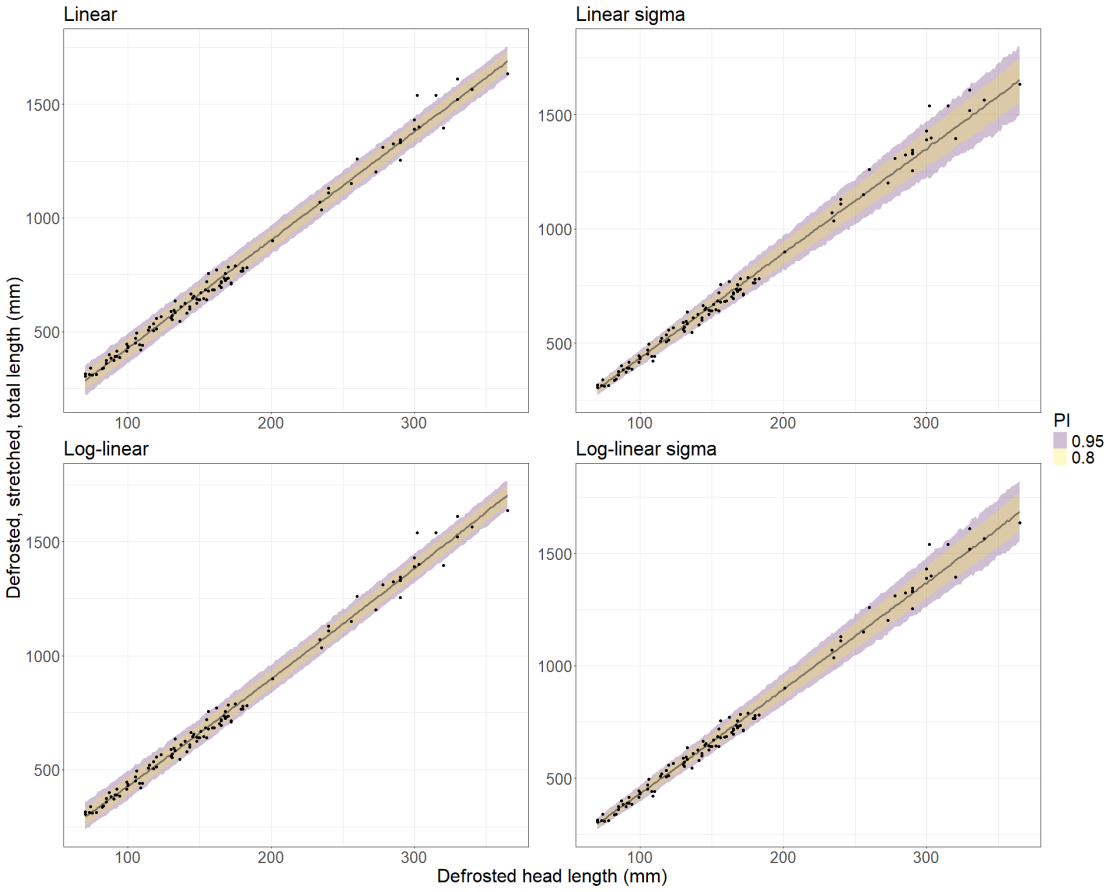


Figure A1.2.15.1: *Predicted fit of the linear and log-linear models (with different error structures) for converting defrosted head length to defrosted, stretched, total length. PI corresponds to 80% and 95% posterior prediction intervals. Defrosted, stretched, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a stretched position. Defrosted head length is the head length measured from a defrosted shark, in a straight line.*

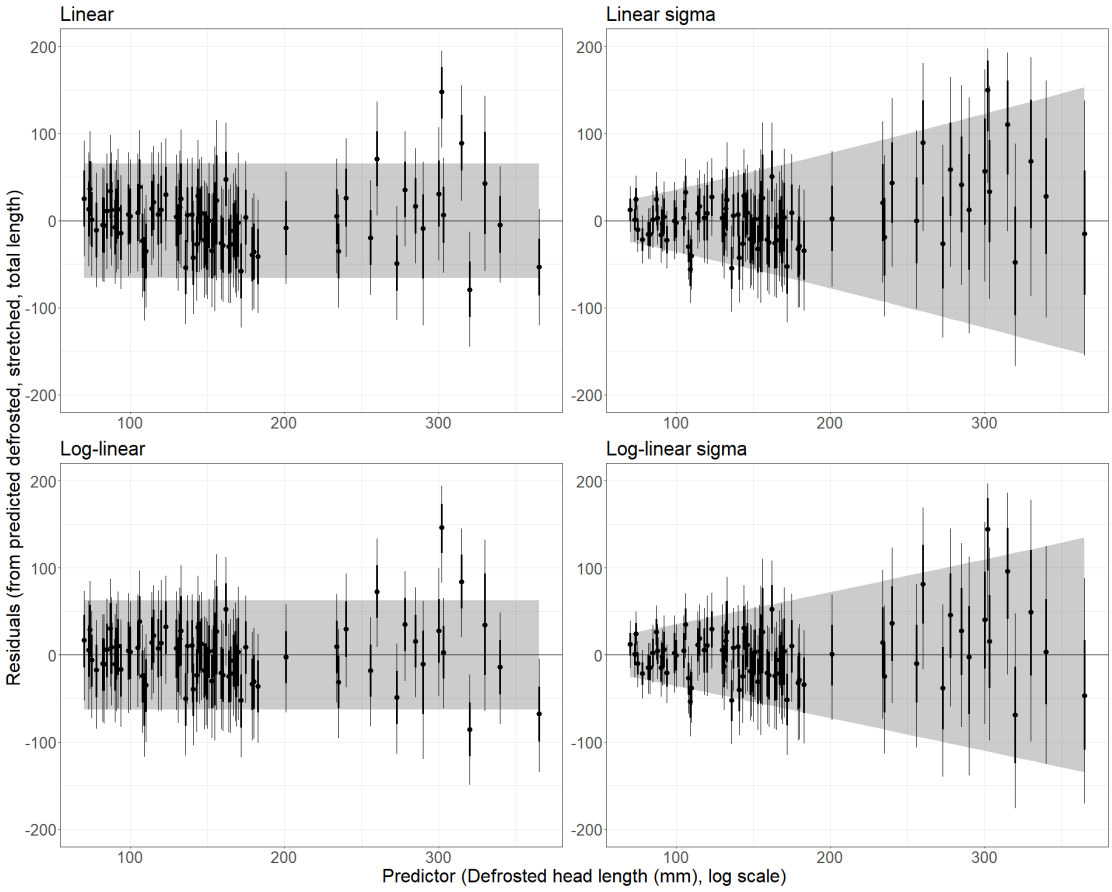


Figure A1.2.15.2: *Residual plots of the linear and log-linear models (with different error structures) for converting defrosted head length to defrosted, stretched, total length. Points represent the point estimates of the residual posterior distributions. Vertical lines indicate the 66% and 95% credible intervals of the residual posterior distributions. The shaded area is the 95% range of the residual variation, as determined by the model's error structure. Defrosted, stretched, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a stretched position. Defrosted head length is the head length measured from a defrosted shark, in a straight line.*

A1.2.16: dss ~ ddso - Defrosted, stretched, total length ~ defrosted, stretched, over-the-body dorsal origin to caudal tip length

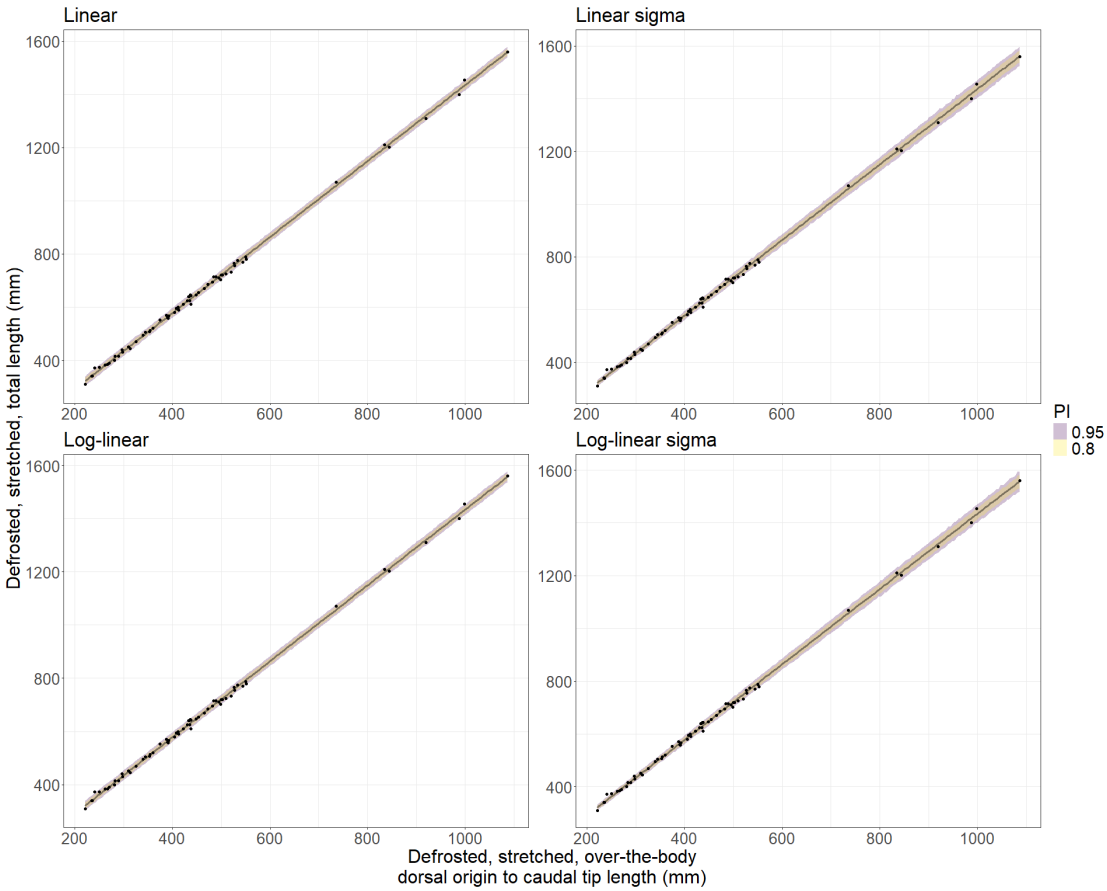


Figure A1.2.16.1: *Predicted fit of the linear and log-linear models (with different error structures) for converting defrosted, stretched, over-the-body dorsal origin to caudal tip length to defrosted, stretched, total length. PI corresponds to 80% and 95% posterior prediction intervals. Defrosted, stretched, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a stretched position. Defrosted, stretched, over-the-body dorsal origin to caudal tip length is the first dorsal fin origin to caudal tip length measured from a defrosted shark, over the curvature of the body, with the tail in a stretched position.*

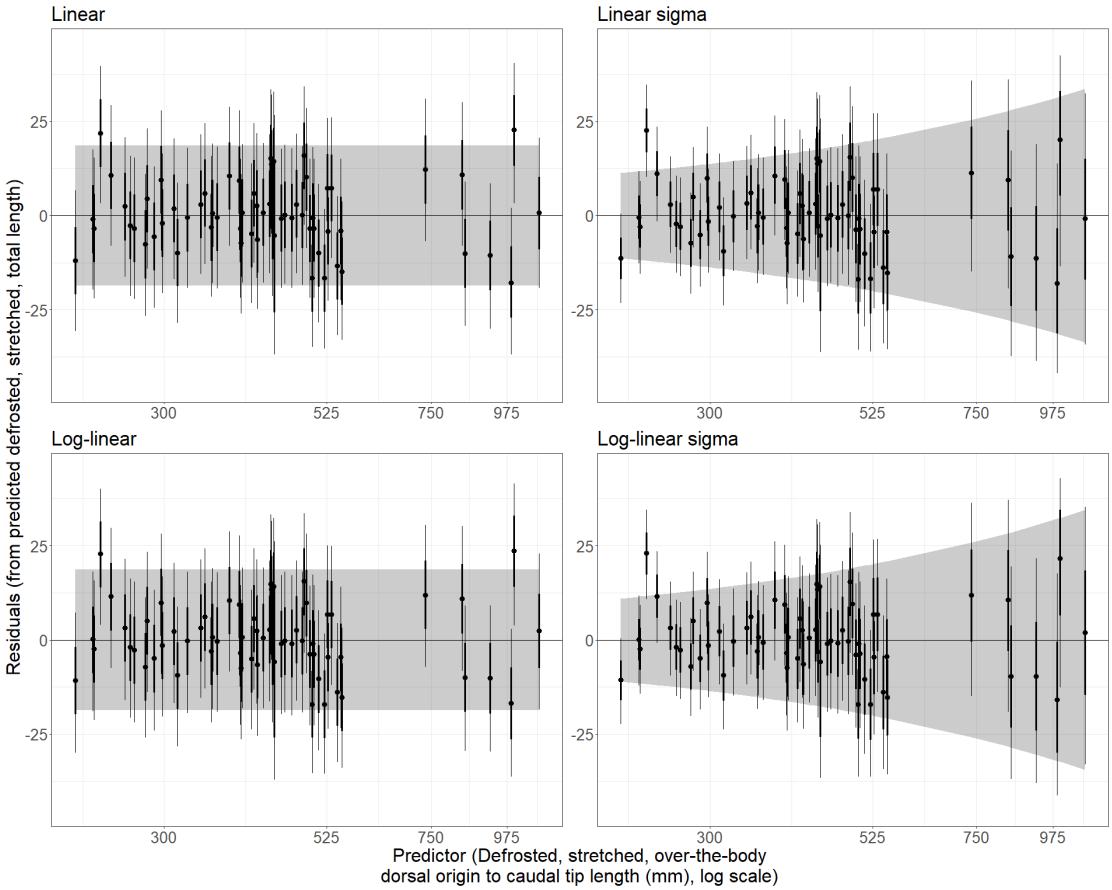


Figure A1.2.16.2: *Residual plots of the linear and log-linear models (with different error structures) for converting defrosted, stretched, over-the-body dorsal origin to caudal tip length to defrosted, stretched, total length. Points represent the point estimates of the residual posterior distributions. Vertical lines indicate the 66% and 95% credible intervals of the residual posterior distributions. The shaded area is the 95% range of the residual variation, as determined by the model's error structure. Defrosted, stretched, total length is the total length measured from a defrosted shark, in a straight line, with the tail in a stretched position. Defrosted, stretched, over-the-body dorsal origin to caudal tip length is the first dorsal fin origin to caudal tip length measured from a defrosted shark, over the curvature of the body, with the tail in a stretched position.*

A1.3: Estimated conversion parameters

Table A1.3.1: *Point estimates of the alpha (α) and beta (β) parameters (± SE, standard error of the posterior) from the log-linear sigma model for converting between length variants ($y_i = exp(\alpha + \beta\ log(x_i))$) for school sharks captured in New Zealand.*

Conversion	Response variable	Predictor variable	α (± SE)	β (± SE)
fts~dts	Fresh, natural, total length	Defrosted, natural, total length	0.0965±0.0385	0.9922±0.0060
fts~dhls	Fresh, natural, total length	Defrosted head length	1.30±0.07	1.042±0.014
fts~dpls	Fresh, natural, total length	Defrosted preoral length	2.23±0.07	1.068±0.016
dts~dto	Defrosted, natural, total length	Defrosted, natural, over-the-body total length	-0.0158±0.0087	0.9996±0.0014
dts~dss	Defrosted, natural, total length	Defrosted, stretched, total length	-0.0067±0.0078	0.9981±0.0012
dts~dso	Defrosted, natural, total length	Defrosted, stretched, over-the-body total length	-0.021±0.011	0.9978±0.0017
dts~dfs	Defrosted, natural, total length	Defrosted fork length	0.1930±0.0129	0.992±0.002
dts~dps	Defrosted, natural, total length	Defrosted precaudal length	0.353±0.011	0.9810±0.0017
dts~ddso	Defrosted, natural, total length	Defrosted, stretched, over-the-body dorsal origin to caudal tip length	0.443±0.034	0.9844±0.0056
dts~dhls	Defrosted, natural, total length	Defrosted head length	1.223±0.047	1.048±0.009
dts~dpls	Defrosted, natural, total length	Defrosted preoral length	2.176±0.051	1.071±0.012
dss~dts	Defrosted, stretched, total length	Defrosted, natural, total length	0.00816±0.00769	1.017±0.001
dss~dto	Defrosted, stretched, total length	Defrosted, natural, over-the-body total length	-0.0163±0.0095	1.002±0.001
dss~dso	Defrosted, stretched, total length	Defrosted, stretched, over-the-body total length	-0.0243±0.0076	1.001±0.001
dss~dfs	Defrosted, stretched, total length	Defrosted fork length	0.197±0.011	0.9946±0.0017
dss~dps	Defrosted, stretched, total length	Defrosted precaudal length	0.3632±0.0095	0.9826±0.0015
dss~ddso	Defrosted, stretched, total length	Defrosted, stretched, over-the-body dorsal origin to caudal tip length	0.416±0.028	0.9920±0.0046
dss~dhls	Defrosted, stretched, total length	Defrosted head length	1.24±0.05	1.050±0.009
dss~dpls	Defrosted, stretched, total length	Defrosted preoral length	2.182±0.047	1.074±0.011
dts~fts	Defrosted, natural, total length	Fresh, natural, total length	-0.0759±0.0404	1.005±0.006
dhls~fts	Defrosted head length	Fresh, natural, total length	-1.171±0.081	0.948±0.013
dpls~fts	Defrosted preoral length	Fresh, natural, total length	-2.00±0.09	0.923±0.013
dto~dts	Defrosted, natural, over-the-body total length	Defrosted, natural, total length	0.0172±0.0088	1.000±0.001

Conversion	Response variable	Predictor variable	α (± SE)	β (± SE)
dso~dts	Defrosted, stretched, over-the-body total length	Defrosted, natural, total length	0.023±0.011	1.002±0.002
dfs~dts	Defrosted fork length	Defrosted, natural, total length	-0.190±0.013	1.019±0.002
dps~dts	Defrosted precaudal length	Defrosted, natural, total length	-0.357±0.011	1.020±0.002
ddso~dts	Defrosted, stretched, over-the-body dorsal origin to caudal tip length	Defrosted, natural, total length	-0.437±0.037	1.019±0.006
dhls~dts	Defrosted head length	Defrosted, natural, total length	-1.16±0.13	0.952±0.019
dpls~dts	Defrosted preoral length	Defrosted, natural, total length	-1.929±0.065	0.9182±0.0097
dto~dss	Defrosted, natural, over-the-body total length	Defrosted, stretched, total length	0.0181±0.0094	0.9971±0.0015
dso~dss	Defrosted, stretched, over-the-body total length	Defrosted, stretched, total length	0.0252±0.0075	0.9986±0.0012
dfs~dss	Defrosted fork length	Defrosted, stretched, total length	-0.196±0.011	1.005±0.002
dps~dss	Defrosted precaudal length	Defrosted, stretched, total length	-0.367±0.010	1.017±0.002
ddso~dss	Defrosted, stretched, over-the-body dorsal origin to caudal tip length	Defrosted, stretched, total length	-0.410±0.031	1.007±0.005
dhls~dss	Defrosted head length	Defrosted, stretched, total length	-1.13±0.05	0.9451±0.0082
dpls~dss	Defrosted preoral length	Defrosted, stretched, total length	-1.946±0.061	0.9180±0.0091

Table A1.3.2: *Point estimates of the sigma (σ) intercept and slope parameters (± SE, standard error of the posterior) from the log-linear sigma model for converting between length variants for school sharks captured in New Zealand.*

Conversion	Response variable	Predictor variable	σ intercept (± SE)	σ slope (± SE)
fts~dts	Fresh, natural, total length	Defrosted, natural, total length	-4.36±1.45	1.07±0.23
fts~dhls	Fresh, natural, total length	Defrosted head length	-1.88±1.08	1.06±0.22
fts~dpls	Fresh, natural, total length	Defrosted preoral length	1.42±0.92	0.543±0.231
dts~dto	Defrosted, natural, total length	Defrosted, natural, over-the-body total length	-4.87±0.91	0.979±0.141
dts~dss	Defrosted, natural, total length	Defrosted, stretched, total length	-5.42±0.83	1.06±0.13
dts~dso	Defrosted, natural, total length	Defrosted, stretched, over-the-body total length	-6.43±0.91	1.24±0.14
dts~dfs	Defrosted, natural, total length	Defrosted fork length	-1.90±0.97	0.621±0.153
dts~dps	Defrosted, natural, total length	Defrosted precaudal length	-3.74±0.78	0.90±0.13
dts~ddso	Defrosted, natural, total length	Defrosted, stretched, over-the-body dorsal origin to caudal tip length	-3.27±1.49	0.91±0.25

Conversion	Response variable	Predictor variable	σ intercept (± SE)	σ slope (± SE)
dts~dhls	Defrosted, natural, total length	Defrosted head length	-1.39±0.86	0.928±0.169
dts~dpls	Defrosted, natural, total length	Defrosted preoral length	0.479±0.709	0.766±0.177
dss~dts	Defrosted, stretched, total length	Defrosted, natural, total length	-5.37±0.83	1.06±0.13
dss~dto	Defrosted, stretched, total length	Defrosted, natural, over-the-body total length	-4.28±0.92	0.899±0.143
dss~dso	Defrosted, stretched, total length	Defrosted, stretched, over-the-body total length	-5.10±0.94	0.988±0.146
dss~dfs	Defrosted, stretched, total length	Defrosted fork length	-3.71±0.89	0.868±0.141
dss~dps	Defrosted, stretched, total length	Defrosted precaudal length	-4.07±0.81	0.927±0.130
dss~ddso	Defrosted, stretched, total length	Defrosted, stretched, over-the-body dorsal origin to caudal tip length	-2.14±1.47	0.71±0.24
dss~dhls	Defrosted, stretched, total length	Defrosted head length	-1.83±0.75	1.02±0.15
dss~dpls	Defrosted, stretched, total length	Defrosted preoral length	0.389±0.677	0.77±0.17
dts~fts	Defrosted, natural, total length	Fresh, natural, total length	-5.02±1.47	1.16±0.23
dhls~fts	Defrosted head length	Fresh, natural, total length	-4.10±1.32	0.918±0.200
dpls~fts	Defrosted preoral length	Fresh, natural, total length	-1.24±1.35	0.348±0.208
dto~dts	Defrosted, natural, over-the-body total length	Defrosted, natural, total length	-4.79±0.90	0.973±0.140
dso~dts	Defrosted, stretched, over-the-body total length	Defrosted, natural, total length	-6.36±0.89	1.25±0.14
dfs~dts	Defrosted fork length	Defrosted, natural, total length	-2.27±0.96	0.643±0.149
dps~dts	Defrosted precaudal length	Defrosted, natural, total length	-4.37±0.80	0.932±0.125
ddso~dts	Defrosted, stretched, over-the-body dorsal origin to caudal tip length	Defrosted, natural, total length	-4.14±1.61	0.945±0.250
dhls~dts	Defrosted head length	Defrosted, natural, total length	1.0±1.1	0.264±0.175
dpls~dts	Defrosted preoral length	Defrosted, natural, total length	-2.19±1.03	0.495±0.159
dto~dss	Defrosted, natural, over-the-body total length	Defrosted, stretched, total length	-4.3±0.9	0.902±0.140
dso~dss	Defrosted, stretched, over-the-body total length	Defrosted, stretched, total length	-5.01±0.94	0.978±0.147
dfs~dss	Defrosted fork length	Defrosted, stretched, total length	-4.16±0.89	0.892±0.138
dps~dss	Defrosted precaudal length	Defrosted, stretched, total length	-4.85±0.84	0.973±0.129
ddso~dss	Defrosted, stretched, over-the-body dorsal origin to caudal tip length	Defrosted, stretched, total length	-2.83±1.56	0.719±0.243

Conversion	Response variable	Predictor variable	σ intercept (± SE)	σ slope (± SE)
dhls~dss	Defrosted head length	Defrosted, stretched, total length	-4.04±0.95	0.892±0.147
dpls~dss	Defrosted preoral length	Defrosted, stretched, total length	-2.47±0.99	0.522±0.152

A1.4: Effect of sex check

Table A1.4.1: *Model comparison results from the log-linear sigma models, with and without the effect of sex, that convert between the 17 pairs of length measurement variants. Conversion are the conversions modelled with length variants expressed in concise subscript. Values in the table are the differences in the Expected Log Predictive Density (ELPD) of the two models from the model with the greatest ELPD (difference = 0) with standard errors of the difference. Models that were selected are highlighted in green. Models where the difference is less than the standard error are highlighted in brown.*

Conversion	Response variable	Predictor variable	Log-linear sigma	Log-linear sigma.sex
fts~dts	Fresh, natural, total length	Defrosted, natural, total length	-1.98±2.69	0
fts~dpls	Fresh, natural, total length	Defrosted preoral length	-0.589±2.297	0
fts~dhls	Fresh, natural, total length	Defrosted head length	0	-0.158±2.370
dts~dto	Defrosted, natural, total length	Defrosted, natural, over-the-body total length	-1.06±2.86	0
dts~dss	Defrosted, natural, total length	Defrosted, stretched, total length	0	-1.572±0.765
dts~dso	Defrosted, natural, total length	Defrosted, stretched, over-the-body total length	0	-1.69±1.01
dts~dps	Defrosted, natural, total length	Defrosted precaudal length	0	-1.814±0.806
dts~dfs	Defrosted, natural, total length	Defrosted fork length	0	-1.677±0.737
dts~ddso	Defrosted, natural, total length	Defrosted, stretched, over-the-body dorsal origin to caudal tip length	0	-0.989±1.097
dss~dts	Defrosted, stretched, total length	Defrosted, natural, total length	0	-1.562±0.746
dss~dto	Defrosted, stretched, total length	Defrosted, natural, over-the-body total length	0	-0.811±1.718
dss~dso	Defrosted, stretched, total length	Defrosted, stretched, over-the-body total length	0	-2.236±0.474
dss~dps	Defrosted, stretched, total length	Defrosted precaudal length	0	-1.21±1.49
dss~dpls	Defrosted, stretched, total length	Defrosted preoral length	-0.508±2.162	0
dss~dhls	Defrosted, stretched, total length	Defrosted head length	0	-2.178±0.515
dss~dfs	Defrosted, stretched, total length	Defrosted fork length	0	-1.31±1.20
dss~ddso	Defrosted, stretched, total length	Defrosted, stretched, over-the-body dorsal origin to caudal tip length	0	-1.5±1.1

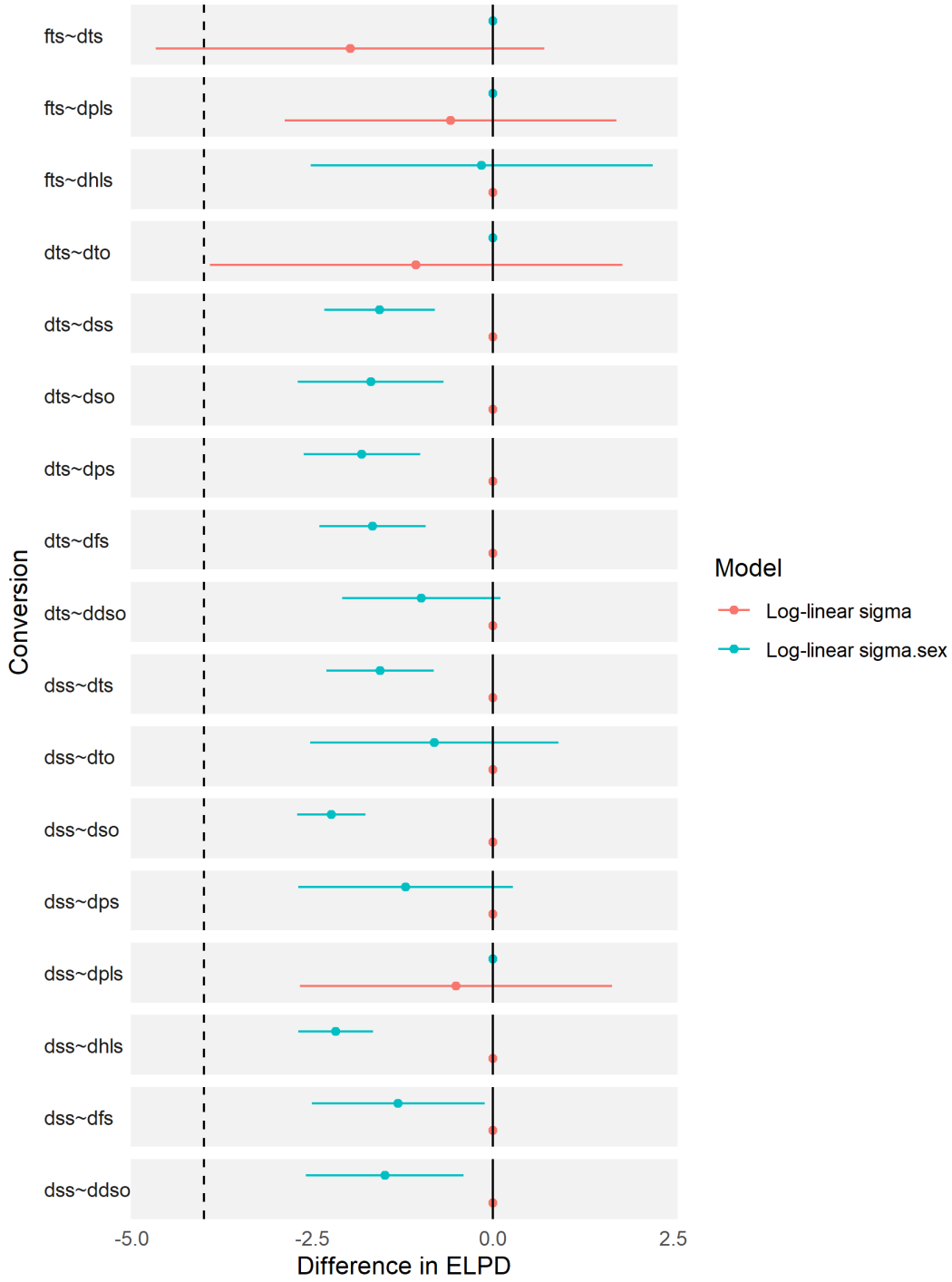


Figure A1.4.1: *Comparison of the difference in ELPD between the log-linear sigma models, with and without the effect of sex, for each of the 17 length variant conversions. Conversions are the length variants given in concise subscript (see Table A1.4.1 and Appendix 1.1 for definitions). The horizontal lines are the standard errors of the difference. The vertical solid line represents a difference of 0, which is the model with the greatest ELPD. The vertical dashed line is a difference of 4. Any differences in model ELPD ≤ 4 can be taken as no evidence of a difference in the predictive accuracy of those models.*

A1.5: Fresh conversions from defrosted models

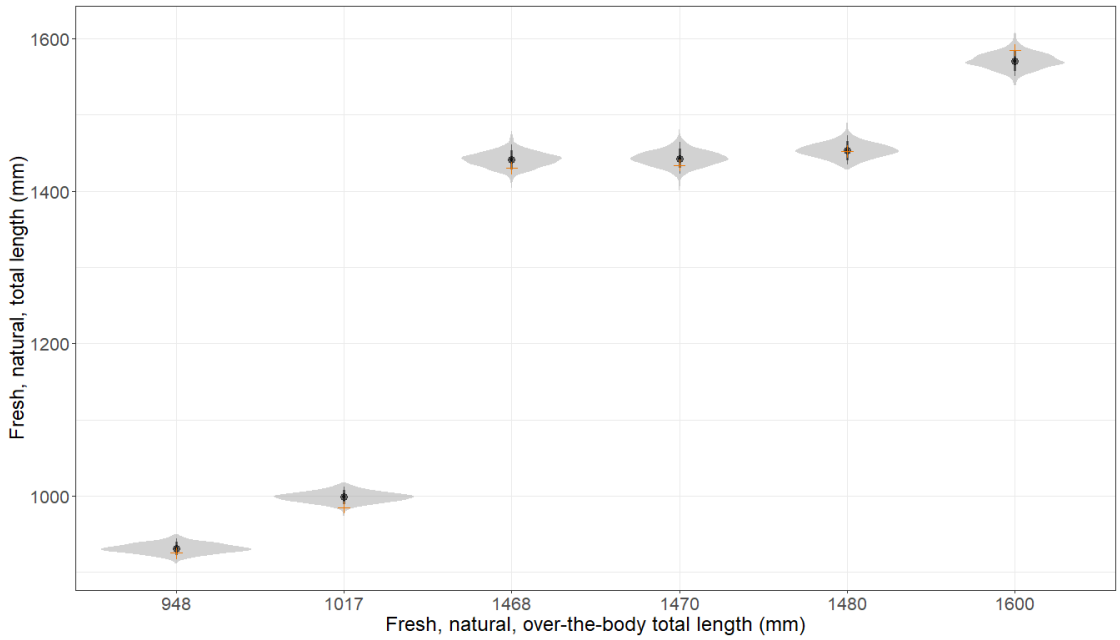


Figure A1.5.1: *Predictions for fresh, natural, total length given fresh, natural, over-the-body total length using log-linear sigma model trained on the same variants measured from defrosted individuals. Fresh, natural, total length: total length, measured in a straight line, tail in natural position, measured from a fresh or live shark. Fresh, natural, over-the-body total length: total length, measured over the curvature of the body, tail in natural position, measured from a fresh or live shark. The filled black circles are the point estimates of the predicted length variants. The black horizontal lines are the 80% and 95% prediction intervals. The grey distributions around the filled points and horizontal lines are the posterior distribution of the predicted length variants. The orange plus symbols are the observed values of the fresh variants.*

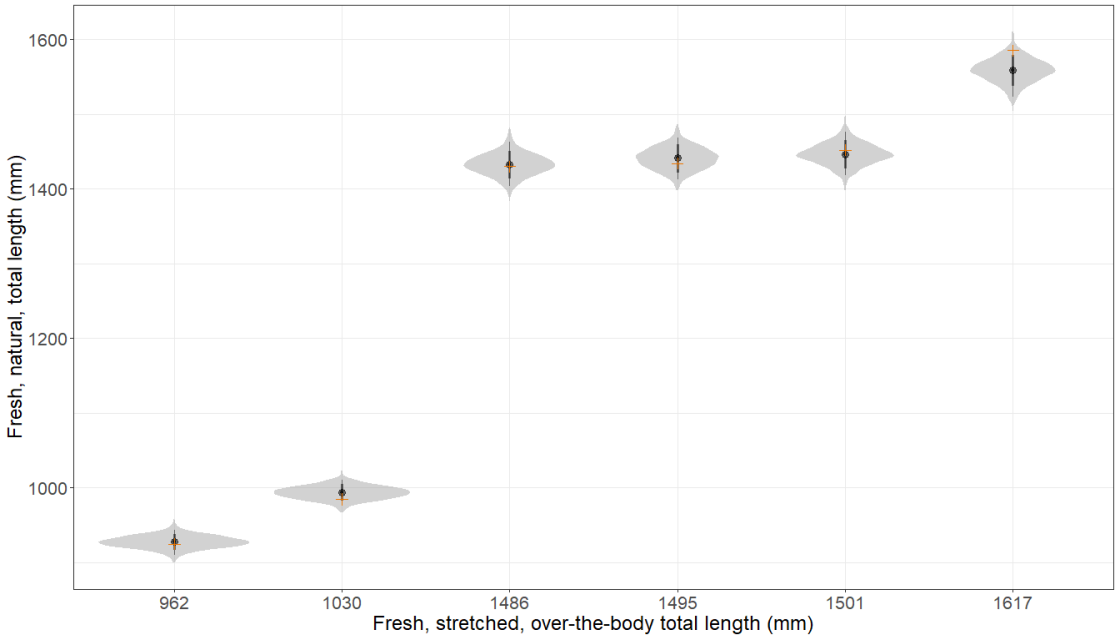


Figure A1.5.2: *Predictions for fresh, natural, total length given fresh, stretched, over-the-body total length using log-linear sigma model trained on the same variants measured from defrosted individuals. Fresh, natural, total length: total length, measured in a straight line, tail in natural position, measured from a fresh or live shark. Fresh, stretched, over-the-body total length: total length, measured over the curvature of the body, tail in stretched position, measured from a fresh or live shark. The filled black circles are the point estimates of the predicted length variants. The black horizontal lines are the 80% and 95% prediction intervals. The grey distributions around the filled points and horizontal lines are the posterior distribution of the predicted length variants. The orange plus symbols are the observed values of the fresh variants.*

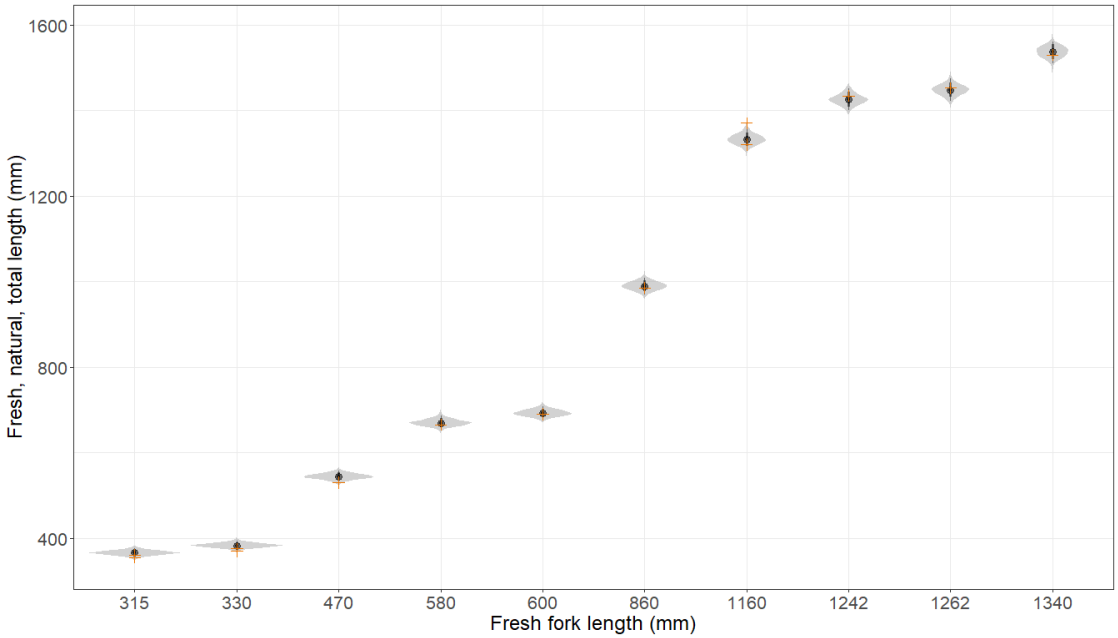


Figure A1.5.3: *Predictions for fresh, natural, total length given fresh fork length using log-linear sigma model trained on the same variants measured from defrosted individuals. Fresh, natural, total length: total length, measured in a straight line, tail in natural position, measured from a fresh or live shark. Fresh fork length: fork length, measured in a straight line, tail in natural position from a fresh or live shark. The filled black circles are the point estimates of the predicted length variants. The black horizontal lines are the 80% and 95% prediction intervals. The grey distributions around the filled points and horizontal lines are the posterior distribution of the predicted length variants. The orange plus symbols are the observed values of the fresh variants.*

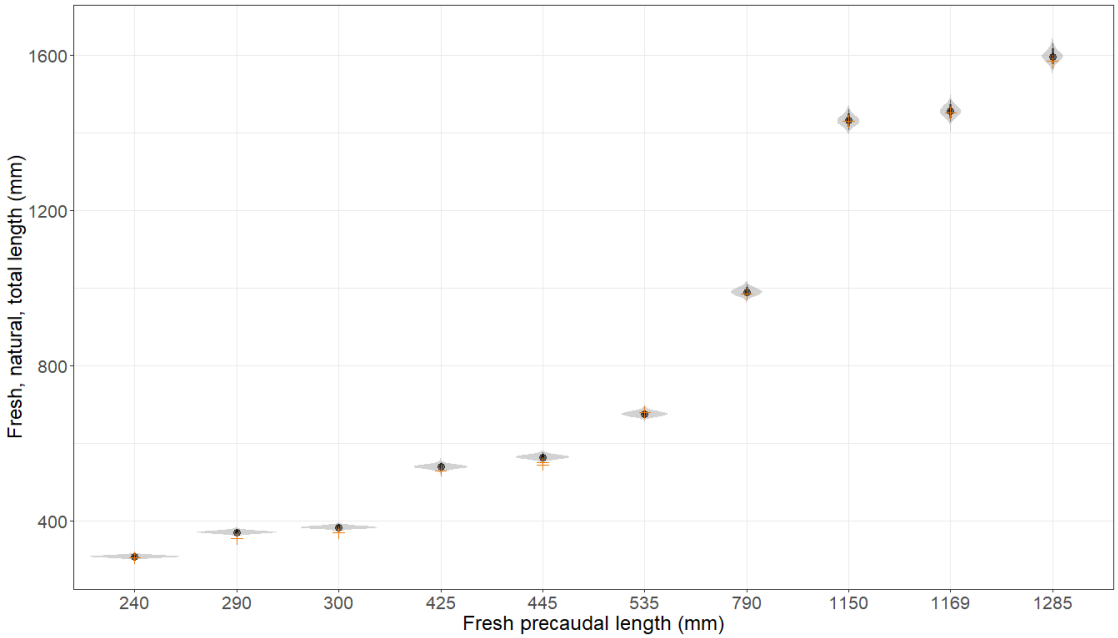


Figure A1.5.4: *Predictions for fresh, natural, total length given fresh precaudal length using log-linear sigma model trained on the same variants measured from defrosted individuals. Fresh, natural, total length: total length, measured in a straight line, tail in natural position, measured from a fresh or live shark. Fresh precaudal length: precaudal length, measured in a straight line from a fresh or live shark. The filled black circles are the point estimates of the predicted length variants. The black horizontal lines are the 80% and 95% prediction intervals. The grey distributions around the filled points and horizontal lines are the posterior distribution of the predicted length variants. The orange plus symbols are the observed values of the fresh variants.*

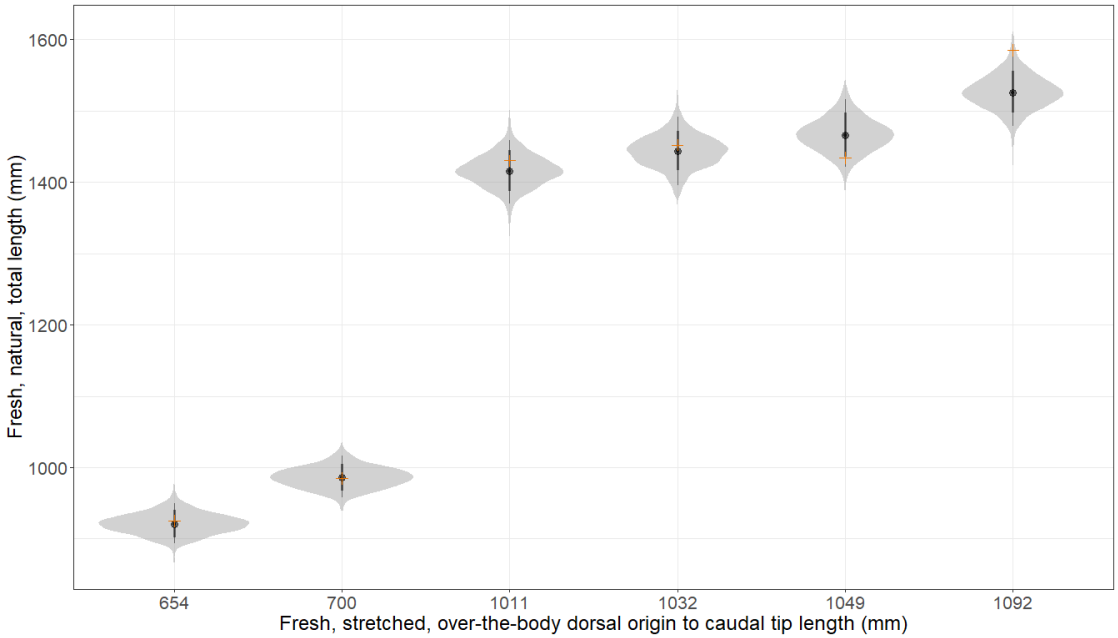


Figure A1.5.5: *Predictions for fresh, natural, total length given fresh, stretched, over-the-body dorsal origin to caudal tip length using log-linear sigma model trained on the same variants measured from defrosted individuals. Fresh, natural, total length: total length, measured in a straight line, tail in natural position, measured from a fresh or live shark. Fresh, stretched, over-the-body dorsal origin to caudal tip length: dorsal origin to caudal tip length, measured over the curvature of the body, tail in a stretched position, measured from a fresh or live shark. The filled black circles are the point estimates of the predicted length variants. The black horizontal lines are the 80% and 95% prediction intervals. The grey distributions around the filled points and horizontal lines are the posterior distribution of the predicted length variants. The orange plus symbols are the observed values of the fresh variants.*

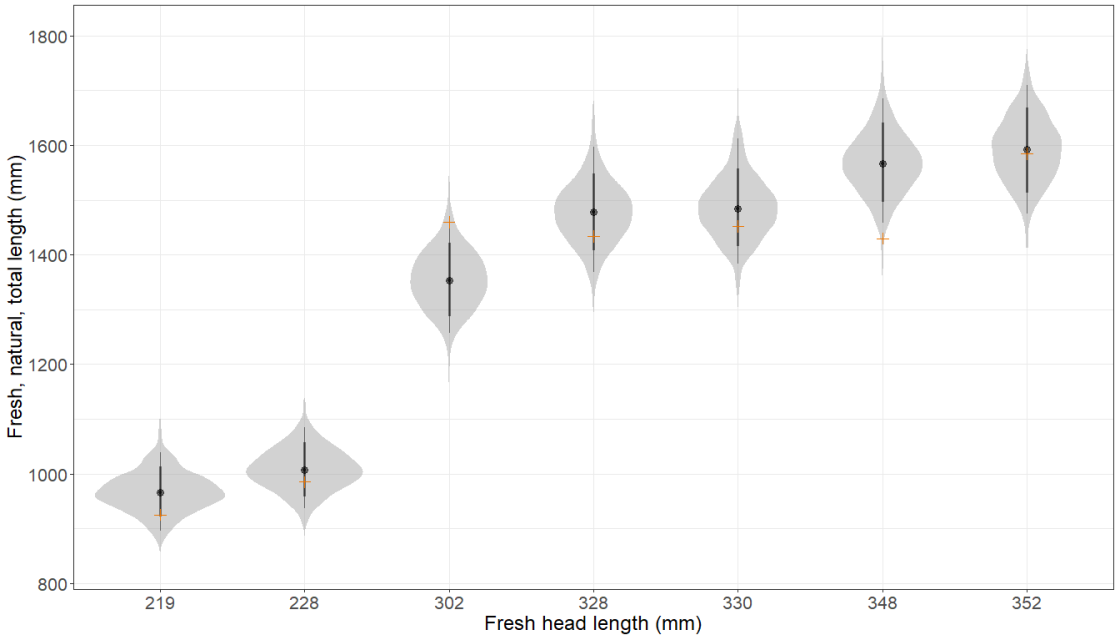


Figure A1.5.6: *Predictions for fresh, natural, total length given fresh head length using log-linear sigma model trained on the same variants measured from defrosted individuals. Fresh, natural, total length: total length, measured in a straight line, tail in natural position, measured from a fresh or live shark. Fresh head length: head length, measured in a straight line from a fresh or live shark. The filled black circles are the point estimates of the predicted length variants. The black horizontal lines are the 80% and 95% prediction intervals. The grey distributions around the filled points and horizontal lines are the posterior distribution of the predicted length variants. The orange plus symbols are the observed values of the fresh variants.*

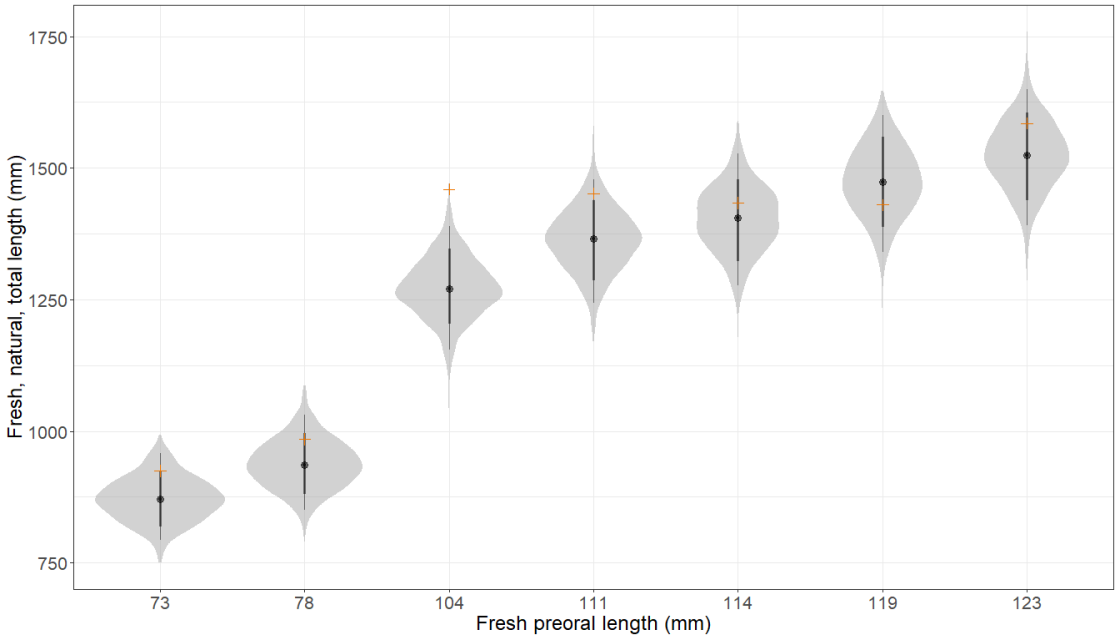


Figure A1.5.7: *Predictions for fresh, natural, total length given fresh preoral length using log-linear sigma model trained on the same variants measured from defrosted individuals. Fresh, natural, total length: total length, measured in a straight line, tail in natural position, measured from a fresh or live shark. Fresh preoral length: preoral length, measured in a straight line from a fresh or live shark. The filled black circles are the point estimates of the predicted length variants. The black horizontal lines are the 80% and 95% prediction intervals. The grey distributions around the filled points and horizontal lines are the posterior distribution of the predicted length variants. The orange plus symbols are the observed values of the fresh variants.*

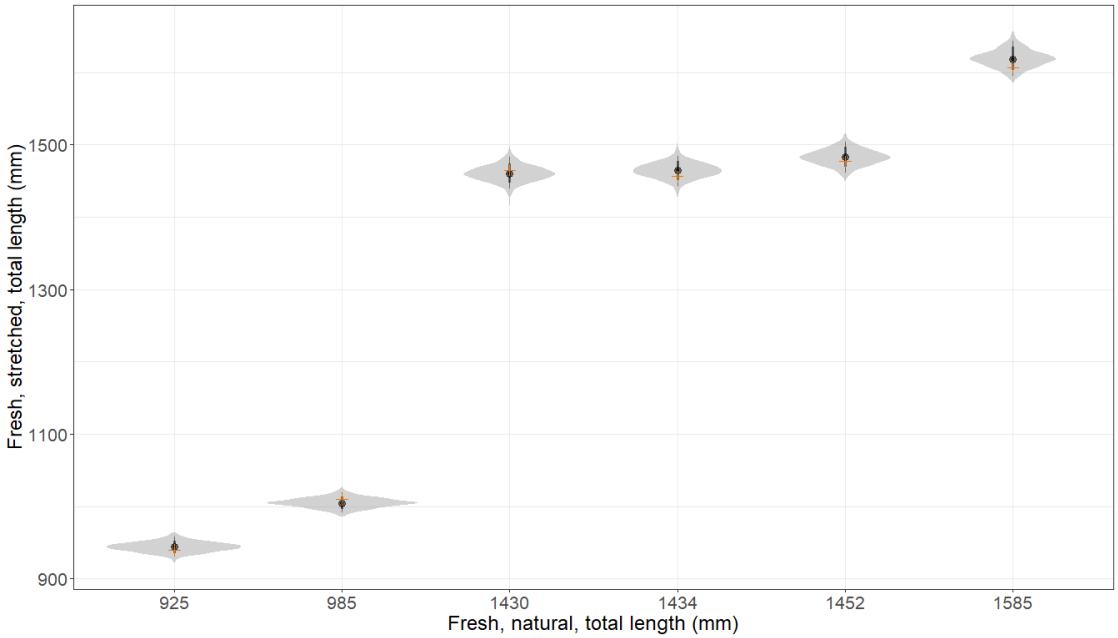


Figure A1.5.8: *Predictions for fresh, stretched, total length given fresh, natural, total length using log-linear sigma model trained on the same variants measured from defrosted individuals. Fresh, stretched, total length: total length, measured in a straight line, tail in stretched position, measured from a fresh or live shark. Fresh, natural, total length: total length, measured in a straight line, tail in natural position, measured from a fresh or live shark. The filled black circles are the point estimates of the predicted length variants. The black horizontal lines are the 80% and 95% prediction intervals. The grey distributions around the filled points and horizontal lines are the posterior distribution of the predicted length variants. The orange plus symbols are the observed values of the fresh variants.*

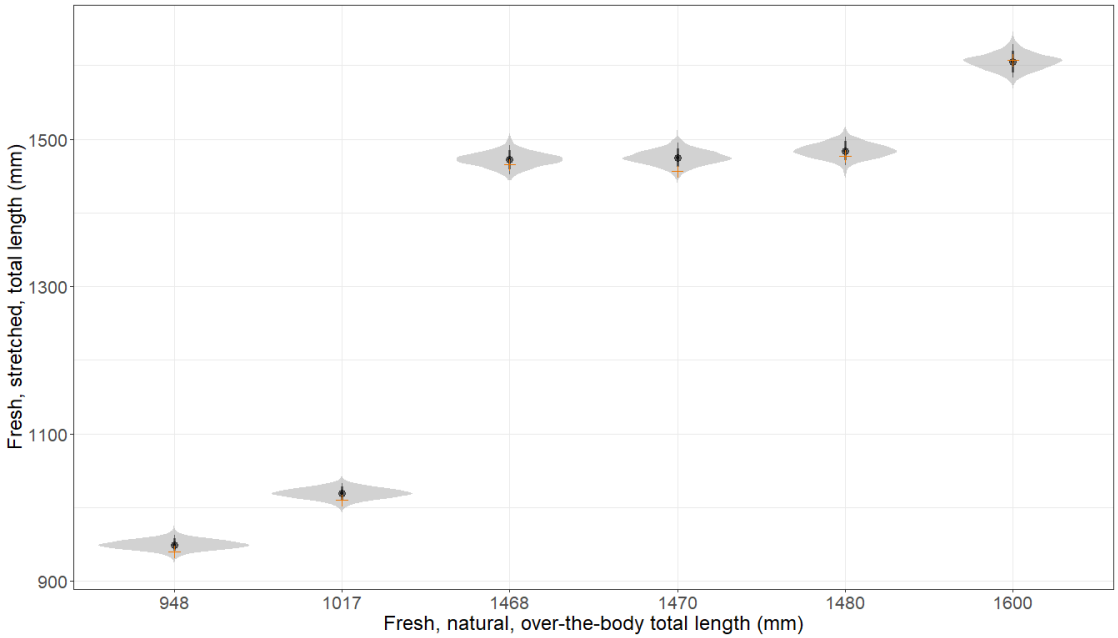


Figure A1.5.9: *Predictions for fresh, stretched, total length given fresh, natural, over-the-body total length using log-linear sigma model trained on the same variants measured from defrosted individuals. Fresh, stretched, total length: total length, measured in a straight line, tail in stretched position, measured from a fresh or live shark. Fresh, natural, over-the-body total length: total length, measured over the curvature of the body, tail in natural position, measured from a fresh or live shark. The filled black circles are the point estimates of the predicted length variants. The black horizontal lines are the 80% and 95% prediction intervals. The grey distributions around the filled points and horizontal lines are the posterior distribution of the predicted length variants. The orange plus symbols are the observed values of the fresh variants.*

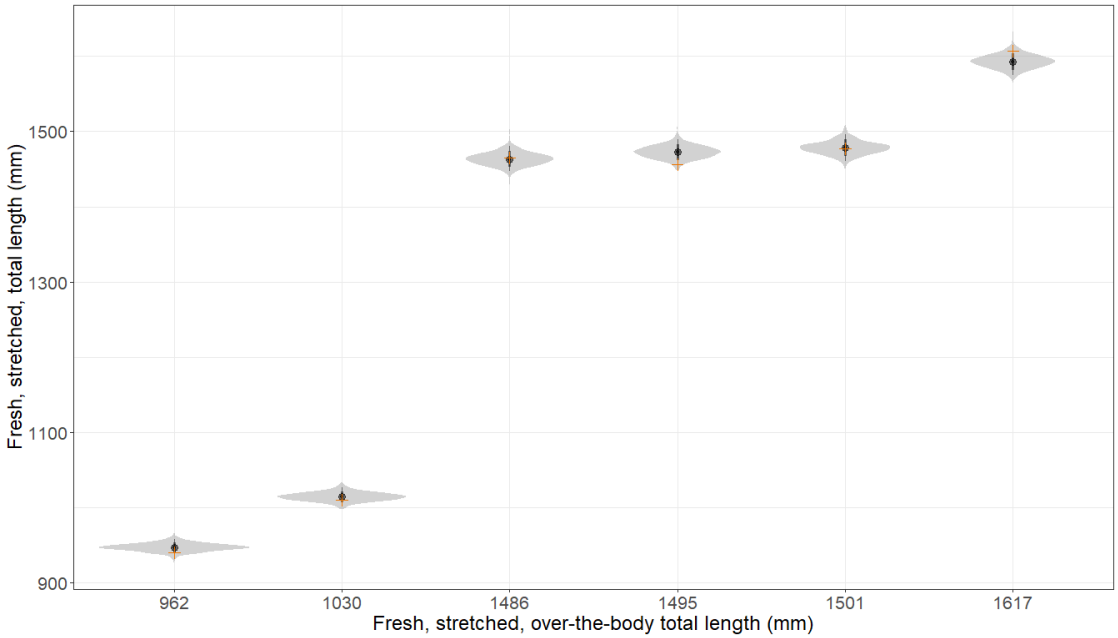


Figure A1.5.10: *Predictions for fresh, stretched, total length given fresh, stretched, over-the-body total length using log-linear sigma model trained on the same variants measured from defrosted individuals. Fresh, stretched, total length: total length, measured in a straight line, tail in stretched position, measured from a fresh or live shark. Fresh, stretched, over-the-body total length: total length, measured over the curvature of the body, tail in stretched position, measured from a fresh or live shark. The filled black circles are the point estimates of the predicted length variants. The black horizontal lines are the 80% and 95% prediction intervals. The grey distributions around the filled points and horizontal lines are the posterior distribution of the predicted length variants. The orange plus symbols are the observed values of the fresh variants.*

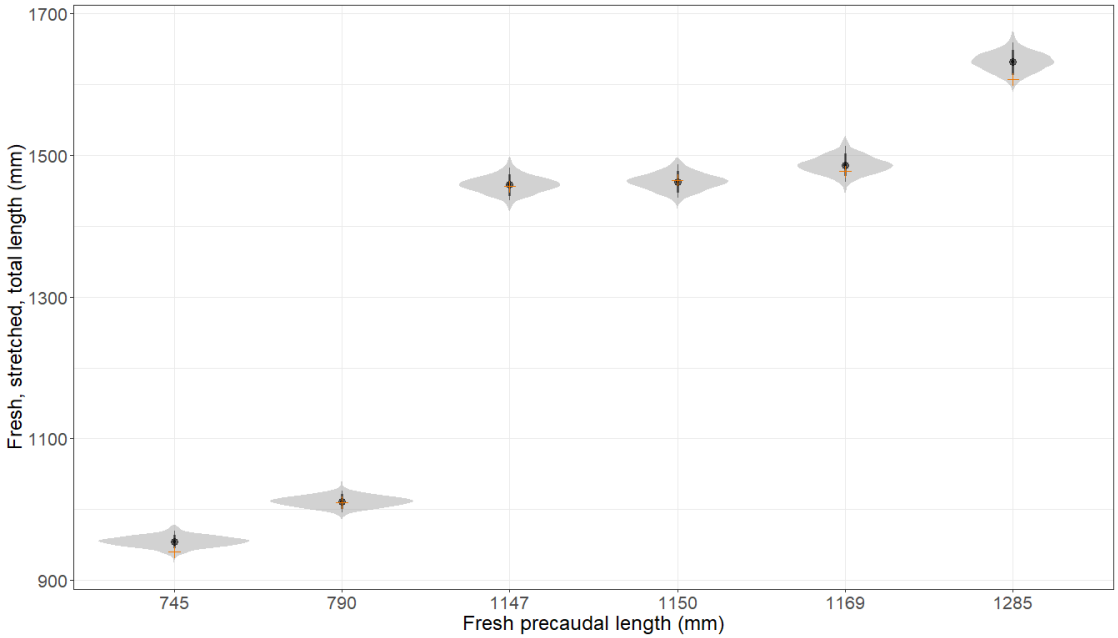


Figure A1.5.11: *Predictions for fresh, stretched, total length given fresh precaudal length using log-linear sigma model trained on the same variants measured from defrosted individuals. Fresh, stretched, total length: total length, measured in a straight line, tail in stretched position, measured from a fresh or live shark. Fresh precaudal length: precaudal length, measured in a straight line from a fresh or live shark. The filled black circles are the point estimates of the predicted length variants. The black horizontal lines are the 80% and 95% prediction intervals. The grey distributions around the filled points and horizontal lines are the posterior distribution of the predicted length variants. The orange plus symbols are the observed values of the fresh variants.*

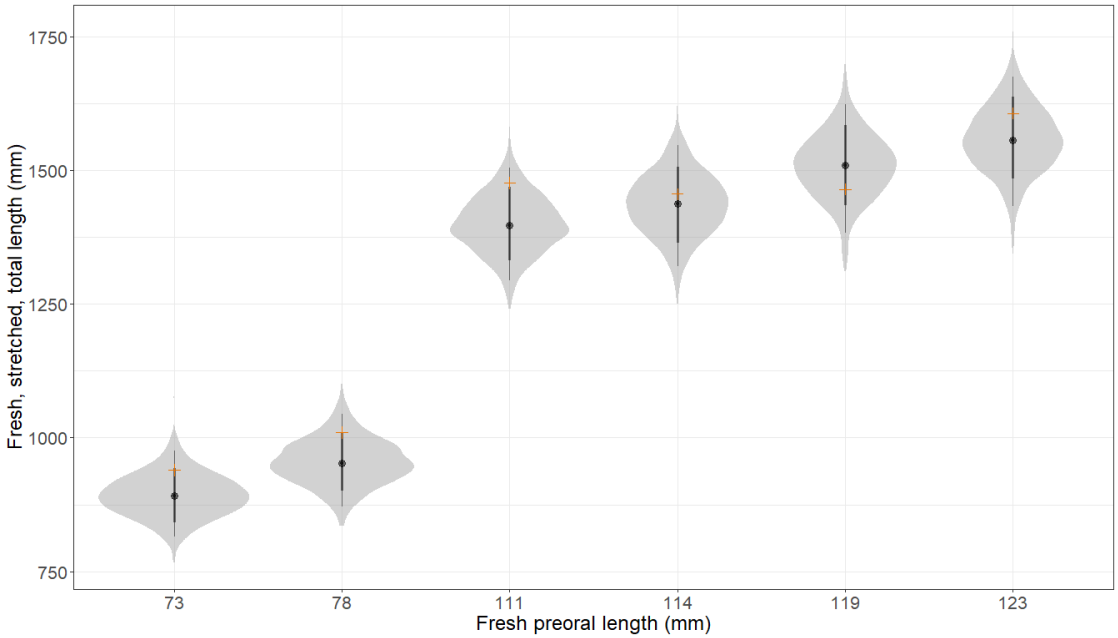


Figure A1.5.12: *Predictions for fresh, stretched, total length given fresh preoral length using log-linear sigma model trained on the same variants measured from defrosted individuals. Fresh, stretched, total length: total length, measured in a straight line, tail in stretched position, measured from a fresh or live shark. Fresh preoral length: preoral length, measured in a straight line from a fresh or live shark. The filled black circles are the point estimates of the predicted length variants. The black horizontal lines are the 80% and 95% prediction intervals. The grey distributions around the filled points and horizontal lines are the posterior distribution of the predicted length variants. The orange plus symbols are the observed values of the fresh variants.*

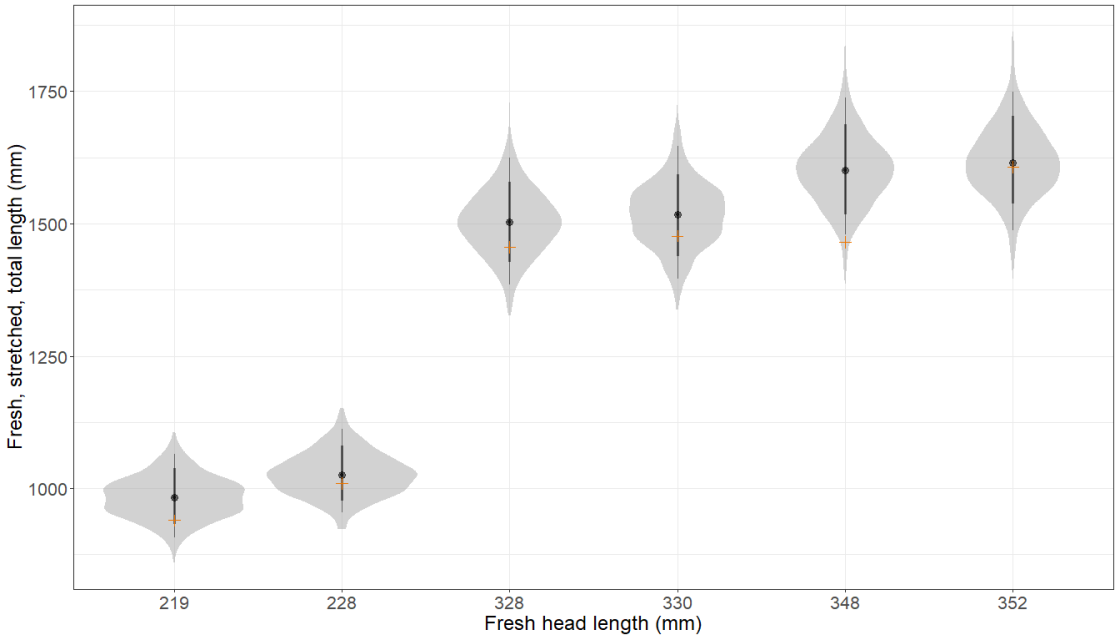


Figure A1.5.13: *Predictions for fresh, stretched, total length given fresh head length using log-linear sigma model trained on the same variants measured from defrosted individuals. Fresh, stretched, total length: total length, measured in a straight line, tail in stretched position, measured from a fresh or live shark. Fresh head length: head length, measured in a straight line from a fresh or live shark. The filled black circles are the point estimates of the predicted length variants. The black horizontal lines are the 80% and 95% prediction intervals. The grey distributions around the filled points and horizontal lines are the posterior distribution of the predicted length variants. The orange plus symbols are the observed values of the fresh variants.*

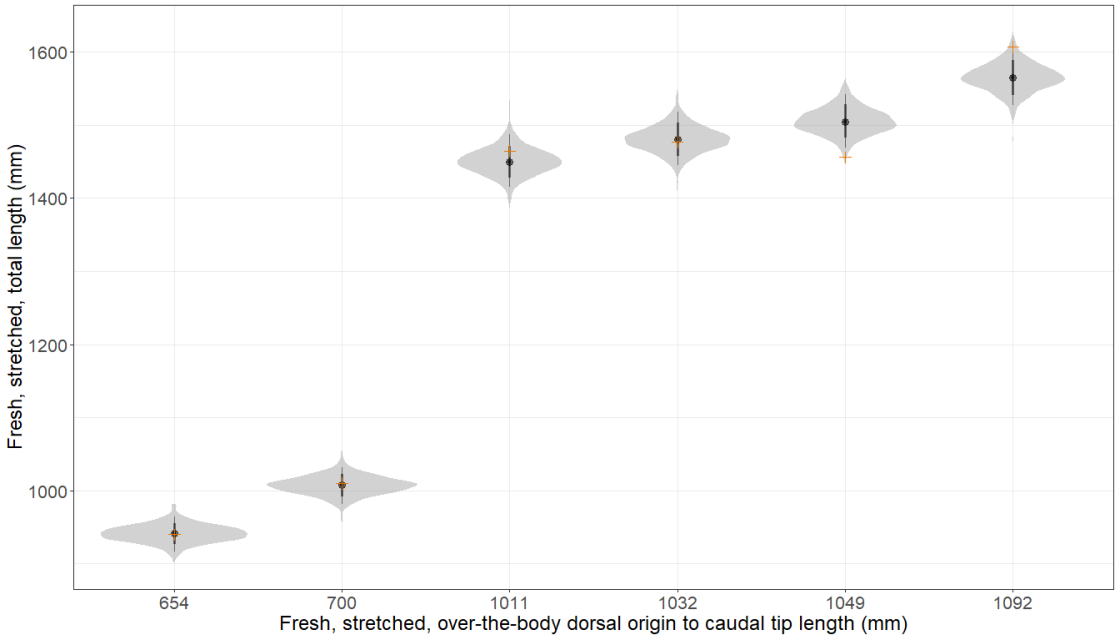


Figure A1.5.14: *Predictions for fresh, stretched, total length given fresh, stretched, over-the-body dorsal origin to caudal tip length using log-linear sigma model trained on the same variants measured from defrosted individuals. Fresh, stretched, total length: total length, measured in a straight line, tail in stretched position, measured from a fresh or live shark. Fresh, stretched, over-the-body dorsal origin to caudal tip length: dorsal origin to caudal tip length, measured over the curvature of the body, tail in a stretched position, measured from a fresh or live shark. The filled black circles are the point estimates of the predicted length variants. The black horizontal lines are the 80% and 95% prediction intervals. The grey distributions around the filled points and horizontal lines are the posterior distribution of the predicted length variants. The orange plus symbols are the observed values of the fresh variants.*

A1.6: Additive vs multiplication effects between measurements

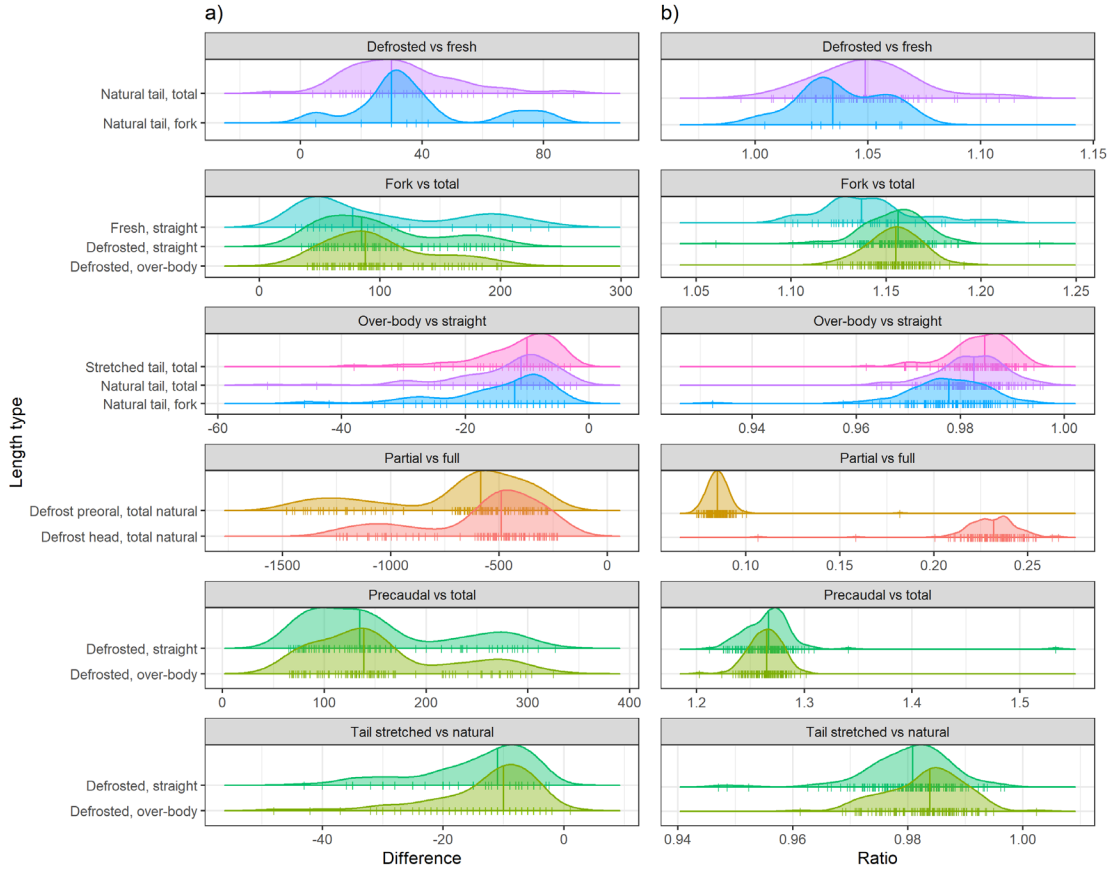


Figure A1.6.1: *Comparisons of effects of varying length measures. a) Additive effects, the difference between two measures. b) Multiplicative effects, the ratio between two measures.*

Appendix 2 – Chapter 3: Life-history stage transitions

A2.1: Reproductive structure diagrams and score definitions

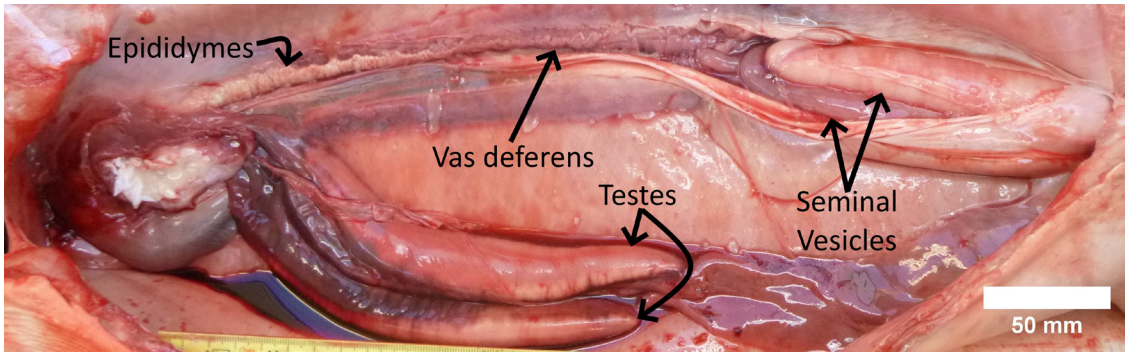


Figure A2.1.1: *Location of internal reproductive structures in a mature male school shark.*

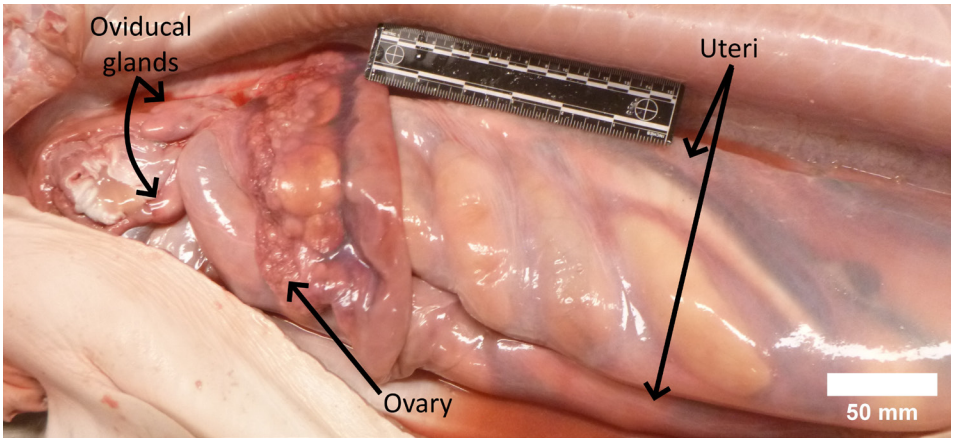
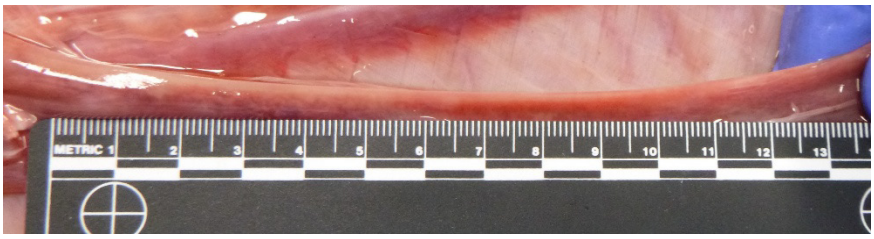


Figure A2.1.2: *Location of reproductive structures in a mature female school shark.*

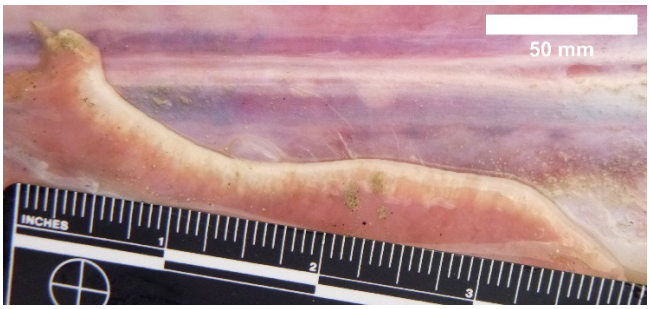
Table A2.1.1: *Indices adopted to assess the stage of reproductive structures in school sharks. Based on reproductive structure assessments from Braccini et al. (2006); Capapé et al. (2005); Centre for Environment, Fisheries & Aquaculture Science (n.d.); Lucifora et al. (2004); Nosal et al. (2021); Peres & Vooren (1991); Walker (2005), and A. Burton personal observations. Examples of the stages for each structure are available in Figures A2.1.3 - A2.1.10.*

Sex	Structure	Score	Definition	Stage assumption
	Neonate scar	1	Open	Neonate
		2	Partially healed	Neonate
		3	Healed	Immature
Male	Testis	1	Little to no development, narrow and threadlike thin strip of tissue. Epigonal gland predominant	Immature
		2	Partially thickened tissue strip (not thickened to full extent). Extensive epigonal gland	Maturing
		3	Enlarged. Lobulation and vascularisation evident. Epigonal gland tissue negligible	Mature
	Epididymides	1	Slightly developed and membranous	Immature
		2	Slightly convoluted, no presence of sperm	Maturing
		3	Highly convoluted, sperm present	Mature
		4	Highly convoluted, sperm absent	Mature
	Vas deferens	1	Linear and thin, no convolution	Immature
		2	Slightly convoluted, no presence of sperm	Maturing
		3	Highly convoluted, sperm present	Mature
		4	Highly convoluted, sperm absent	Mature
	Seminal vesicle	1	Thin translucent walls, seminal fluids absent	Immature
		2	Thickened opaque walls and seminal fluids present	Mature
		3	Thickened opaque walls and seminal fluids absent	Mature
	Clasper	1	Claspers shorter than the pelvic fin, flexible, no calcification, cannot be rotated, rhipidon cannot be splayed	Immature
		2	Claspers longer than the pelvic fin, flexible, partially calcified or soft, difficult to or cannot be rotated forward, if can be rotated by resistance is encountered, rhipidon unable or difficult to be splayed	Maturing
		3	Claspers elongated, longer than pelvic fin, rigid, calcified, can be rotated anteriorly, rhipidon can be splayed, spermatozoa may be present in the groove	Mature
Female	Ovary	1	Small, membranous/gelatinous, undeveloped. Largest follicles are translucent white and <2-3mm diameter	Immature
		2	Largest oocytes (typically white to cream) are yolking (start of yolk deposition) and 3-11mm diameter	Uncertain

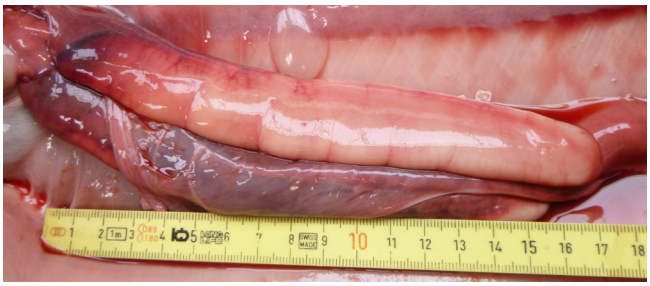
Sex	Structure	Score	Definition	Stage assumption
		3	Largest oocytes with yellowish yolk and ≥12mm diameter	Mature
		4	Yolked oocytes >3mm diameter, extensive corpora atretica and corpora lutea present	Mature
	Oviducal gland	1	Indistinct from the anterior oviduct. Width is not much greater than the width of the oviduct	Immature
		2	Distinct, but only partially formed (slightly rounded). Greater than the width of the oviduct	Maturing
		3	Enlarged and heart-shaped	Mature
	Uterus	1	Uniformly thin tubular structure	Immature
		2	Thin tubular structure partially enlarged posteriorly	Immature
		3	Uniformly enlarged tubular structure	Uncertain
		4	In utero eggs present without macroscopically visible embryos present	Mature, pregnant
		5	In utero embryos are macroscopically visible	Mature, pregnant
		6	Enlarged tubular structure distended and/or flaccid, and potentially vascularised	Mature, post-partum



(a) Testes: Stage 1



(b) Testes: Stage 2



(c) Testes: Stage 3

Figure A2.1.3: *Examples of the stages of Testes in school sharks.*

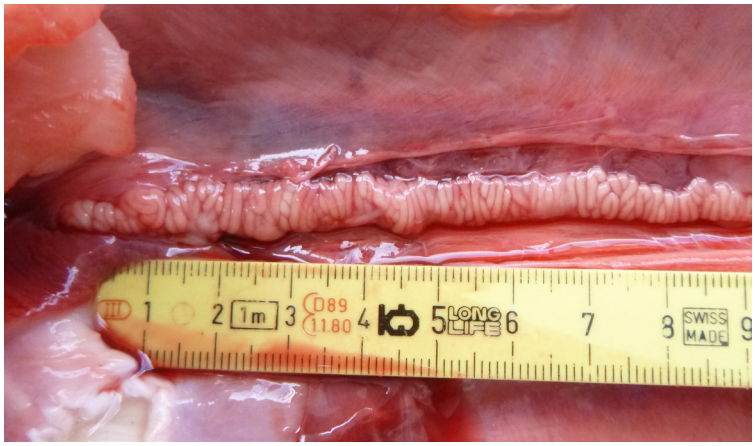


Figure A2.1.4: *Example of Stage 3 of the Epididymis in school sharks.*

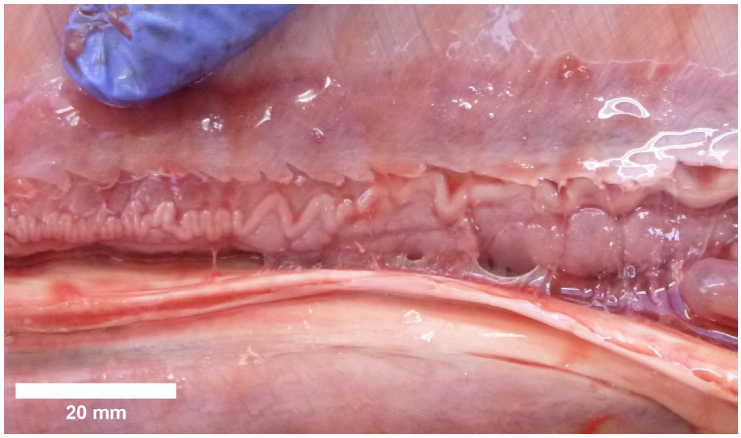


Figure A2.1.5: *Example of Stage 3 of the Vas deferens in school sharks.*

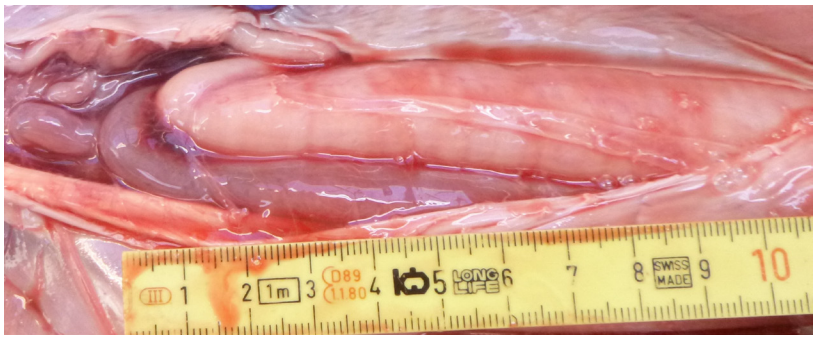
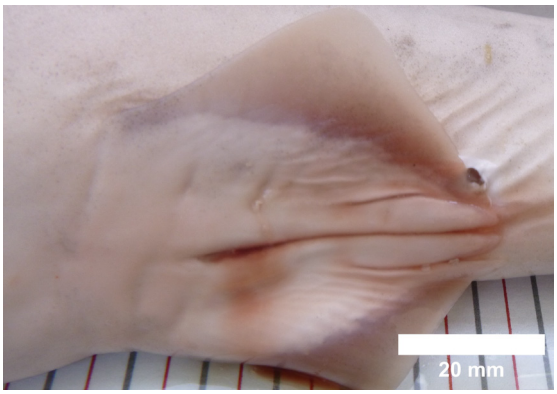
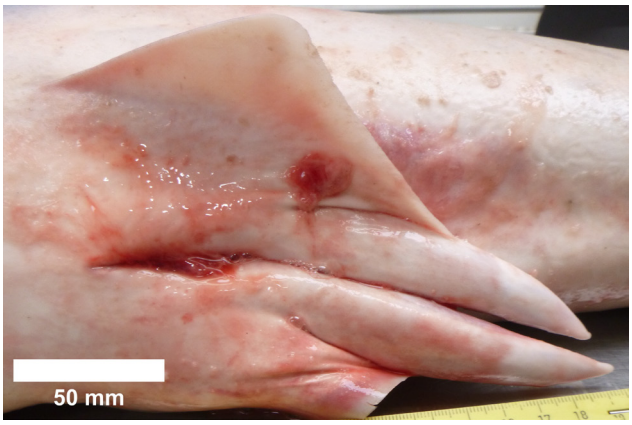


Figure A2.1.6: *Example of Stage 2 of the Seminal vesicle in school sharks.*

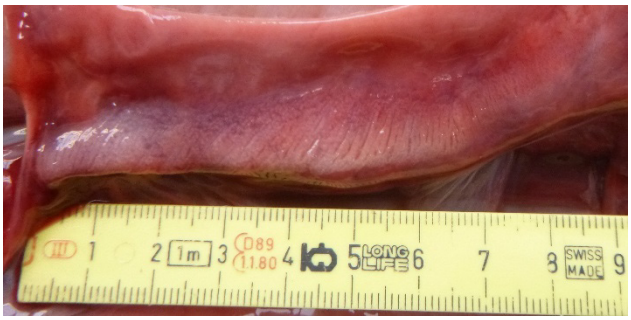


(a) Claspers: Stage 1

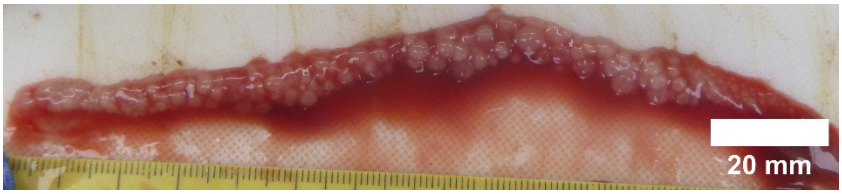


(b) Claspers: Stage 3

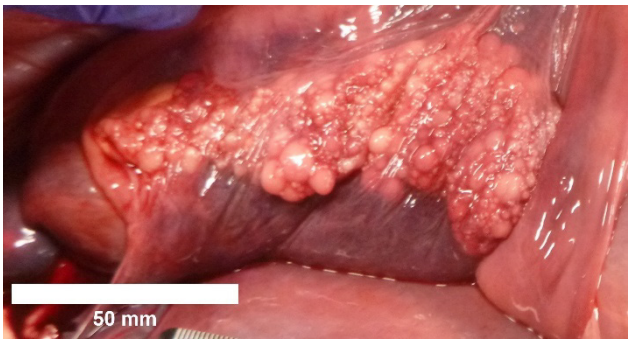
Figure A2.1.7: *Examples of the stages of Claspers in school sharks.*



(a) Ovary: Stage 1

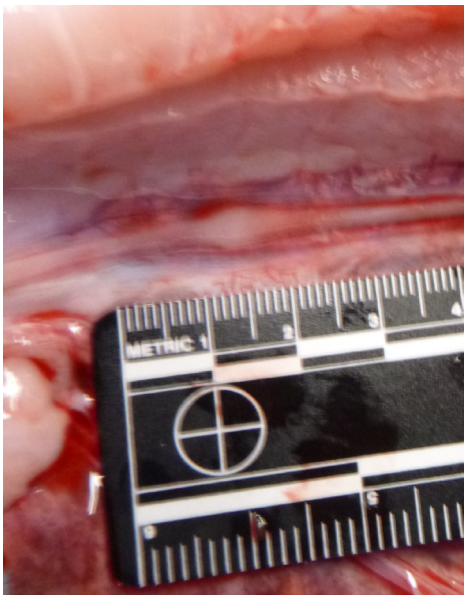


(b) Ovary: Stage 2 (immature)

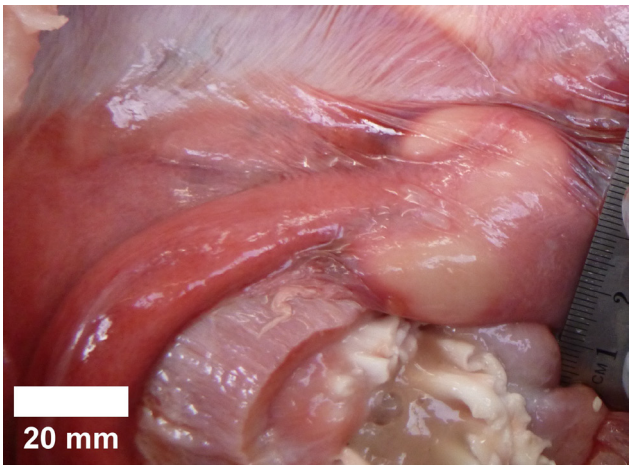


(b) Ovary: Stage 2 (resting mature)

Figure A2.1.8: *Examples of the stages of the Ovary in school sharks.*

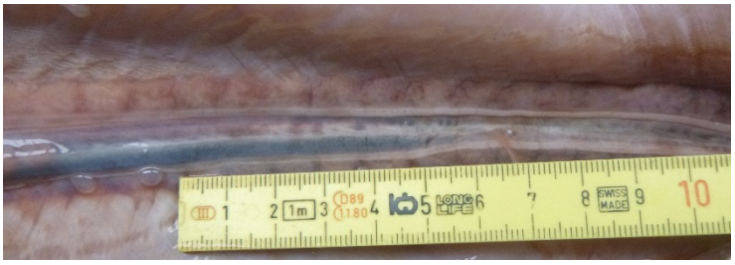


(a) Oviducal gland: Stage 1

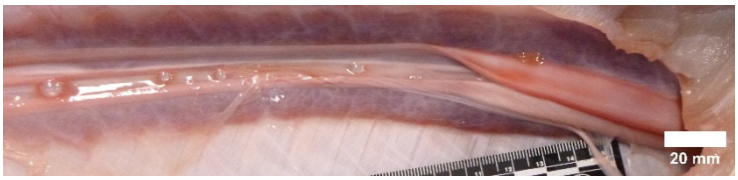


(b) Oviducal gland: Stage 3

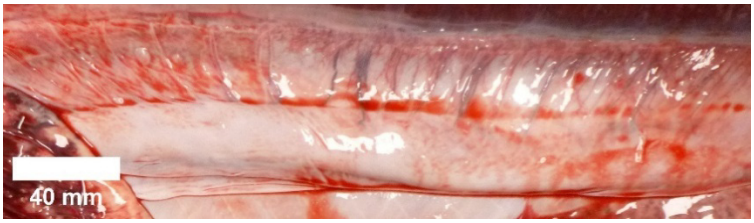
Figure A2.1.9: *Examples of the stages of Oviducal glands in school sharks.*



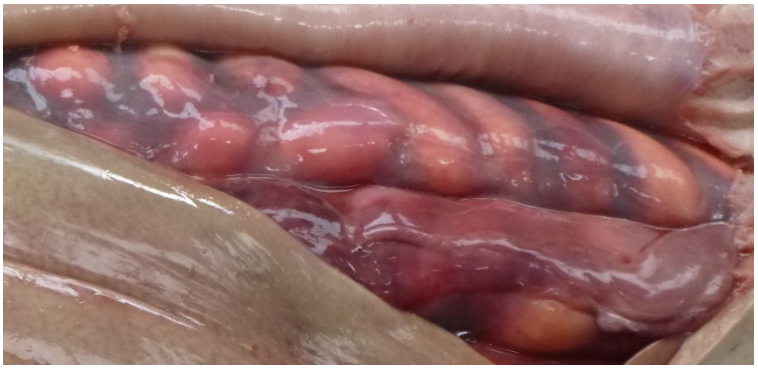
(a) Uterus: Stage 1



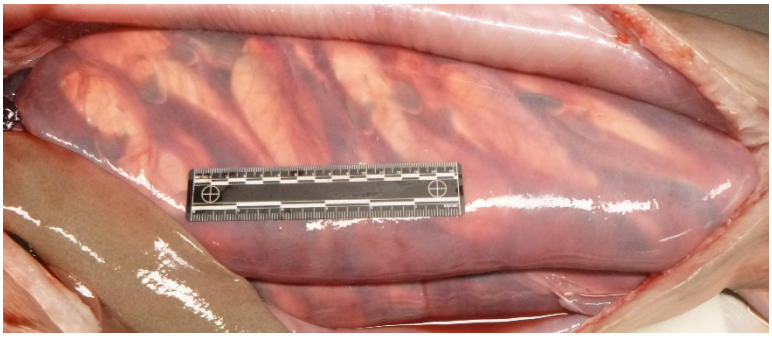
(b) Uterus: Stage 2



(c) Uterus: Stage 3



(d) Uterus: Stage 4



(e) Uterus: Stage 5

Figure A2.1.10: *Examples of the stages of Uteri in school sharks.*

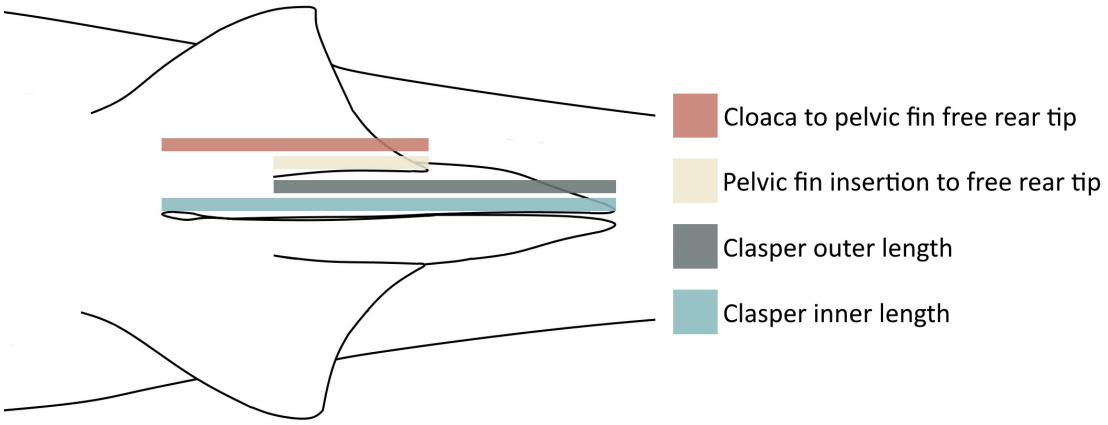


Figure A2.1.11: *Lengths of the claspers and pelvic fins. Definitions of length variants are available in Table A2.1.2.*

Table A2.1.2: *Definition of pelvic fin and clasper length measurements. Descriptions exclude whether the measurement was taken in a straight line or over-the-body of the shark.*

Length	Definition
Cloaca to pelvic fin free rear tip	From the apex of the cloaca to the apex of the free rear tip of the pelvic fin.
Pelvic fin insertion to free rear tip	From the insertion to the apex of the free rear tip of the pelvic fin.
Clasper outer length	From the insertion of the pelvic fin to the distal tip of the clasper.
Clasper inner length	From the apex of the cloaca to the distal tip of the clasper.

A2.2: Maturation order of male reproductive structures

Estimates of the length-at-maturity of each male reproductive structure are derived from the UGGC model, using the same priors and truncation points used for estimating length-at-maturity for male school sharks (see Chapter 3, section '*3.3.5.2: Estimating length-at-transition'* for details).

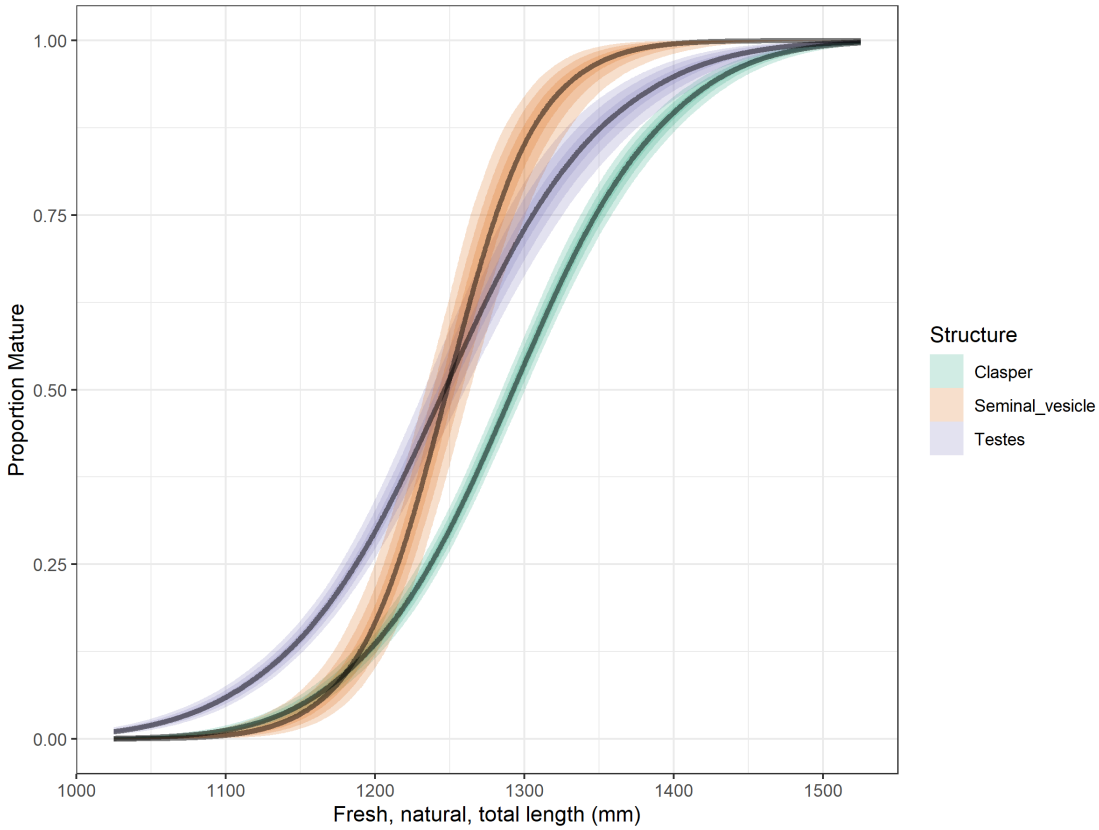


Figure A2.2.1: *Maturation order of male school shark reproductive structures. Shaded areas are the 95% credible intervals. Fresh, natural, total length is the total length measured in a straight line from a fresh animal, with the tail in a natural position.*

A2.3: Models for converting clasper and testes measurements to life-history stages

A2.3.1: Clasper inner length

A Bayesian logistic regression with a probit link was applied to truncated clasper inner length data (Figure A2.3.1.1) to estimate the life-history stage of individuals whose life-history stage was classified as unknown but had clasper inner length measured.

The logistic regression was defined as:

$$\begin{aligned} y_i &\sim \text{Binomial}(1, p_i) \\ probit(p_i) &= \beta_0 + \beta_1 \text{C}_i \end{aligned}$$

where C_i is the clasper inner length.

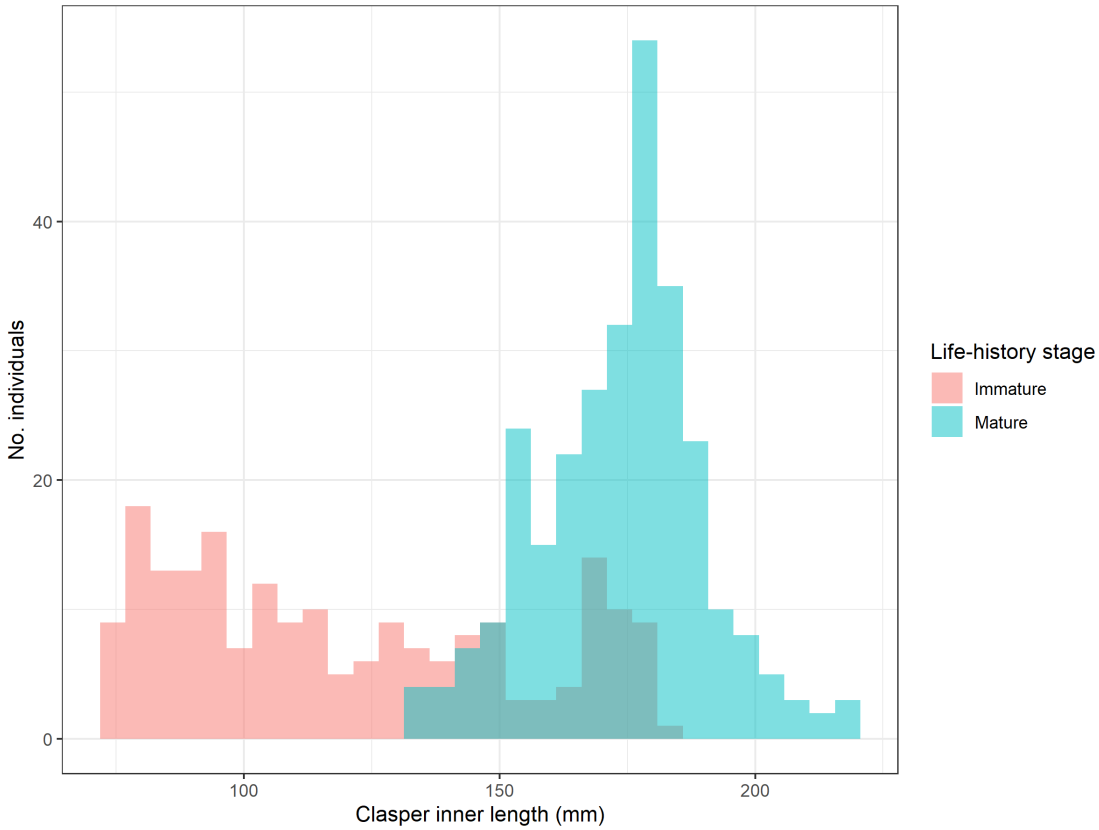


Figure A2.3.1.1: *Distribution of clasper inner lengths of immature and mature male school sharks within the truncation points.*

The priors for the model parameters were based on prior simulations (Figure A2.3.1.2) and the clasper inner length value where 50% of individuals were expected to be mature (e.g., 150mm)

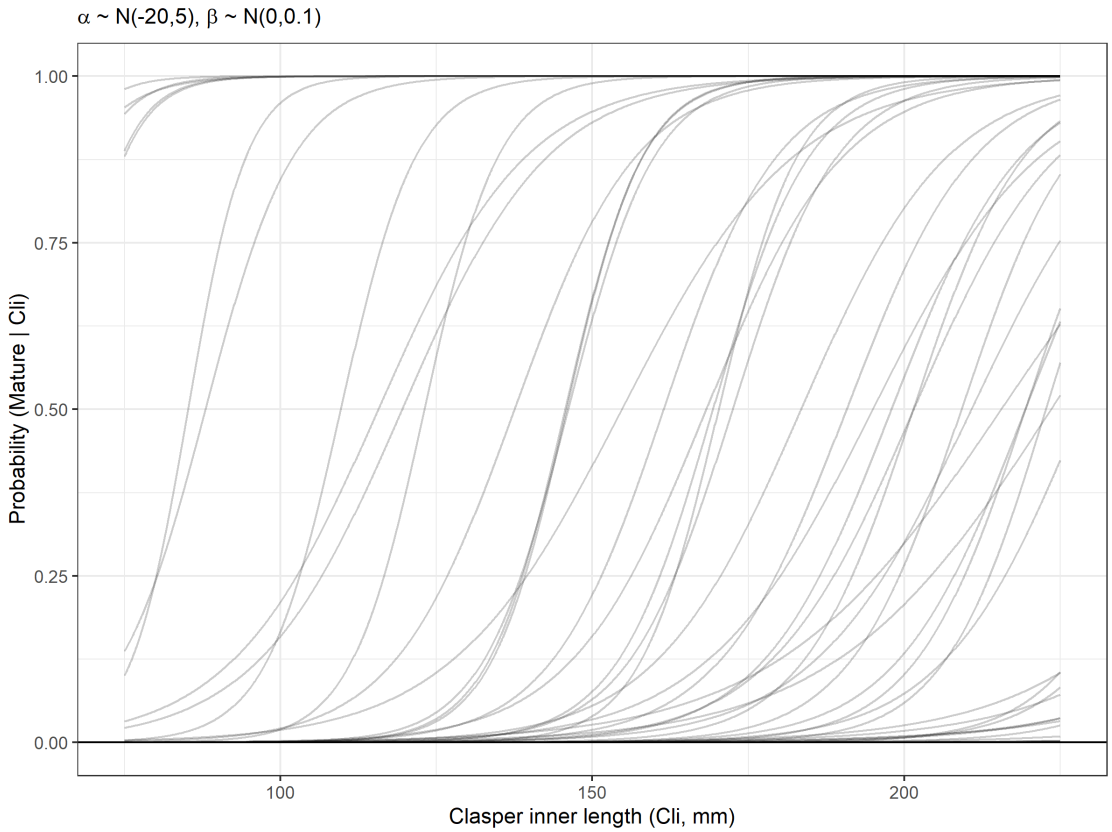


Figure A2.3.1.2: *Simulation of parameter priors for the probit logistic regression used to classify life-history stage based on clasper inner length.*

The priors for modelling the life-history stage given clasper inner length were as follows:

$$\begin{aligned} \beta_0 &\sim \mathcal{N}(-20,5) \\ \beta_1 &\sim \mathcal{N}(0,0.1) \end{aligned}$$

The lower and upper truncation bounds of the data were chosen as:

$$\begin{aligned} \text{Lower} &= 75 \\ \text{Upper} &= 225 \end{aligned}$$

Logistic regression with a probit link, applied to truncated clasper inner length data, was chosen over the Uniform-Gaussian Generative Classifier (UGGC) model because the within-sample classification rate for each life-history stage was reasonable (True positive rate: Immature - 75%, Mature - 93%). Additionally, the UGGC model for classifying life-history stage based on clasper inner length is still under development.

A2.3.2: Testes weight (left)

A Bayesian logistic regression with a probit link was applied to truncated left testis weight data (Figure A2.3.2.1) to estimate the life-history stage of individuals that had their stage classified as unknown but had left testis weight measured. Left testis weight was chosen as it was the most frequently recorded testis weight for individuals with an unknown life-history stage. The ratio between left and right testis weight was approximately 1:1, on average. Given the ratio between left and right testis weights, left testis weight was assumed to be equivalent to the right testis weight when only the right testis weight was recorded, and half of the total testes weight when only the combined weight of individuals was recorded.

The logistic regression was defined as:

$$\begin{aligned} y_i &\sim \text{Binomial}(1, p_i) \\ probit(p_i) &= \beta_0 + \beta_1 \text{Ts}_i \end{aligned}$$

where Ts_i is the left testis weight.

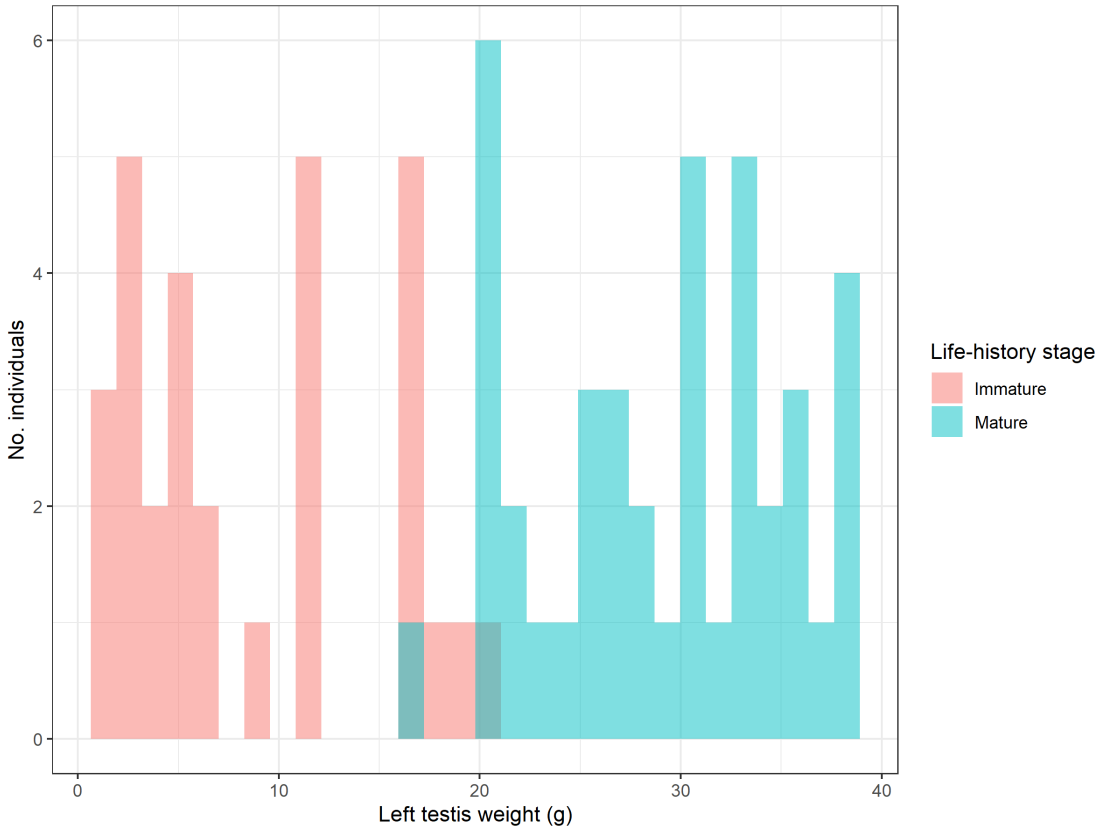


Figure A2.3.2.1: *Distribution of left testis weight of immature and mature male school sharks within the truncation points.*

The priors for the model parameters were based on prior simulations (Figure A2.3.2.2) and the left testis weight value where 50% of individuals were expected to be mature (e.g., 20g).

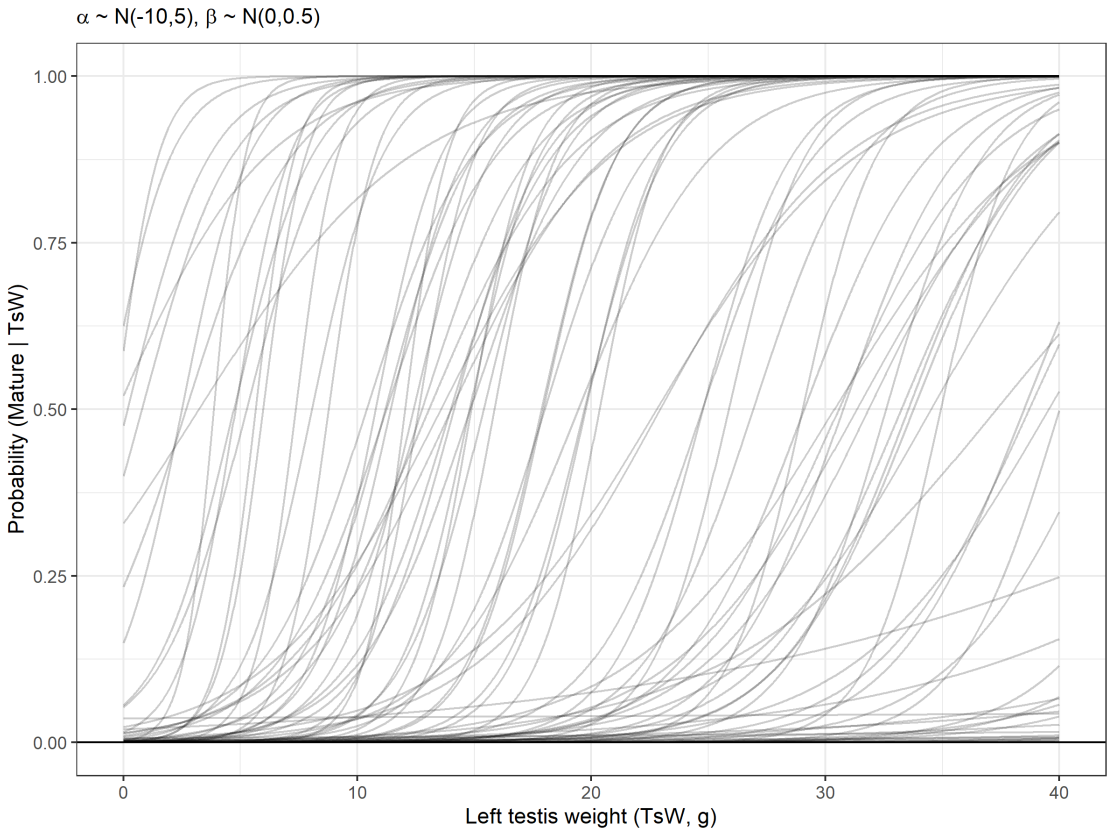


Figure A2.3.2.2: *Simulation of parameter priors for the probit logistic regression used to classify life-history stage based on left testis weight.*

The priors for modelling the life-history stage given left testis weight were as follows:

$$\begin{aligned} \beta_0 &\sim \mathcal{N}(-10,5) \\ \beta_1 &\sim \mathcal{N}(0,0.5) \end{aligned}$$

The lower and upper truncation bounds of the data were chosen as:

$$\begin{aligned} \text{Lower} &= 0 \\ \text{Upper} &= 40 \end{aligned}$$

Logistic regression with a probit link, applied to truncated left testis weight data, was chosen over the UGGC model because both models had the same within-sample classification rate for each life-history stage (True positive rate: Immature - 97%, Mature - 98%). Since the logistic regression was the simpler of the two models, it was selected.

A2.4: Prior simulations and model diagnostics for the male length-at-maturity model

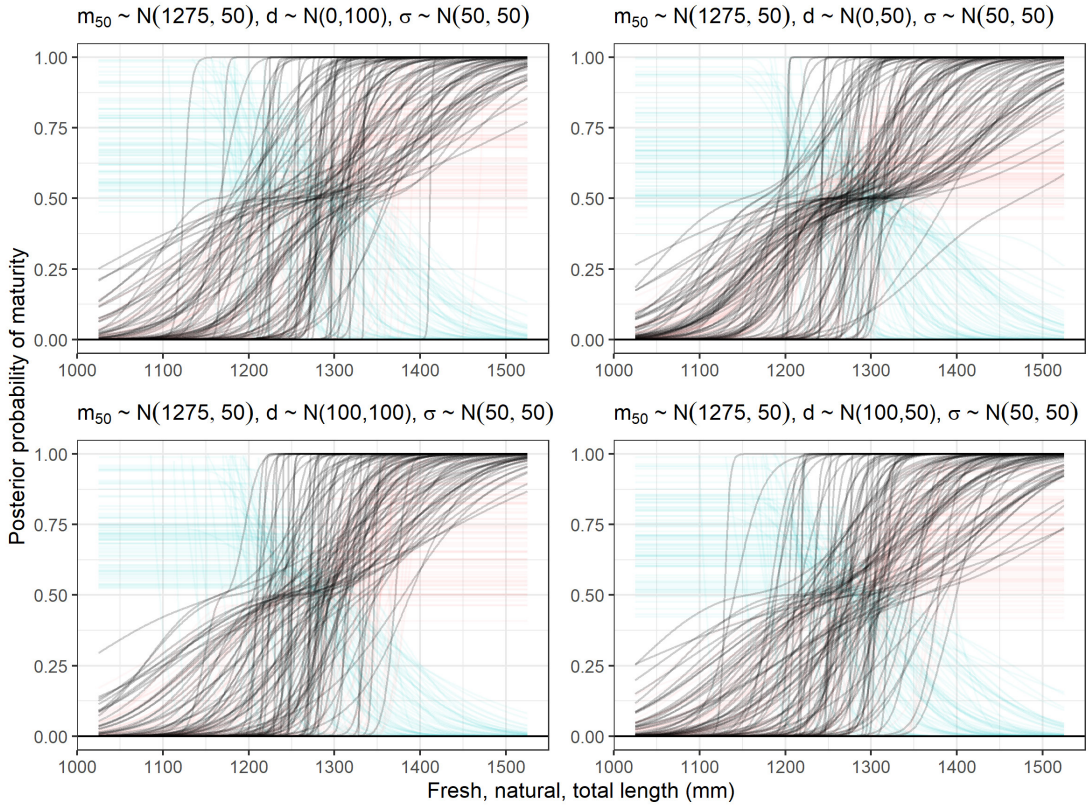


Figure A2.4.1: *Simulation of parameter priors for the hierarchical Bayesian Uniform-Gaussian generative model used to estimate male length-at-maturity. Fresh, natural, total length is the total length, measured in a straight line, tail in natural position, measured from a fresh or live shark.*

Table A2.4.1: *Model summary of the hierarchical Bayesian Uniform-Gaussian generative model used to estimate length-at-maturity for male school sharks.* LCI_{95} *is the lower bound of the 95% credible interval.* UCI_{95} *is the upper bound of the 95% credible interval.*

Parameter	Population	Estimate	Estimate standard deviation	Estimate standard error	LCI_{95}	UCI_{95}	Effective sample size	Rhat
mu_m50		1273.22	14.55	0.19	1243.72	1302.07	5963	1
d		147.20	14.61	0.15	118.34	175.76	9644	1
z[1]	Australia	1.1082	0.5757	0.0072	0.0592	2.2939	6467	1
z[2]	New Zealand	0.2180	0.4817	0.0056	-0.7117	1.1849	7334	1
z[3]	Northeast Atlantic	-0.6214	0.5326	0.0059	-1.7251	0.3788	8187	1
z[4]	Northeast Pacific	0.0144	0.8604	0.0069	-1.6896	1.7113	15389	1
z[5]	South Africa	0.4517	0.4750	0.0058	-0.4402	1.4274	6719	1

Parameter	Population	Estimate	Estimate standard deviation	Estimate standard error	LCI_{95}	UCI_{95}	Effective sample size	Rhat
z[6]	Southwest Atlantic	-1.1933	0.5903	0.0069	-2.4424	-0.1253	7235	1
sigma_x		81.744	3.776	0.039	74.434	89.256	9638	1
sigma_alpha		33.08	12.84	0.16	16.39	64.96	6394	1
alpha[1]	Australia	32.63	15.36	0.19	2.41	63.91	6590	1
alpha[2]	New Zealand	6.44	15.67	0.19	-24.66	38.17	6797	1
alpha[3]	Northeast Atlantic	-18.66	16.53	0.19	-52.33	13.64	7449	1
alpha[4]	Northeast Pacific	0.614	28.433	0.229	-55.666	57.358	15406	1
alpha[5]	South Africa	13.25	15.11	0.19	-16.51	43.73	6485	1
alpha[6]	Southwest Atlantic	-35.27	15.44	0.19	-67.91	-5.06	6586	1
m50_pop[1]	Australia	1305.846	6.264	0.044	1293.514	1318.063	20075	1
m50_pop[2]	New Zealand	1279.654	7.028	0.045	1265.869	1293.378	24819	1
m50_pop[3]	Northeast Atlantic	1254.559	10.000	0.065	1234.356	1274.027	23572	1
m50_pop[4]	Northeast Pacific	1273.830	29.438	0.238	1215.297	1332.893	15283	1
m50_pop[5]	South Africa	1286.467	5.526	0.036	1275.709	1297.328	23713	1
m50_pop[6]	Southwest Atlantic	1237.943	6.638	0.047	1224.884	1250.722	20068	1
mu0_pop[1]	Australia	1232.247	10.700	0.099	1211.230	1253.062	11706	1
mu0_pop[2]	New Zealand	1206.055	9.590	0.081	1186.994	1224.593	13885	1
mu0_pop[3]	Northeast Atlantic	1180.96	12.94	0.11	1154.86	1206.17	14960	1
mu0_pop[4]	Northeast Pacific	1200.23	30.55	0.25	1138.78	1260.94	14506	1
mu0_pop[5]	South Africa	1212.868	9.981	0.090	1193.026	1232.339	12395	1
mu0_pop[6]	Southwest Atlantic	1164.34	11.48	0.11	1141.79	1187.09	11794	1
mu1_pop[1]	Australia	1379.445	8.408	0.072	1363.334	1396.262	13614	1
mu1_pop[2]	New Zealand	1353.253	10.656	0.093	1332.257	1373.819	13277	1
mu1_pop[3]	Northeast Atlantic	1328.159	11.806	0.092	1305.131	1351.251	16511	1
mu1_pop[4]	Northeast Pacific	1347.43	30.11	0.25	1288.53	1408.63	15084	1
mu1_pop[5]	South Africa	1360.066	8.257	0.075	1343.970	1376.659	12259	1
mu1_pop[6]	Southwest Atlantic	1311.542	7.943	0.067	1296.151	1327.275	14265	1
C0_pop[1]	Australia	309.697	7.959	0.062	294.067	325.236	16536	1
C0_pop[2]	New Zealand	283.505	7.298	0.050	269.323	297.766	21392	1
C0_pop[3]	Northeast Atlantic	258.411	11.147	0.077	236.134	280.191	20762	1
C0_pop[4]	Northeast Pacific	277.68	29.76	0.24	218.04	337.43	15099	1
C0_pop[5]	South Africa	290.318	7.718	0.055	275.148	305.642	19502	1
C0_pop[6]	Southwest Atlantic	241.795	8.733	0.069	224.777	259.110	16270	1
C1_pop[1]	Australia	248.0056	6.5994	0.0456	235.1377	260.9731	20950	1

Parameter	Population	Estimate	Estimate standard deviation	Estimate standard error	LCI_{95}	UCI_{95}	Effective sample size	Rhat
C1_pop[2]	New Zealand	274.197	8.600	0.060	257.728	291.024	20770	1
C1_pop[3]	Northeast Atlantic	299.292	10.208	0.067	279.460	319.692	23140	1
C1_pop[4]	Northeast Pacific	280.02	29.60	0.24	220.32	338.45	15408	1
C1_pop[5]	South Africa	267.385	5.471	0.039	256.572	278.012	19438	1
C1_pop[6]	Southwest Atlantic	315.908	6.347	0.043	303.742	328.488	22214	1
lp__		-16223.293	2.531	0.034	-16229.004	-16219.254	5457	1

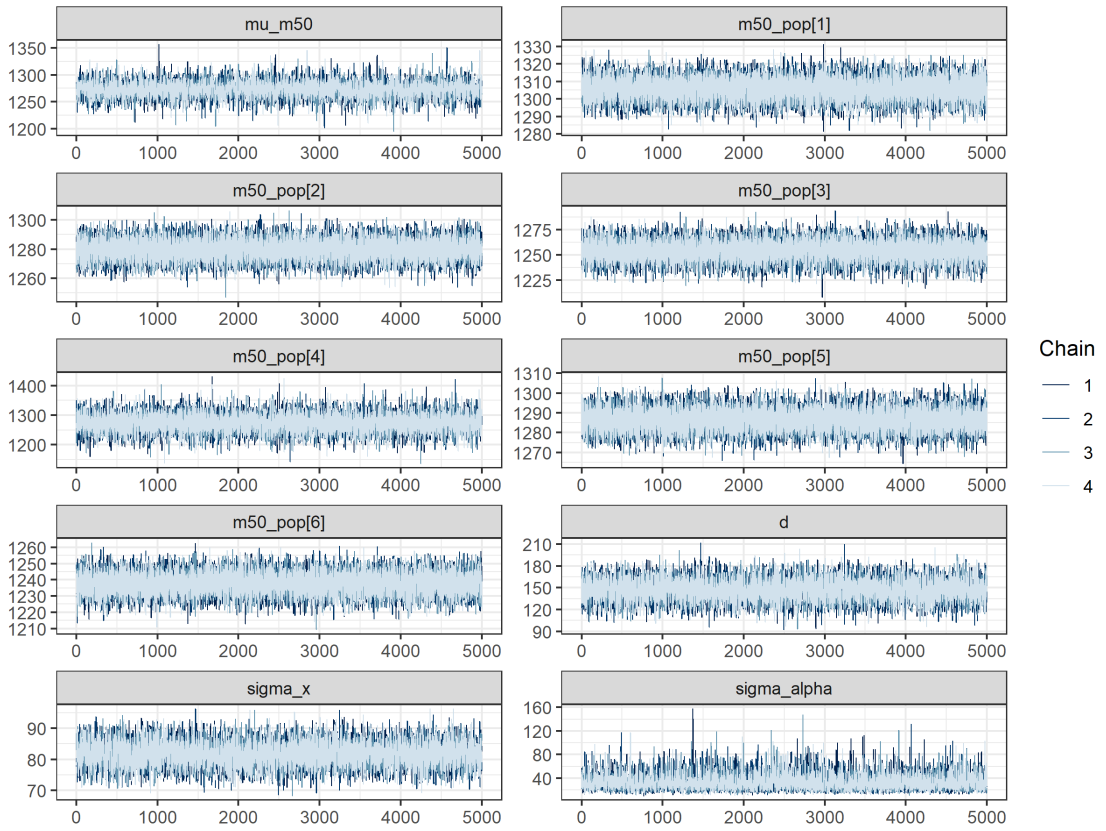


Figure A2.4.2: *Trace plots for each parameter of the hierarchical Bayesian Uniform-Gaussian generative model used to estimate length-at-maturity for male school sharks.*

A2.5: Female length-at-maturity

After standardising length and life-history stage data, data for 1,677 female school sharks from all six populations were useable. As with males, there were varying degrees of data imbalance between immature and mature life-history stages across the populations (Figure A2.5.1). Additionally, some populations had greater spatio-temporal and gear representation than others (Figures A2.5.2a and A2.5.2b). Unfortunately, due to a lack of data around the point at transition, the hierarchical Uniform-Gaussian Generative Classifier model variant could only be applied to estimate female length-at-maturity for the Australian, South African, and Southwest Atlantic populations.

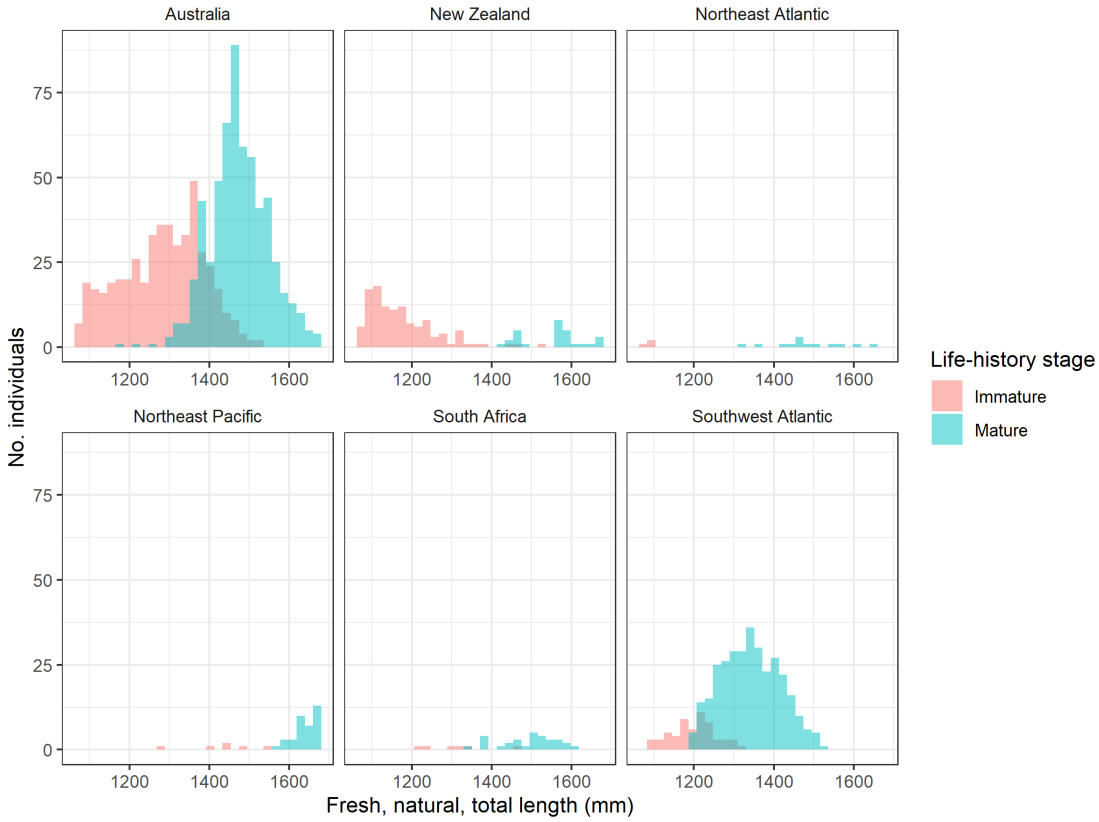
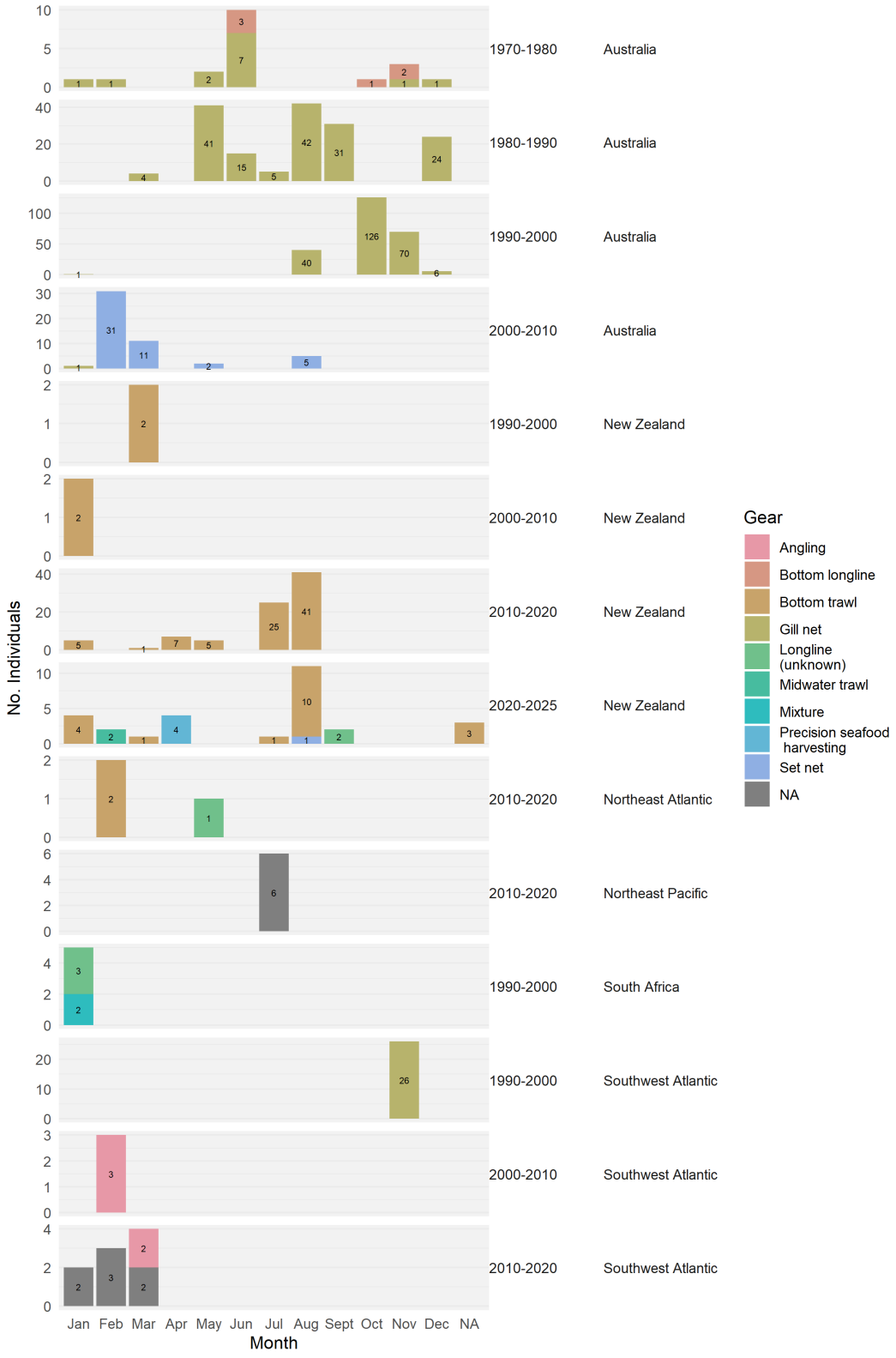
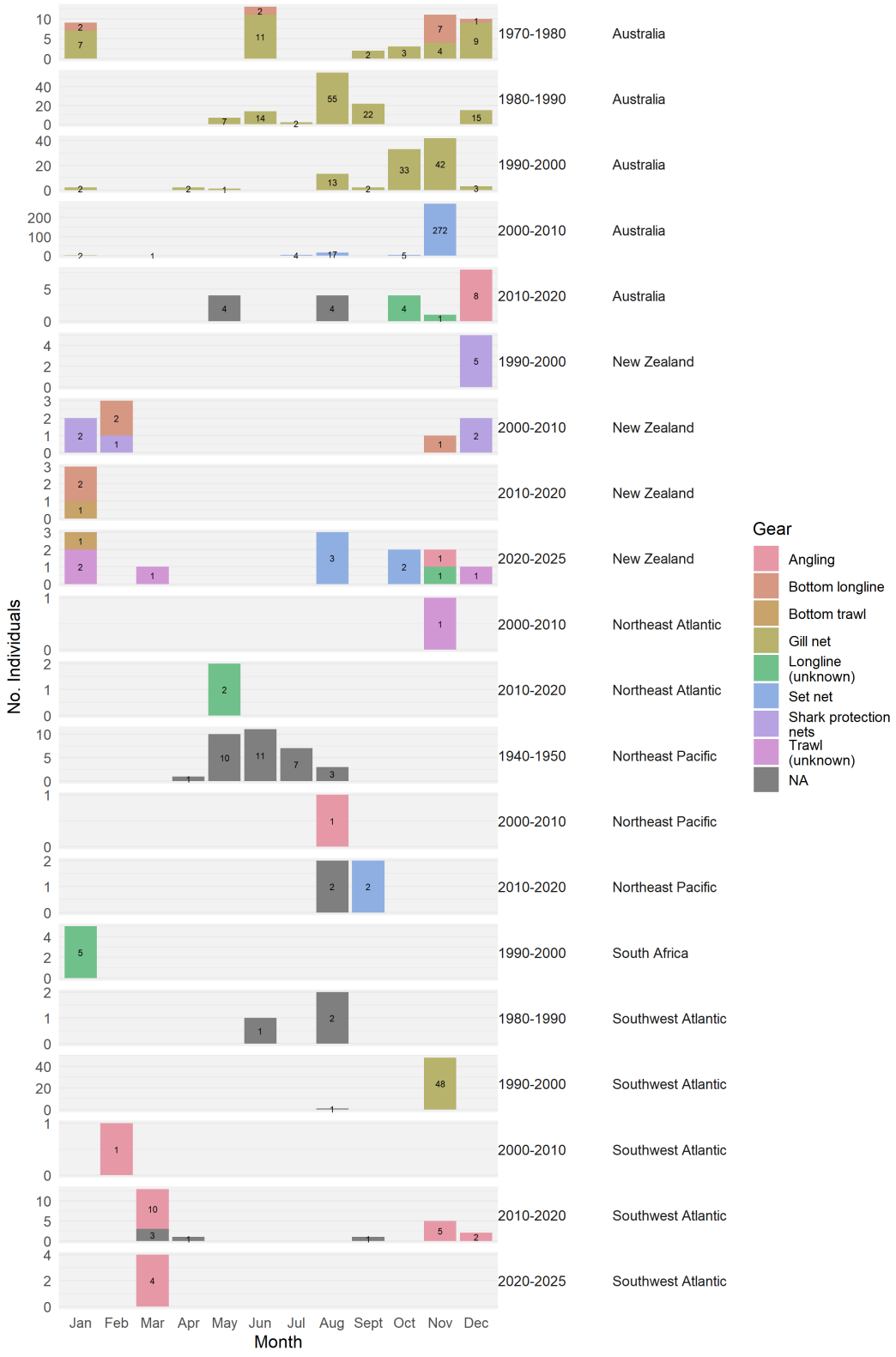


Figure A2.5.1: *Distribution of lengths of immature and mature female school sharks for each population, within the truncation points. Fresh, natural, total length is the total length measured in a straight line from a fresh animal, with the tail in a natural position.*


No. Individuals
Month
Jan Feb Mar Apr May Jun Jul Aug Sept Oct Nov Dec NA
1970-1980 Australia
1980-1990 Australia
1990-2000 Australia
2000-2010 Australia
1990-2000 New Zealand
2000-2010 New Zealand
2010-2020 New Zealand
2020-2025 New Zealand
2010-2020 Northeast Atlantic
2010-2020 Northeast Pacific
1990-2000 South Africa
1990-2000 Southwest Atlantic
2000-2010 Southwest Atlantic
2010-2020 Southwest Atlantic
Gear
Angling
Bottom longline
Bottom trawl
Gill net
Longline (unknown)
Midwater trawl
Mixture
Precision seafood harvesting
Set net
NA

a) Immature



b) Mature

Figure A2.5.2: *Number of female school sharks captured per gear type, month, and time period in each population.*

The priors used for modelling length-at-maturity for female school sharks were as follows:

$$\begin{aligned} m_{50} &\sim \mathcal{N}(1375,50) \\ d &\sim \mathcal{N}(0,100) \\ \sigma &\sim \mathcal{N}^{+}(0,50) \\ \sigma_{\alpha} &\sim \mathcal{N}^{+}(0,50) \end{aligned}$$

The lower and upper truncation values were chosen as:

$$\begin{aligned} L &= 1075 \\ U &= 1675 \end{aligned}$$

Posteriors of female length-at-maturity for each population were summarised as point estimates (i.e., the mean of the posterior distribution) with associated standard deviations and 95% credible intervals. Differences in length-at-maturity between populations and sexes within populations were estimated by examining the posterior distribution of the difference between the estimates of m_{50} for the two populations or sexes being compared.

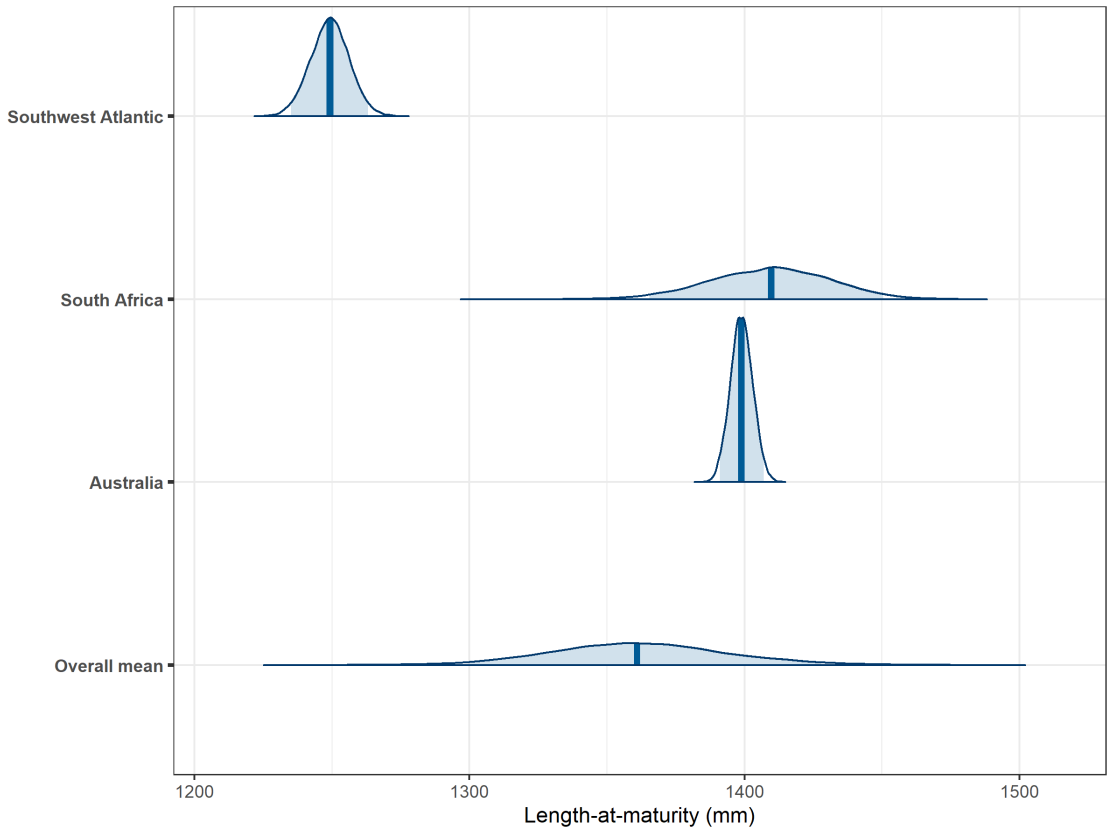


Figure A2.5.3: *The overall and population-specific posteriors of the length-at-maturity for female school sharks. Solid lines indicate the point estimates of length-at-maturity. The light blue shading under the curve visualises the 95% credible interval of the length-at-maturity estimate.*

Table A2.5.1: *Point estimates of length-at-maturity (mm TL; ± standard deviation, SD) for female school sharks for each of the modelled populations.* LCI_{95} *is the lower bound of the 95% credible interval.* UCI_{95} *is the upper bound of the 95% credible interval. Maturity length range is the total length range (mm, fresh, natural, total length) of mature individuals from the datasets received for each population for this study.*

Population	Length-at-maturity (±SD)	LCI_{95}	UCI_{95}	Maturity length range
Australia	1399±4	1391	1407	1176 - 1749
South Africa	1409±22	1365	1450	1350 - 1634
Southwest Atlantic	1249±7	1235	1263	1191 - 1530

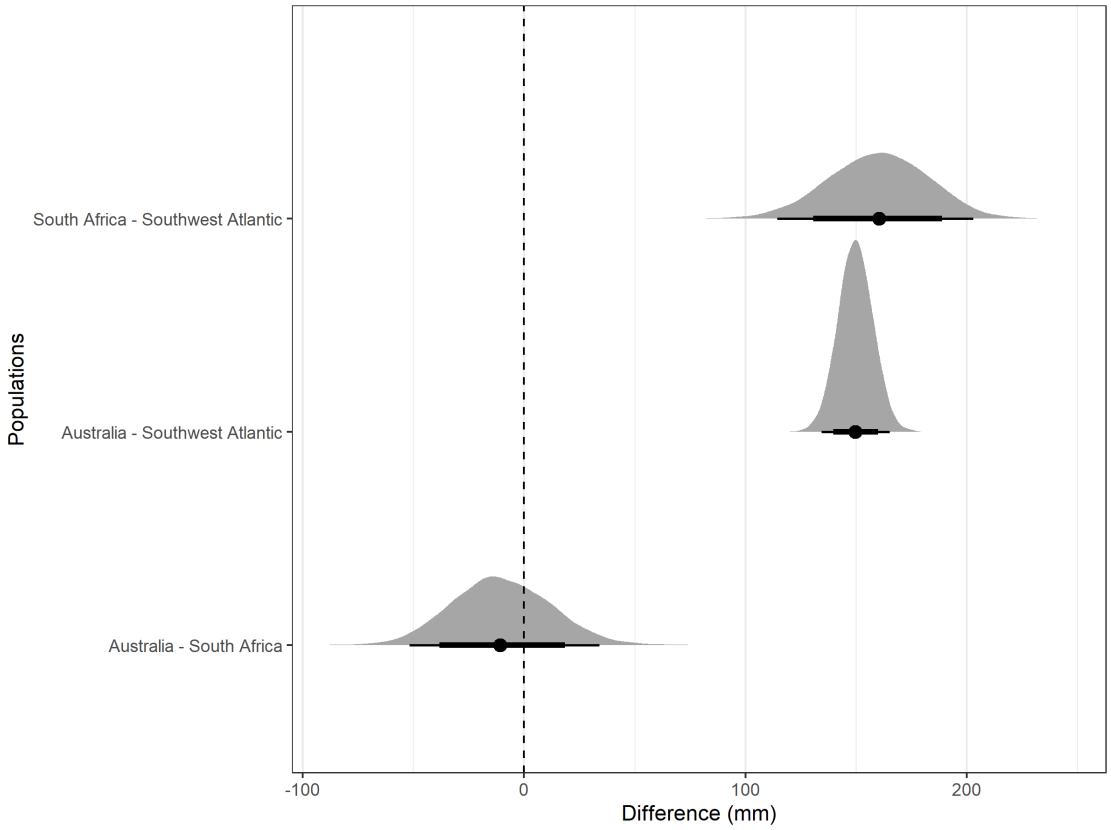


Figure A2.5.4: *Posterior distributions of the differences in length-at-maturity for female school sharks between pairs of populations. The points are the average difference between populations. The thicker lines are the 80% credible intervals, and the thinner lines are the 95% credible intervals.*

Point estimates of female length-at-maturity ranged between 1249 and 1409mm TL (Figure A2.5.3; Table A2.5.1). Pairwise comparisons suggest that length-at-maturity is similar between the Australian and South African populations, while both populations differ from the Southwest Atlantic by 155 mm TL, on average (Figure A2.5.4). However, due to the high uncertainty in the female length-at-maturity estimate for the South African population, I am uncertain as to how reflective the estimated difference is of the true difference between the populations.

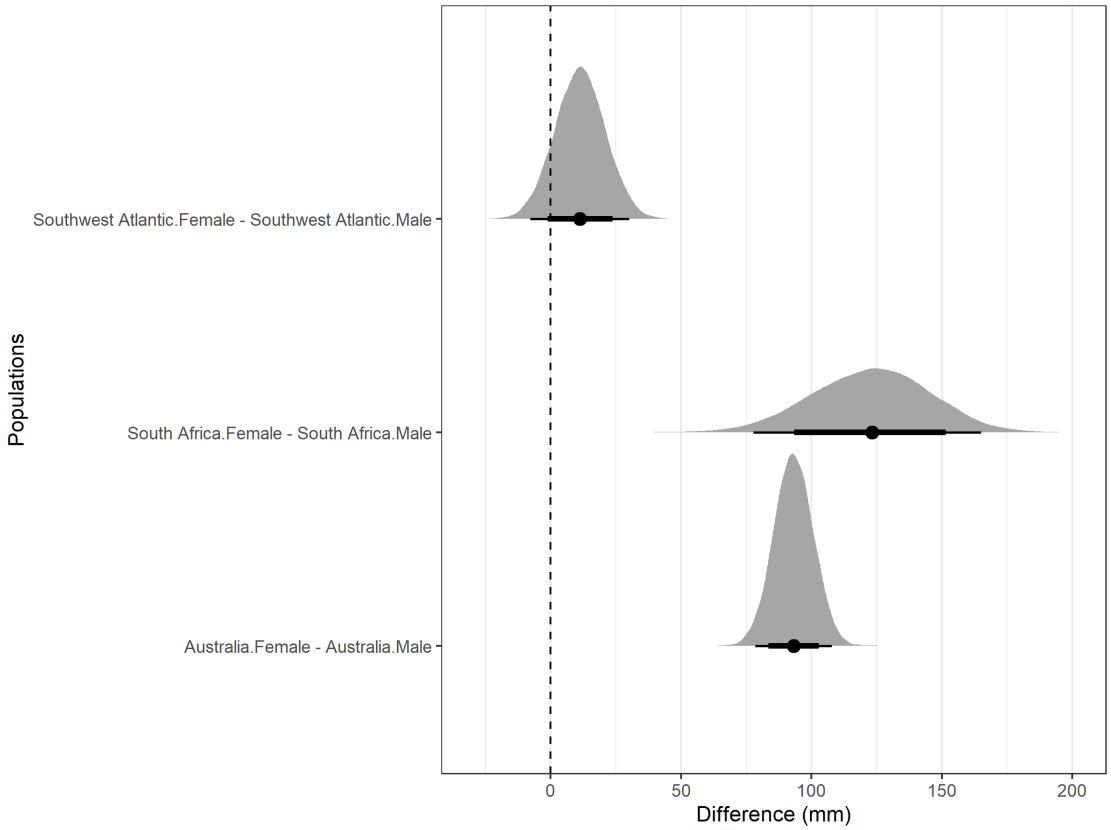


Figure A2.5.5: *Posterior distributions of the differences in length-at-maturity between sexes for each modelled population. The points are average difference between sexes for specific populations. The thicker lines are the 80% credible intervals, and the thinner lines are the 95% credible intervals.*

Pairwise comparisons of length-at-maturity between sexes suggest that, on average, female school sharks in the Australian population mature 93mm TL larger than males (Figure A2.5.5). However, due to the high uncertainty in the female length-at-maturity estimate for the South African population, I cannot determine whether the observed difference between sexes accurately reflects the true difference in the population parameters. Similarly, given that sexual dimorphism in length-at-maturity has been reported for some shark species (e.g., Grant et al., 2018), I am uncertain whether the estimated female length-at-maturity for the Southwest Atlantic population, and difference from male length-at-maturity, is representative of the true population parameters or underestimated due to the representativeness of the data (Figures A2.5.1 and A2.5.2).

If the observed difference in length-at-maturity between male and female school sharks in the Australian population is consistent across all populations, then females are likely to mature at a similarly greater length than males in other populations as well. Using this assumption, potential female length-at-maturity were estimated for each populations, where direct modelling was not possible, by adding the posterior distribution of the sex-based difference in the Australian population to the posterior distributions of male length-at-maturity for each population (see Chapter 3; Figure 3.4 for the posteriors of male length-at-maturity estimates). This approach was applied to the South African and Southwest Atlantic populations due to the high uncertainty in their

modelled female length-at-maturity estimates. These estimated values are provided in Figure A2.5.6 and Table A2.5.2.

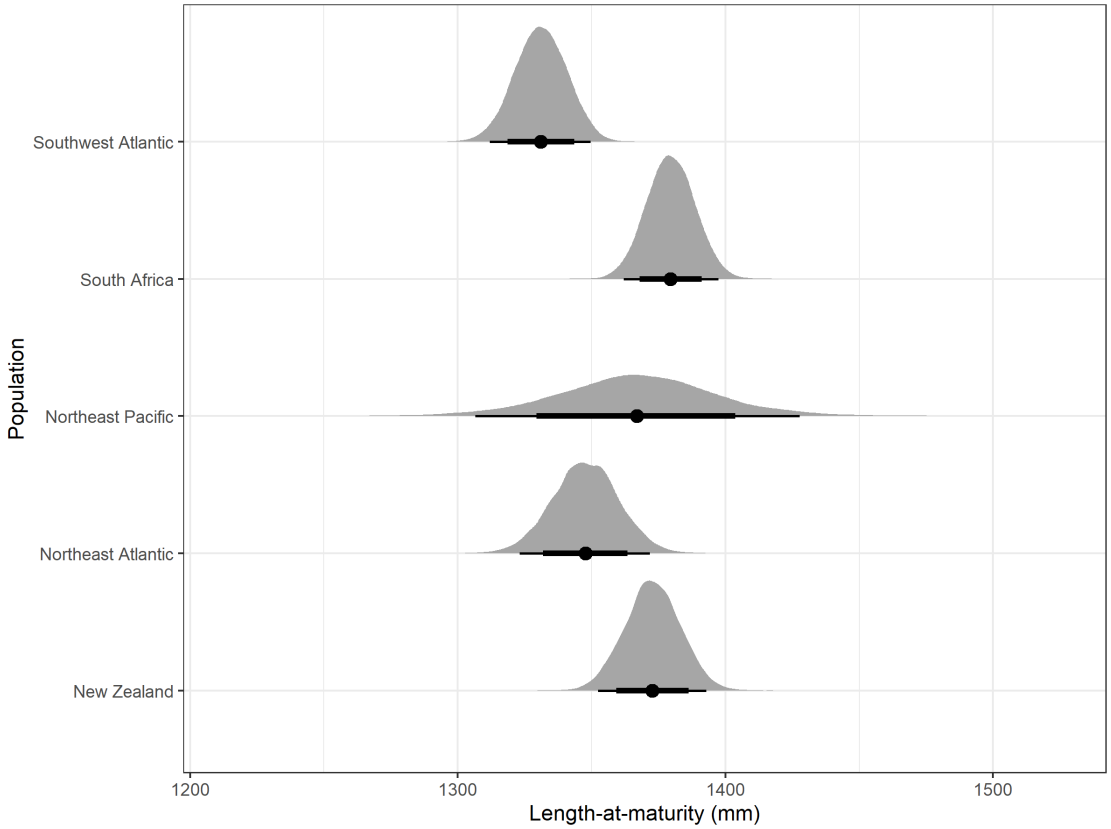


Figure A2.5.6: *Estimated potential posteriors of female length-at-maturity for populations where male length-at-maturity was modelled, based on the observed difference between sexes in the Australian population. Points are the point estimates of possible length-at-maturity. The thicker lines are the 80% credible intervals, and the thinner lines are the 95% credible intervals.*

Table A2.5.2: *Point estimates of possible female length-at-maturity (mm TL; ± standard deviation, SD), inferred for populations where male length-at-maturity was modelled, using the observed sex-based difference from the Australian population.* LCI_{95} *is the lower bound of the 95% credible interval.* UCI_{95} *is the upper bound of the 95% credible interval. Maturity length range is the total length range (mm, fresh, natural, total length) of mature individuals from the datasets received for each population for this study.*

Population	Length-at-maturity (±SD)	LCI_{95}	UCI_{95}	Maturity length range
New Zealand	1373±10	1352	1393	1430 - 2348
Northeast Atlantic	1348±12	1323	1372	1312 - 1948
Northeast Pacific	1367±30	1307	1428	1570 - 1938
South Africa	1380±9	1362	1397	1350 - 1634
Southwest Atlantic	1331±10	1312	1350	1191 - 1530

A2.6: Length-at-birth

After standardising length and life-history stage data, data for 2,264 prenate and 1,360 juvenile school sharks from five populations were useable. Similar to females and males, there were varying degrees of data imbalance between immature and mature life-history stages (Figure A2.6.1), as well as spatio-temporal and gear representation across populations. Due to limited data around the point at transition for some populations, the hierarchical Uniform-Gaussian Generative Classifier model variant could only be applied to estimate length-at-birth for the Australian, Northeast Atlantic, and Southwest Atlantic populations. Data for both sexes were combined as there was insufficient data to model length-at-birth for each sex. However, it is likely that length-at-birth does not differ between the sexes.

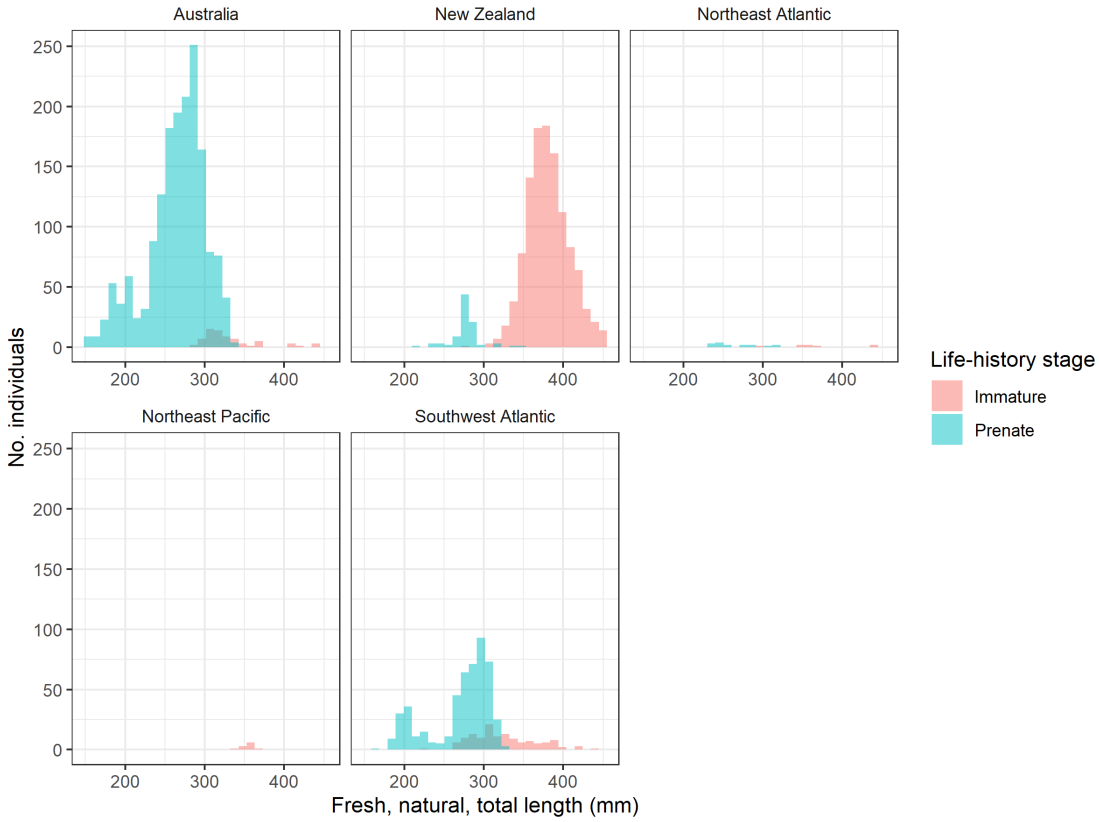


Figure A2.6.1: *Distribution of lengths of prenate and immature school sharks for each population, within the truncation points. Fresh, natural, total length is the total length measured in a straight line from a fresh animal, with the tail in a natural position.*

The priors used for modelling length-at-birth for school sharks were as follows:

$$\begin{aligned} m_{50} &\sim \mathcal{N}(300,50) \\ d &\sim \mathcal{N}(0,100) \\ \sigma &\sim \mathcal{N}^{+}(0,50) \\ \sigma_{\alpha} &\sim \mathcal{N}^{+}(0,50) \end{aligned}$$

The lower and upper truncation values were chosen as:

$$\begin{aligned} L &= 150 \\ U &= 450 \end{aligned}$$

Posteriors of length-at-birth for each population were summarised as point estimates (i.e., the mean of the posterior distribution) with associated standard deviations and 95% credible intervals. Differences in length-at-birth between populations were estimated by examining the posterior distribution of the difference between the estimates of m_{50} for the two populations being compared.

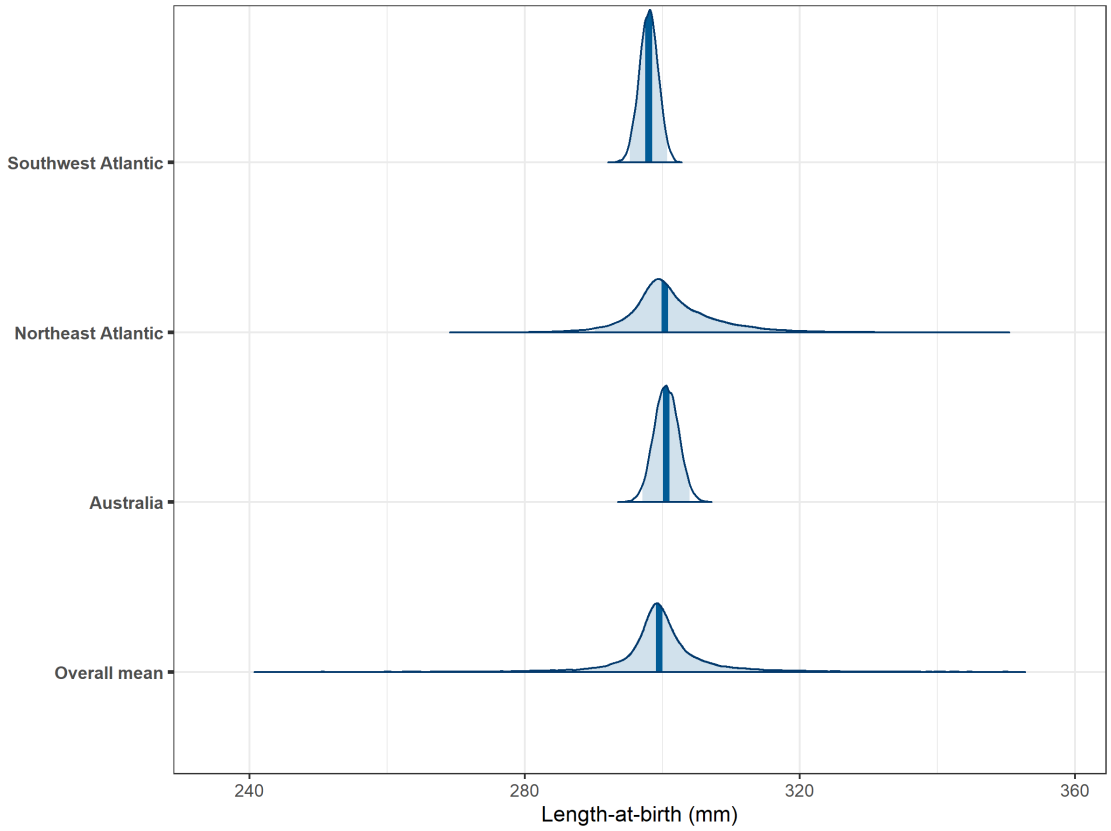


Figure A2.6.2: *The overall and population-specific posteriors of the length-at-birth for school sharks. Solid lines indicate the point estimates of length-at-birth. The light blue shading under the curve visualises the 95% credible interval of the length-at-birth estimate.*

Table A2.6.1: *Point estimates of length-at-birth (mm TL; ± standard deviation, SD) for school sharks for each of the modelled populations.* LCI_{95} *is the lower bound of the 95% credible interval.* UCI_{95} *is the upper bound of the 95% credible interval.*

Population	Length-at-birth (±SD)	LCI_{95}	UCI_{95}
Australia	301±2	297	304
Northeast Atlantic	301±6	290	317
Southwest Atlantic	298±1	295	301

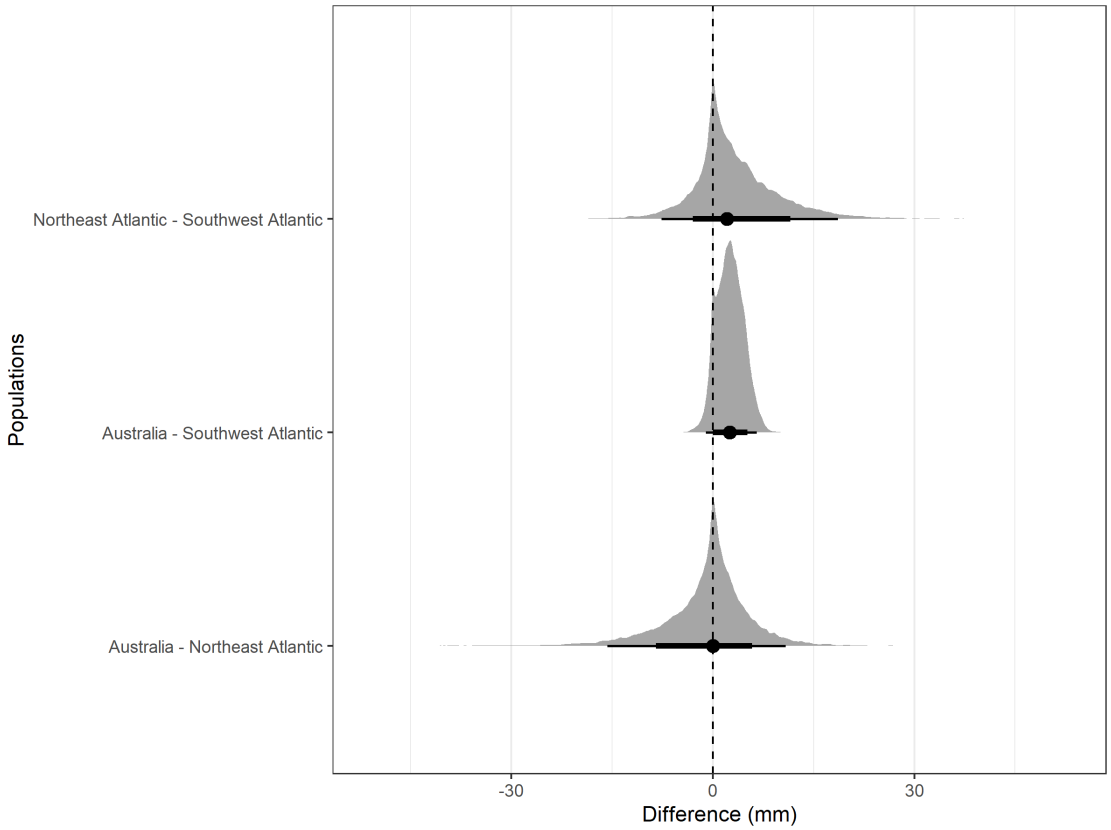


Figure A2.6.3: *Posterior distributions of the differences in length-at-birth for school sharks between pairs of populations. The points are the average difference between populations. The thicker lines are the 80% credible intervals, and the thinner lines are the 95% credible intervals.*

Point estimates of length-at-birth ranged between 298 and 301mm TL (Figure A2.6.2; Table A2.6.1). Pairwise comparisons suggest that length-at-birth is similar between all modelled populations (Figure A2.6.3). Based on the similarities of length-at-birth estimates between modelled populations and available data for the New Zealand population (Figure A2.6.1; Figure A2.6.3), it is likely that the New Zealand school shark population also have a length-at-birth of approximately 300mm TL.

A2.7: Age-at-maturity

Table A2.7.1: *Variants of the von Bertalanffy growth function. For the purposes of this study, L_t is the length-at-maturity, L_∞ is the asymptotic length, L_0 is the length at birth, k is the growth rate, t_0 is the theoretical age at zero length, and t is the age-at-maturity.*

Model	Equation	Equation to solve t
von Bertalanffy growth function, two parameter (VBGF 2p)	$L_t = L_\infty - (L_\infty - L_0)e^{-kt}$	$t = -\frac{1}{k} ln\left(\frac{L_\infty - L_t}{L_\infty - L_0}\right)$
von Bertalanffy growth function, three parameter (VBGF 3p)	$L_t = L_\infty\left(1 - e^{-k(t-t_0)}\right)$	$t = t_0 - ln(1 - L_t/L_\infty)/k$

Table A2.7.2: *A summary of population-specific growth studies for school sharks. Growth function is the growth function used as specified in Table A2.7.1. Model is whether a sex specific or combined sex model was used. Sample type is the type of data used. L_∞ is the asymptotic length (TL, mm) ± published standard error (SE). L_0 is the length at birth (TL, mm) ± standard deviation (SD) derived from Appendix 2.6. k is the growth rate (year^{-1}) ± published standard error (SE). t_0 is the theoretical age (years) at zero length ± published standard error (SE). * indicate the asymptotic lengths that needed to be converted to the standardised length variant used in Chapter 3.*

Population	Source	Growth function	Model	Sample type	N	Age Range	t_0 (±SE)	L_0 (±SD)	k (±SE)	L_∞ (±SE)
Australia	Grant et al. (1979)	VBGF 3p	Combined-sex	Mark-recapture	103	1-30	-1.27	300±7	0.1600±0.0007	1567.06*±0.14
Australia	Grant et al. (1979)	VBGF 3p	Female-specific	Mark-recapture	50		-1.28	300±7	0.1600±0.0015	1584.56*±0.32
Australia	Grant et al. (1979)	VBGF 3p	Male-specific	Mark-recapture	53		-1.25	300±7	0.1700±0.0012	1550.34*±0.25
Australia	Moulton et al. (1992)	VBGF 3p	Combined-sex	Vertebral counts	655	1-17	-1.29	300±7	0.12	1790*
New Zealand	Francis & Mulligan (1998)	VBGF 3p	Combined-sex	Vertebral counts	254	0-28	-2.37±0.26	300±7	0.100±0.009	1658±6
New Zealand	Francis & Mulligan (1998)	VBGF 3p	Female-specific	Vertebral counts	127	0-28	-2.68±0.38	300±7	0.086±0.011	1792±10
New Zealand	Francis & Mulligan (1998)	VBGF 3p	Male-specific	Vertebral counts	127	0-20	-1.64±0.31	300±7	0.150±0.019	1429±6

Population	Source	Growth function	Model	Sample type	N	Age Range	t_0 (±SE)	L_0 (±SD)	k (±SE)	L_∞ (±SE)
Northeast Atlantic	Dureuil & Worm (2015)	VBGF 2p	Female-specific	Mark-recapture	37	5-25		300±7	0.076	1934*
Northeast Atlantic	Dureuil & Worm (2015)	VBGF 2p	Male-specific	Mark-recapture	16	12-33		300±7	0.081	1708*
South Africa	Freer (1992)	VBGF 3p	Combined-sex	Vertebral counts	58	1-22	-1.33		0.16	1543*
South Africa	McCord (2005)	VBGF 3p	Combined-sex	Vertebral counts	76	0-33	-3.03±0.35		0.19±0.02	1503*±26
South Africa	McCord (2005)	VBGF 3p	Male-specific	Vertebral counts	53	0-33	-2.79±0.44		0.21±0.03	1486*±34
Southwest Atlantic	Ferreira & Vooren (1991)	VBGF 3p	Female-specific	Vertebral counts	164	0-21	-3	300±7	0.075	1596*
Southwest Atlantic	Ferreira & Vooren (1991)	VBGF 3p	Male-specific	Vertebral counts	123	0-12	-2.69	300±7	0.092	1488*

Table A2.7.3: *Summary of methods used in mark-recapture growth studies of school sharks. Length variant is the length variant measured in a study. Age range is the range of ages that were modelled; age range in brackets is where the age data was most concentrated. Length range is the range of lengths used in a study, standardised to the total length variant used in Chapter 3. VBGF parameters refers to how many von Bertalanffy growth function parameters were also presented in the study.*

Population	Source	Capture method	Length variant	Model	Growth function	N	Age range	Length range	VBGF parameters
Australia	Grant et al. (1979)	Gillnet & longline	Fresh, stretched, total length	Combined-sex	Fabens	103	1-30 (5-25)	551-1680	3
Australia	Grant et al. (1979)	Gillnet & longline	Fresh, stretched, total length	Female-specific	Fabens	50			3
Australia	Grant et al. (1979)	Gillnet & longline	Fresh, stretched, total length	Male-specific	Fabens	53			3
Northeast Atlantic	Dureuil & Worm (2015)	Angling & Trawl	Fresh, stretched, total length, over-the-body	Female-specific	Weighted Fabens	37	5-22 (7-15)	818-1709	2

Population	Source	Capture method	Length variant	Model	Growth function	N	Age range	Length range	VBGF parameters
Northeast Atlantic	Dureuil & Worm (2015)	Angling & Trawl	Fresh, stretched, total length, over-the-body	Male-specific	Weighted Fabens	16	12-33 (15-26)	1235-1648	2

Table A2.7.4: *A summary of methods used in vertebral count growth studies of school sharks. Length variant is the length variant measured in a study. "*" assumption of length variant measured based on data collected from a similar region. Section is whether a vertebral section was used to count vertebral rings. Technique is the technique used to amplify the vertebral deposition bands. Age range is the range of ages that were modelled; age range in brackets is where the age data was most concentrated. Length range is the range of lengths used in a study, standardised to the total length variant used in Chapter 3.*

Population	Source	Capture method	Length variant	Vert sample area	Cleaning	Section	Technique	Age calculation	Model	Growth function	N	Age range	Length range
Australia	Moulton et al. (1992)	Gillnet & longline	Fresh, stretched, total length	Behind to head	Mechanical & bleach	Y	Staining	$c_i + (-1 \times b_i) + (1 \times s_i) + P_{\text{year}}$	Combined-sex	VBGF 3p	655	1-17 (1-12)	<686-1663
New Zealand	Francis & Mulligan (1998)	Bottom trawl	Fresh, natural, total length*	Between first dorsal and pelvic fins	Mechanical & bleach	Y	X-ray & micro-scope	$c_i + (-1 \times b_i) + (-1 \times w_i) + P_{\text{year}}$	Combined-sex	VBGF 3p	254	0-28 (0-10)	340-2110
New Zealand	Francis & Mulligan (1998)	Bottom trawl	Fresh, natural, total length*	Between first dorsal and pelvic fins	Mechanical & bleach	Y	X-ray & micro-scope	$c_i + (-1 \times b_i) + (-1 \times w_i) + P_{\text{year}}$	Female-specific	VBGF 3p	127	0-28 (0-10)	350-2110
New Zealand	Francis & Mulligan (1998)	Bottom trawl	Fresh, natural, total length*	Between first dorsal and pelvic fins	Mechanical & bleach	Y	X-ray & micro-scope	$c_i + (-1 \times b_i) + (-1 \times w_i) + P_{\text{year}}$	Male-specific	VBGF 3p	127	0-20 (0-10)	340-1460
South Africa	Freer (1992)	Mixture	Fresh, stretched, total length, over-the-body*	Behind to head	Mechanical & boiled	N	Staining		Combined-sex	VBGF 3p	58	1-22 (1-15)	491-1533

Population	Source	Capture method	Length variant	Vert sample area	Cleaning	Section	Technique	Age calculation	Model	Growth function	N	Age range	Length range
South Africa	McCord (2005)	Longline	Fresh, stretched, total length, over-the-body*	Behind to head	Mechanical	Y	X-ray & micro-scope		Combined-sex	VBGF 3p	76	0-33 (2-20)	546-1616
South Africa	McCord (2005)	Longline	Fresh, stretched, total length, over-the-body*	Behind to head	Mechanical	Y	X-ray & micro-scope		Male-specific	VBGF 3p	53	0-33 (2-20)	546-1616
Southwest Atlantic	Ferreira & Vooren (1991)	Trawl	Fresh, stretched, total length*	Under first dorsal fin		Y	X-ray & micro-scope	$c_i + (-1 \times b_i)$	Female-specific	VBGF 3p	164	0-21 (0-6)	336-1114
Southwest Atlantic	Ferreira & Vooren (1991)	Trawl	Fresh, stretched, total length*	Under first dorsal fin		Y	X-ray & micro-scope	$c_i + (-1 \times b_i)$	Male-specific	VBGF 3p	127	0-12 (0-5)	317-1343

Terms used in the age calculation are defined as the following: c_i is the number of bands counted for a given vertebra; b_i is an indicator for whether the birth band was observed; w_i is an indicator for whether the winter band would have been deposited in a vertebra based on the capture date; s_i is an indicator for whether the outer margin of the vertebra was stained; and P_{year} is the portion of the year between the capture date and the arbitrary birth date (specified in each study).

Age-at-maturity is the age at which the probability of observing each stage is equal (i.e. probability = 0.5). Due to a lack of data on the age of individuals, age-at-maturity could not be modelled directly. Instead, age-at-maturity was estimated from the posteriors of population-specific length-at-maturity estimates from two- and three-parameter variants of the von Bertalanffy growth function (VBGF) and published, population-specific growth parameters for school sharks (Table A2.7.1 and Table A2.7.2). No published studies from the Northeast Pacific population were available to the best of our knowledge, so growth parameters from the Northeast Atlantic population were used to estimate age-at-maturity. Estimates of asymptotic length, L_{∞}, were converted to the standardised length variant used in Chapter 3, where necessary, using the methods described in Chapter 3, section '*3.3.4: Data standardisation*'. Estimates of length at birth, L_0, were made using the UGGC model fit to prenate and immature individuals; see Appendix 2.6. The methods used to estimate the von Bertalanffy growth function parameters are summarised in Tables A2.7.3 and A2.7.4. Calculations of age-at-maturity did not include the uncertainty associated with the growth parameters as the calculation would have treated the parameter uncertainties as mutually exclusive when, in fact, the parameter uncertainties interact. Inappropriately accounting for the interaction of the parameter posteriors could result in biased estimates.

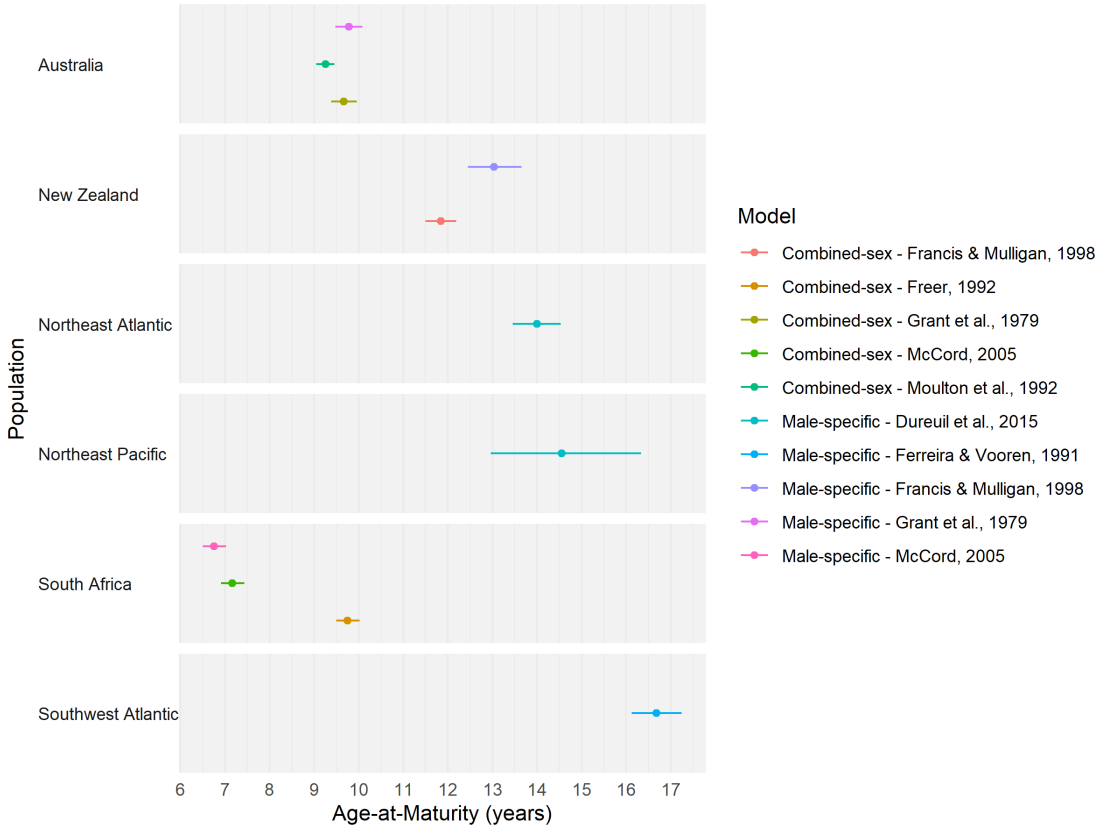


Figure A2.7.1: *Age-at-maturity estimates for male school sharks from each population based on population-specific growth parameters. Points are the point estimates of age-at-maturity for each population. The horizontal lines are the 95% credible intervals of the age-at-maturity estimates. Model is the growth model used to calculate the age-at-maturity estimate.*

Table A2.7.5: *Point estimates of age-at-maturity (years) for male school sharks for each of the modelled populations. Model is whether a sex specific or combined sex model was used.* LCI_{95} *is the lower bound of the 95% credible interval.* UCI_{95} *is the upper bound of the 95% credible interval.*

Population	Source	Model	Age-at-Maturity	LCI_{95}	UCI_{95}
Australia	Moulton et al. (1992)	Combined-sex	9.3	9.0	9.5
Australia	Grant et al. (1979)	Combined-sex	9.7	9.4	10.0
Australia	Grant et al. (1979)	Male-specific	9.8	9.5	10.1
New Zealand	Francis & Mulligan (1998)	Combined-sex	11.8	11.5	12.2
New Zealand	Francis & Mulligan (1998)	Male-specific	13.0	12.5	13.7
Northeast Atlantic	Dureuil & Worm (2015)	Male-specific	14.0	13.5	14.5
Northeast Pacific	Dureuil & Worm (2015)	Male-specific	14.6	13.0	16.3
South Africa	McCord (2005)	Combined-sex	7.2	6.9	7.4
South Africa	McCord (2005)	Male-specific	6.8	6.5	7.0
South Africa	Freer (1992)	Combined-sex	9.8	9.5	10.0
Southwest Atlantic	Ferreira & Vooren (1991)	Male-specific	16.7	16.1	17.2

Appendix 3 – Chapter 4: Juvenile growth

A3.1: Growth model prior simulations

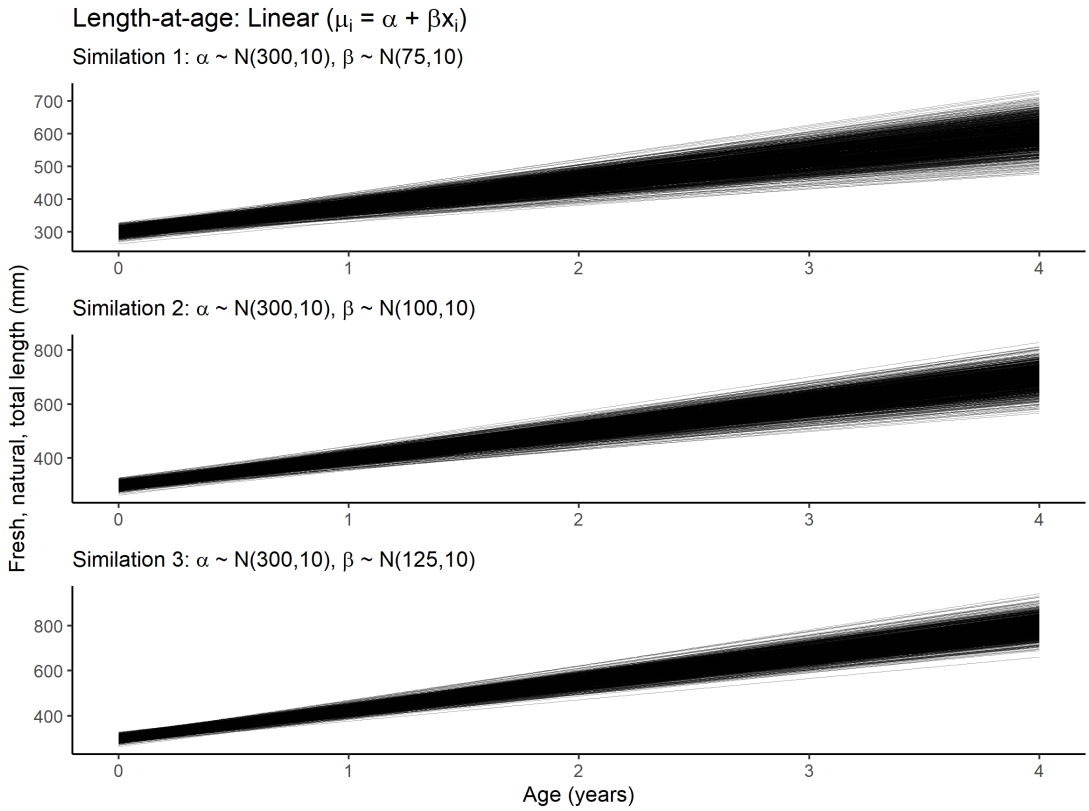


Figure A3.1.1: *Prior simulations for the linear length-at-age model. Fresh, natural, total length is the total length measured from a fresh shark, in a straight line, with the tail in a natural position.*

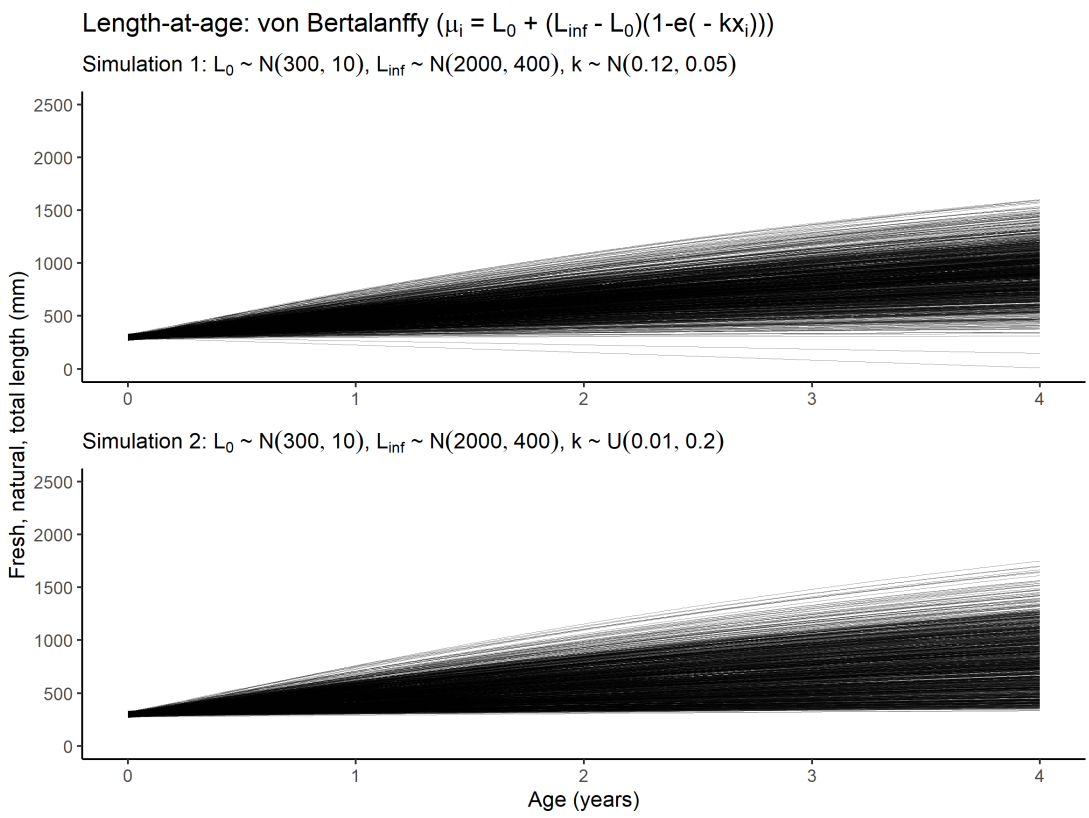


Figure A3.1.2: *Prior simulations for the von Bertalanffy length-at-age model. Fresh, natural, total length is the total length measured from a fresh shark, in a straight line, with the tail in a natural position.*

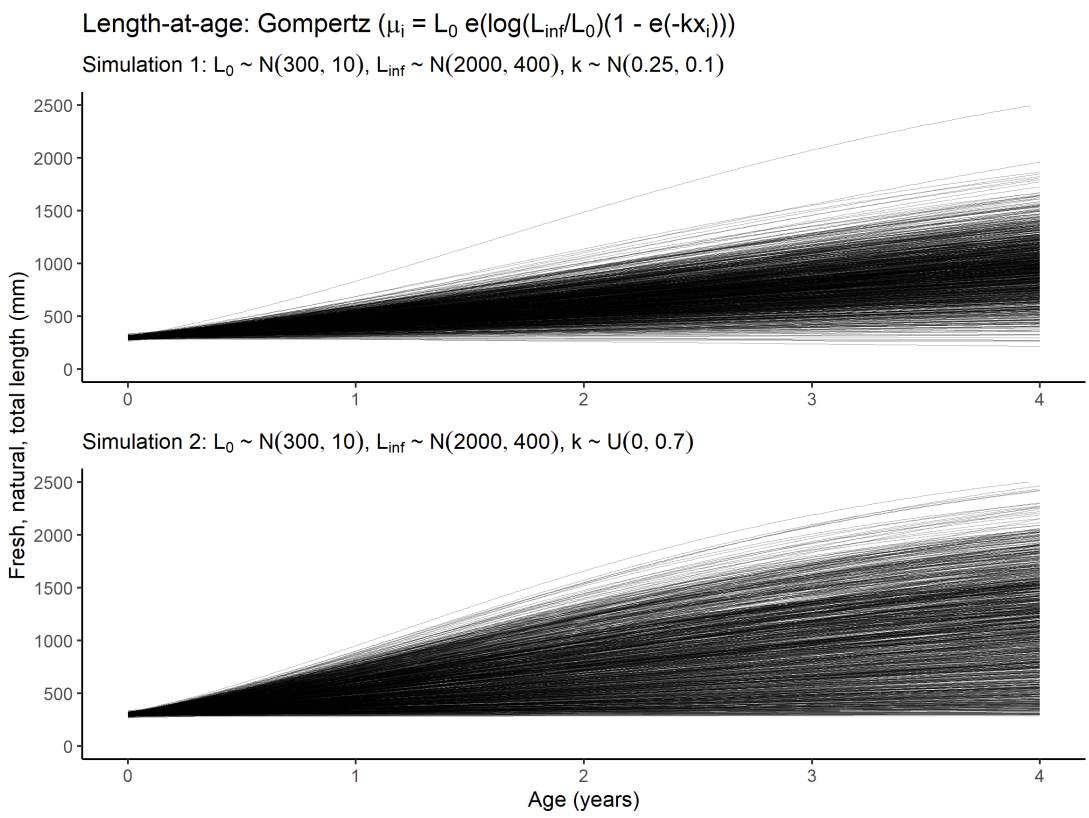


Figure A3.1.3: *Prior simulations for the Gompertz length-at-age model. Fresh, natural, total length is the total length measured from a fresh shark, in a straight line, with the tail in a natural position.*

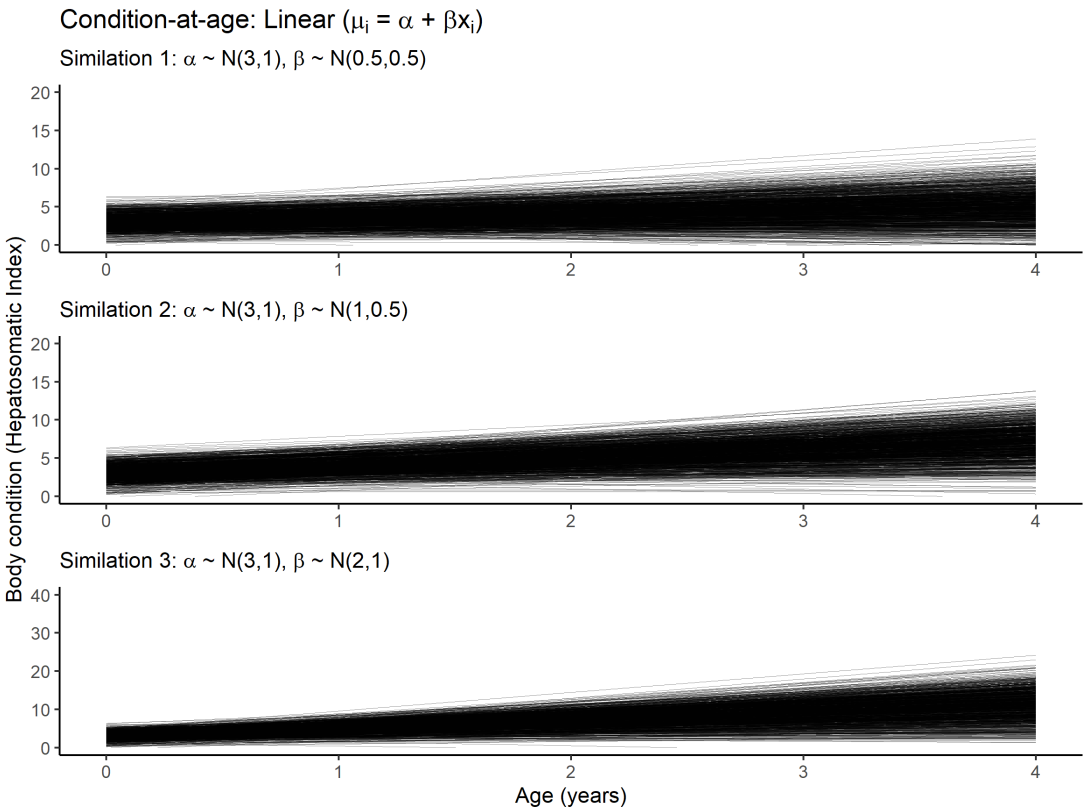


Figure A3.1.4: *Prior simulations for the linear condition-at-age model.*

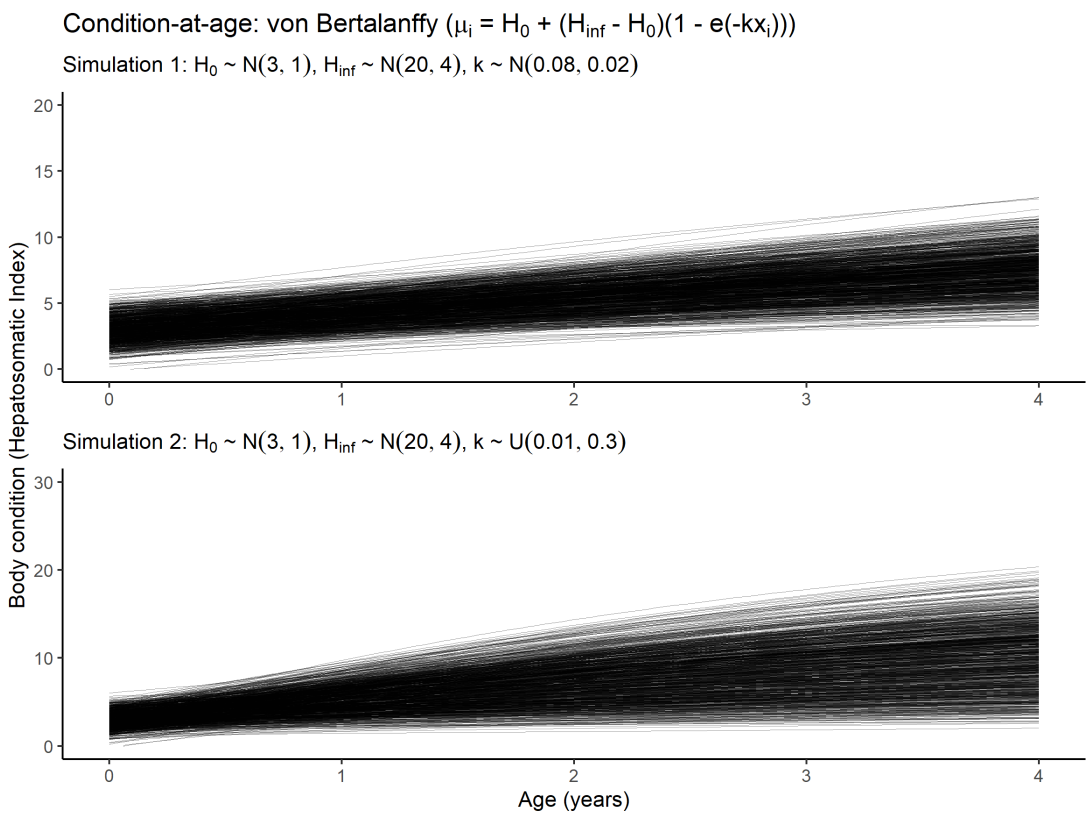


Figure A3.1.5: *Prior simulations for the von Bertalanffy condition-at-age model.*

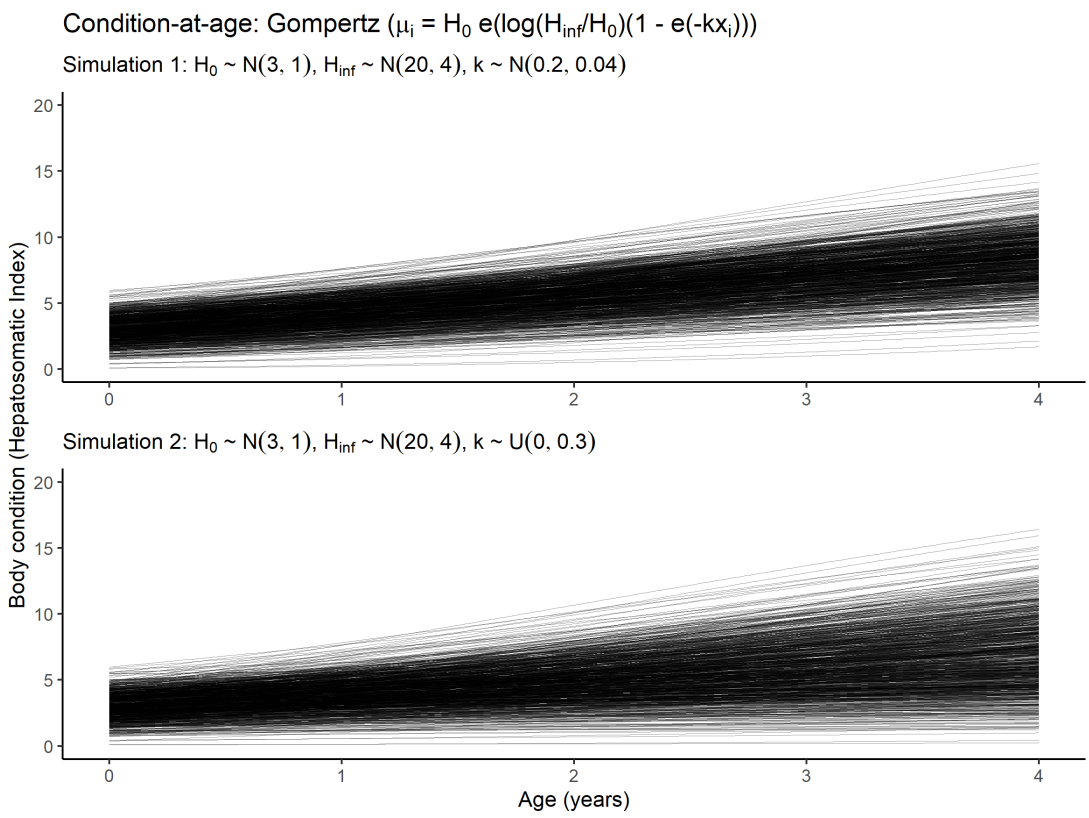


Figure A3.1.6: *Prior simulations for the Gompertz condition-at-age model.*

A3.2: Analysis of juvenile growth with older individuals

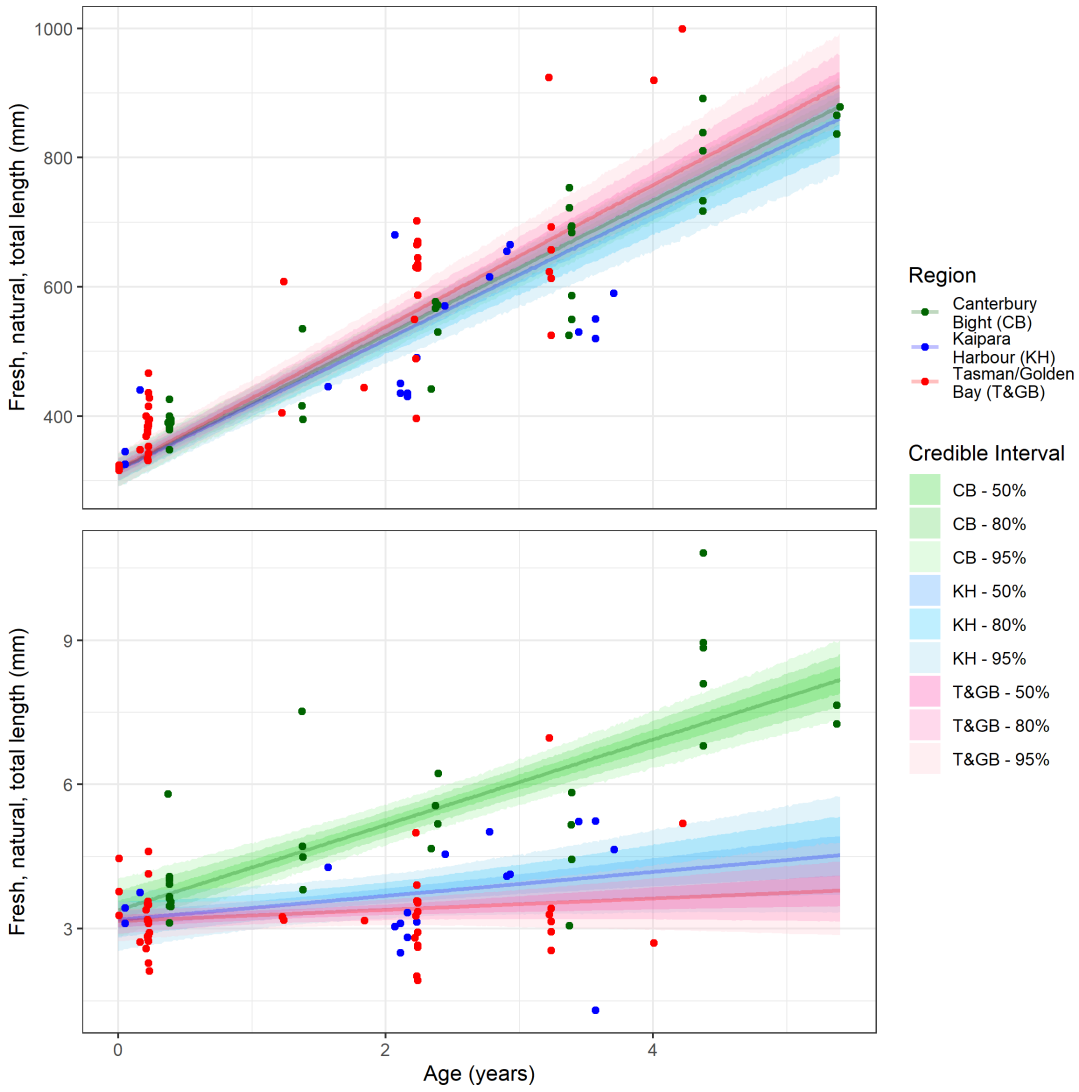


Figure A3.2.1: *The predicted fit of the linear model with varying slopes for location to length-at-age (above) and condition-at-age data (below) including individuals ≥ 4 years. Fresh, natural, total length is the total length measured from a fresh shark, in a straight line, with the tail in a natural position. Credible interval represents the 50%, 80%, and 95% credible intervals.*

Appendix 4 – Chapter 5: Movement & Habitat Use

A4.1: Mini-PAT tether specifications

Table A4.1.1: *Tether specifications for each shark. Tether length is the length between attachment points for the anchor and the tag.*

Shark ID	Anchor	Tether type	Tether length
Judy (20P1826)	Wildlife Computers small titanium anchor	Standard Wildlife Computers shrink-wrapped (Ancor marine grade heat shrink) stainless steel	~125mm
Sue (20P1813)	Wildlife Computers small titanium anchor	Standard Wildlife Computers shrink-wrapped (Ancor marine grade heat shrink) stainless steel	~125mm
Eleanor (20P1812)	Wildlife Computers small titanium anchor	Standard Wildlife Computers shrink-wrapped (Ancor marine grade heat shrink) stainless steel	~125mm
Shana (20P1821)	Wildlife Computers small titanium anchor	Standard Wildlife Computers shrink-wrapped (Ancor marine grade heat shrink) stainless steel	~125mm
Ruth (20P1824)	Wildlife Computers small titanium anchor	Standard Wildlife Computers shrink-wrapped (Ancor marine grade heat shrink) stainless steel	~125mm
Tindale-Marine (20P1825)	Wildlife Computers small titanium anchor	Standard Wildlife Computers shrink-wrapped (Ancor marine grade heat shrink) stainless steel	~125mm
Sharky (21P0890)	Wildlife Computers small titanium anchor	Standard Wildlife Computers shrink-wrapped (Ancor marine grade heat shrink) stainless steel	~125mm
Lorraine (21P0893)	Wildlife Computers small titanium anchor	Standard Wildlife Computers shrink-wrapped (Ancor marine grade heat shrink) stainless steel	~125mm
Sloan (21P0900)	Wildlife Computers small titanium anchor	Standard Wildlife Computers shrink-wrapped (Ancor marine grade heat shrink) stainless steel	~125mm
Alison (21P0881)	Wildlife Computers small titanium anchor	400lb (2.05mm) clear Momoi's Hi-catch nylon mono-line X-Hard monofilament with shrink wrapped (Ancor marine grade heat shrink) bronze crimps	160mm
Natalie (21P0911)	Wildlife Computers small titanium anchor	Standard Wildlife Computers shrink-wrapped (Ancor marine grade heat shrink) stainless steel	~125mm
Zoe (21P0882)	Wildlife Computers small titanium anchor	400lb (2.05mm) clear Momoi's Hi-catch nylon mono-line X-Hard monofilament with shrink wrapped (Ancor marine grade heat shrink) bronze crimps	161mm
Emily (21P0888)	Wildlife Computers small titanium anchor	400lb (2.05mm) clear Momoi's Hi-catch nylon mono-line X-Hard monofilament with shrink wrapped (Ancor marine grade heat shrink) bronze crimps	162mm
Dianne (21P0884)	Wildlife Computers small titanium anchor	400lb (2.05mm) clear Momoi's Hi-catch nylon mono-line X-Hard monofilament with shrink wrapped (Ancor marine grade heat shrink) bronze crimps	175mm
Michelle (21P0899)	Wildlife Computers small titanium anchor	Standard Wildlife Computers shrink-wrapped (Ancor marine grade heat shrink) stainless steel	~125mm
Karla (21P0578)	Wildlife Computers small titanium anchor	Standard Wildlife Computers shrink-wrapped (Ancor marine grade heat shrink) stainless steel	~125mm
Paula (21P0892)	Wildlife Computers small titanium anchor	400lb (2.05mm) clear Momoi's Hi-catch nylon mono-line X-Hard monofilament with shrink wrapped (Ancor marine grade heat shrink) bronze crimps	180mm
Louie (21P0920)	Wildlife Computers small titanium anchor	Standard Wildlife Computers shrink-wrapped (Ancor marine grade heat shrink) stainless steel	127mm

Shark ID	Anchor	Tether type	Tether length
Anna (21P0912)	Wildlife Computers small titanium anchor	Standard Wildlife Computers shrink-wrapped (Ancor marine grade heat shrink) stainless steel	131mm
Kelly (21P0887)	Wildlife Computers small titanium anchor	400lb (2.05mm) clear Momoi's Hi-catch nylon mono-line X-Hard monofilament with shrink wrapped (Ancor marine grade heat shrink) bronze crimps	175mm
Heidi (21P0919)	Wildlife Computers small titanium anchor	Standard Wildlife Computers shrink-wrapped (Ancor marine grade heat shrink) stainless steel	125mm
Sarah (21P0883)	Wildlife Computers small titanium anchor	400lb (2.05mm) clear Momoi's Hi-catch nylon mono-line X-Hard monofilament with shrink wrapped (Ancor marine grade heat shrink) bronze crimps	165mm
Marie (21P0879)	Wildlife Computers small titanium anchor	400lb (2.05mm) clear Momoi's Hi-catch nylon mono-line X-Hard monofilament with shrink wrapped (Ancor marine grade heat shrink) bronze crimps	170mm
Caitlyn (21P0896)	Wildlife Computers small titanium anchor	Standard Wildlife Computers shrink-wrapped (Ancor marine grade heat shrink) stainless steel	125mm
Etoile (21P0880)	Wildlife Computers small titanium anchor	400lb (2.05mm) clear Momoi's Hi-catch nylon mono-line X-Hard monofilament with shrink wrapped (Ancor marine grade heat shrink) bronze crimps	156mm

A4.2: Animal release condition stage definitions

Table A4.2.1: *Definitions of animal condition recorded at release.*

Score	Definition
1	Good. No revival time required; rapid swimming upon release, usually with a vigorous splash
2	Fair. No revival time required; slow but strong swimming upon release
3	Poor. Short revival time (up to 30 s) required; once revived, slow and sometimes atypical swimming upon release
4	Very poor. Long revival time (>30 s) required; once revived, limited or no swimming observed upon release, but respiration observed
5	Moribund or dead. Dead upon removal from gear or moribund and unable to revive even after a long submergence time

A4.3: Definitions of regions for examining connectivity in mark-recapture data

Table A4.3.1: *The name, abbreviation, and identifying number of regions used to assess connectivity in mark-recapture data.*

Abbreviation	Name	Grid ID
CRO	Cape Reinga offshore	1
GEB	Great Exhibition Bay Inshore	2
NEI	Northland East Inshore	3
OHG	Outer Hauraki Gulf	4
IHG	Inner Hauraki Gulf	5
CoI	Coromandel Inshore	6
BoP	Bay of Plenty Inshore	7
TaH	Tauranga Harbour	8

Abbreviation	Name	Grid ID
WhI	Whakatane Inshore	9
CKI	Cape Kidnappers Inshore	10
TBI	Tologa Bay Inshore	11
HBI	Hawkes Bay Inshore	12
WaI	Wairarapa Inshore	13
MaI	Masterton Inshore	14
CS	Cook Strait	15
KaiI	Kaikoura Inshore	16
KaiO	Kaikoura Offshore	17
PegB	Pegasus Bay	18
CanB	Canterbury Bight	19
OtI	Otago Inshore	20
MilI	Milton Inshore	21
FS	Foveaux Strait	22
StEI	Stewart Island East Inshore	23
SnS	Snares Islands South Inshore	24
SnN	Snares Islands North Inshore	25
Pyr	Puysegur Bank	26
FiS	Fiordland South Inshore	27
FiN	Fiordland North Inshore	28
JBI	Jackson Bay Inshore	29
GmI	Greymouth Inshore	30
WpI	Westport Inshore	31
Man	Mangarakau Inshore	32
STB	South Taranaki Bight	33
GTB	Golden Tasman Bay	34
KaC	Kapiti Coast	35
CaE	Cape Egmont	36
NTB	North Taranaki Bight Inshore	37
WWC	Waikato West Inshore	38
MaH	Manukau Harbour	39
KaH	Kaipara Harbour	40
AWC	Auckland West Coast Inshore	41
NWC	Northland West Coast Inshore	42
CRTK	Cape Reinga Inshore	43
TKO	Three Kings Offshore	44
NWO	North Island West Coast Offshore	45
NTS	North Taranaki Bight Shelf Break	46
CI1	Chatham Island1	47

Abbreviation	Name	Grid ID
Km1	Kermadecs1	48
NNE	North Island Northeast Offshore	49
NSE	North Island Southeast Offshore	50
CR	Chatham Rise	51
SSE	South Island Southeast Offshore	52
AntI	Antipodes Island	53
BouI	Bounty Islands	54
SSW	South Island Southwest Offshore	55
SNW	South Island Northwest Offshore	56
OtO	Otago Offshore	57
MilO	Milton Offshore	58
StEO	Stewart Island East offshore	59
StSO	Stewart Island South offshore	60
Akl	Auckland Islands	61
Cam	Campbell Island	62
Tas	Tasmania	63
BS	Bass Strait	64
SA	South Australia	65
WA	Western Australia	66

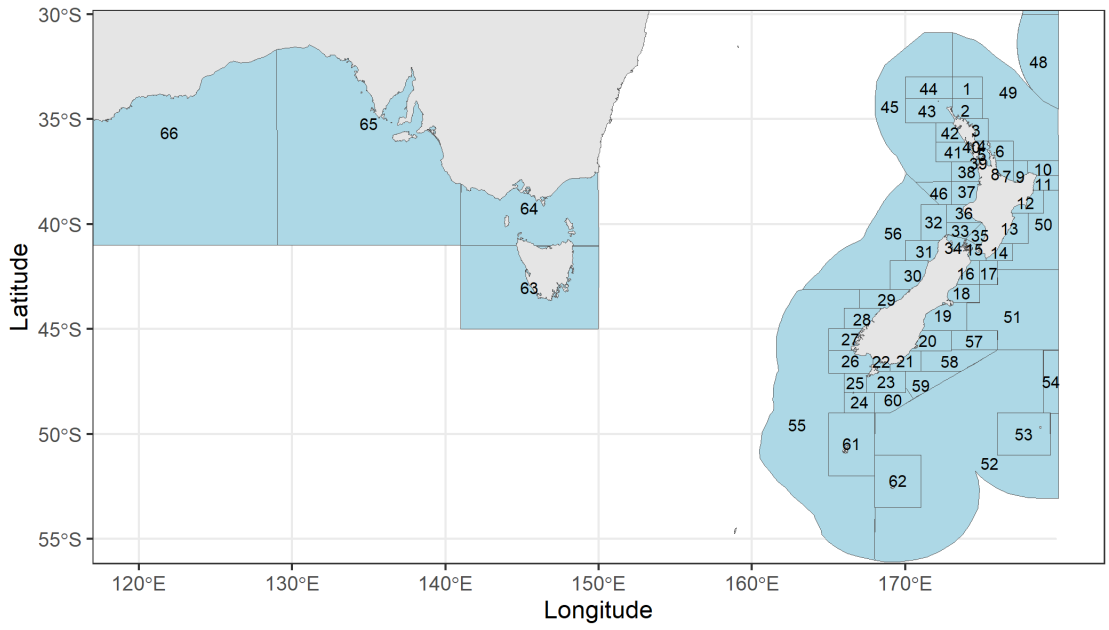


Figure A4.3.1: *The spatial definition of regions used to assess connectivity in mark-recapture data. Numbers are the grid identification numbers, which are defined in Table A4.3.1.*

A4.4: Maximum likelihood tracks of satellite tagged school sharks

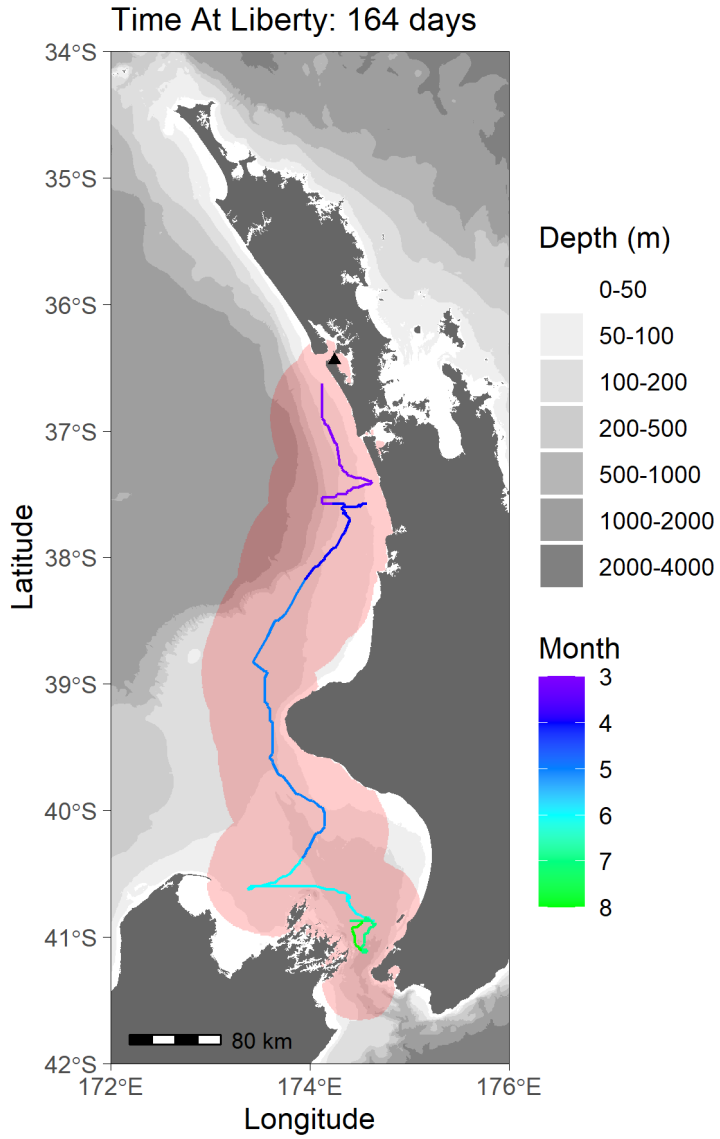


Figure A4.4.1: *The maximum likelihood track of Tindale-Marine (20P1825). The black triangle is the release location. Month represents where the shark was at a given time. The red shaded area represents the 95% confidence interval of the track.*

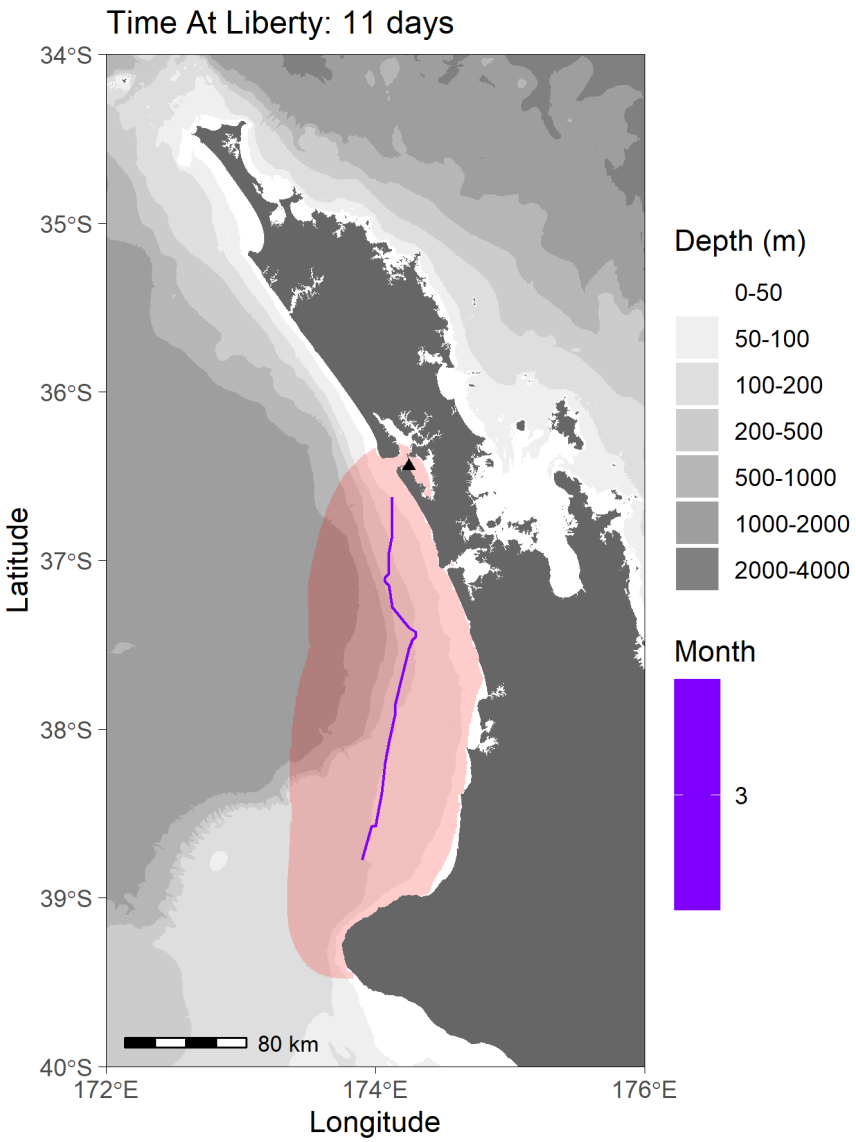


Figure A4.4.2: *The maximum likelihood track of Judy (20P1826). The black triangle is the release location. Month represents where the shark was at a given time. The red shaded area represents the 95% confidence interval of the track.*

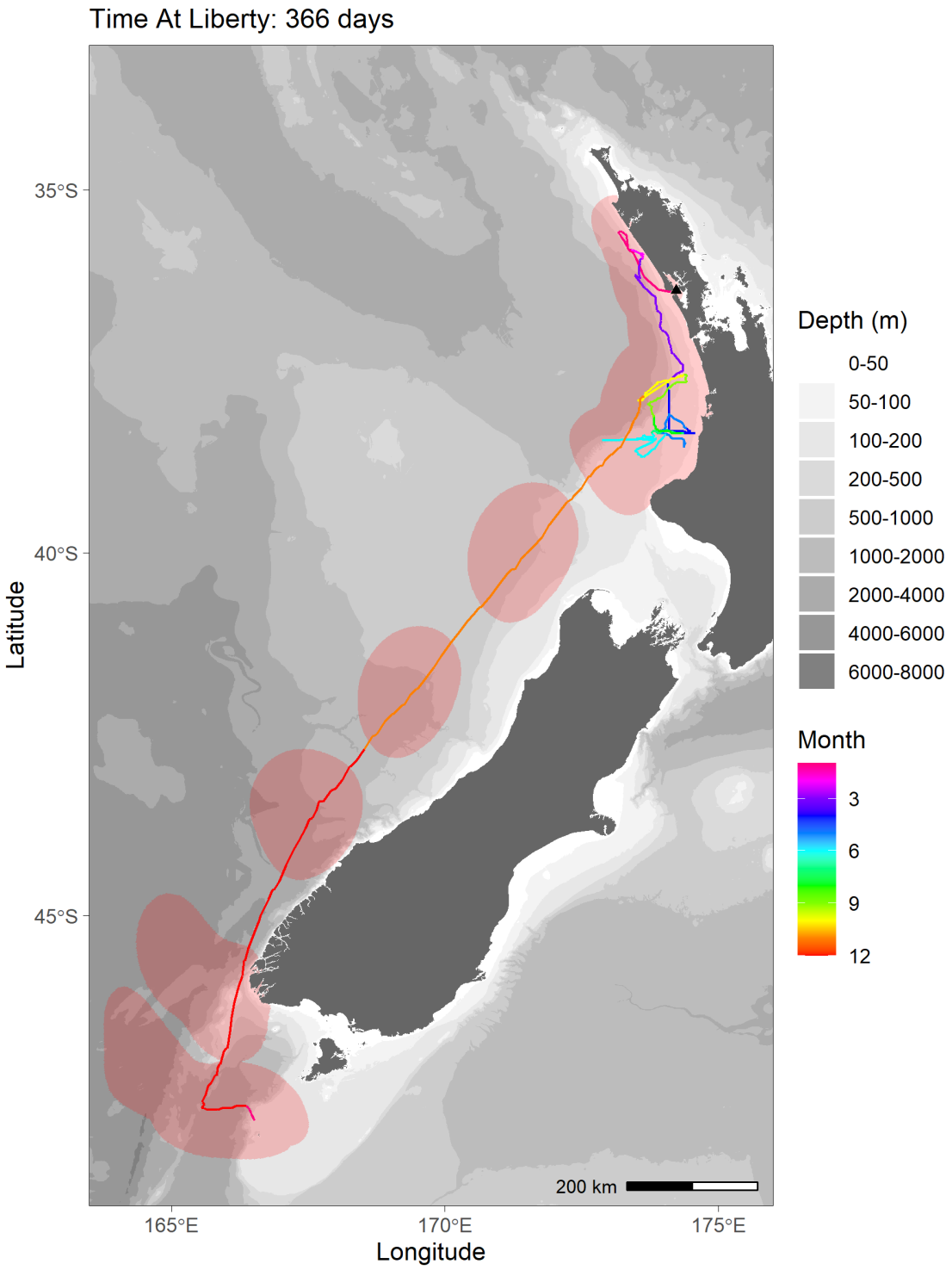


Figure A4.4.3: *The maximum likelihood track of Zoe (21P0882). The black triangle is the release location. Month represents where the shark was at a given time. The red shaded area represents the 95% confidence interval of the track.*

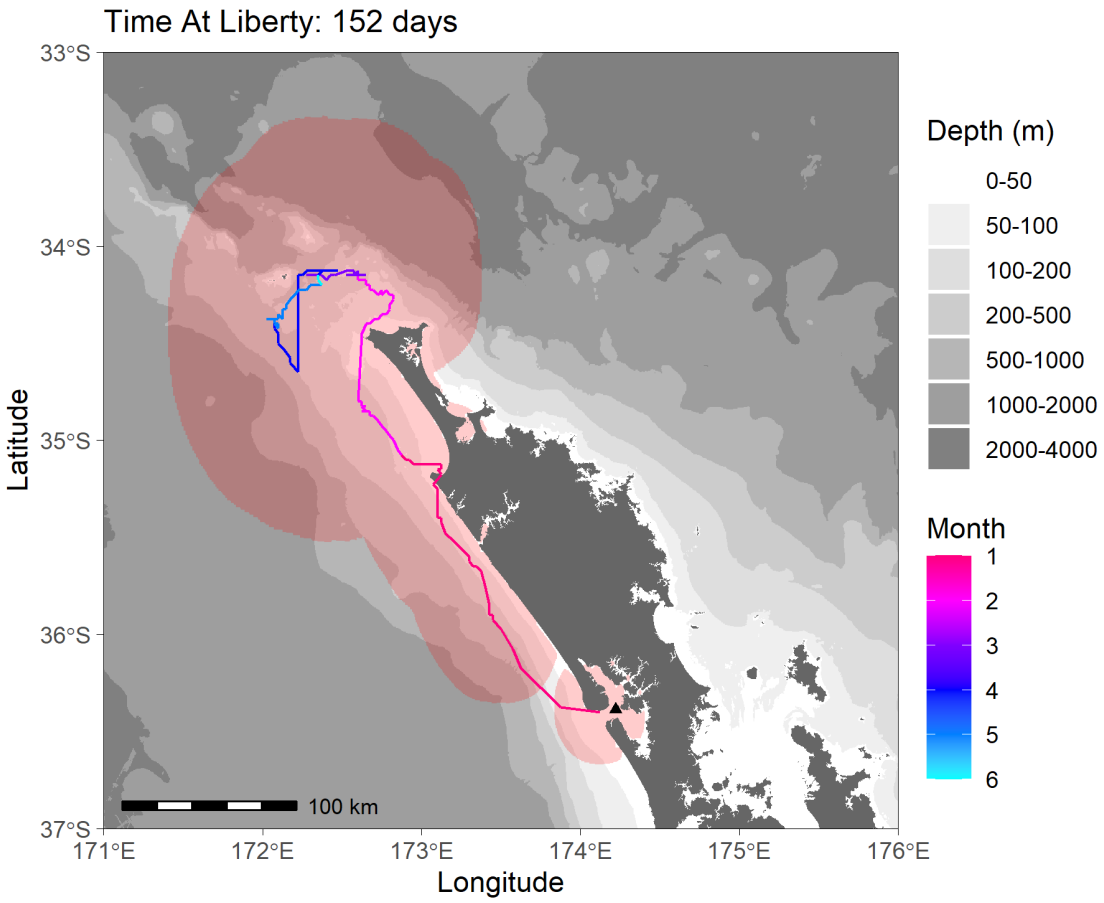


Figure A4.4.4: *The maximum likelihood track of Sharky (21P0890). The black triangle is the release location. Month represents where the shark was at a given time. The red shaded area represents the 95% confidence interval of the track.*

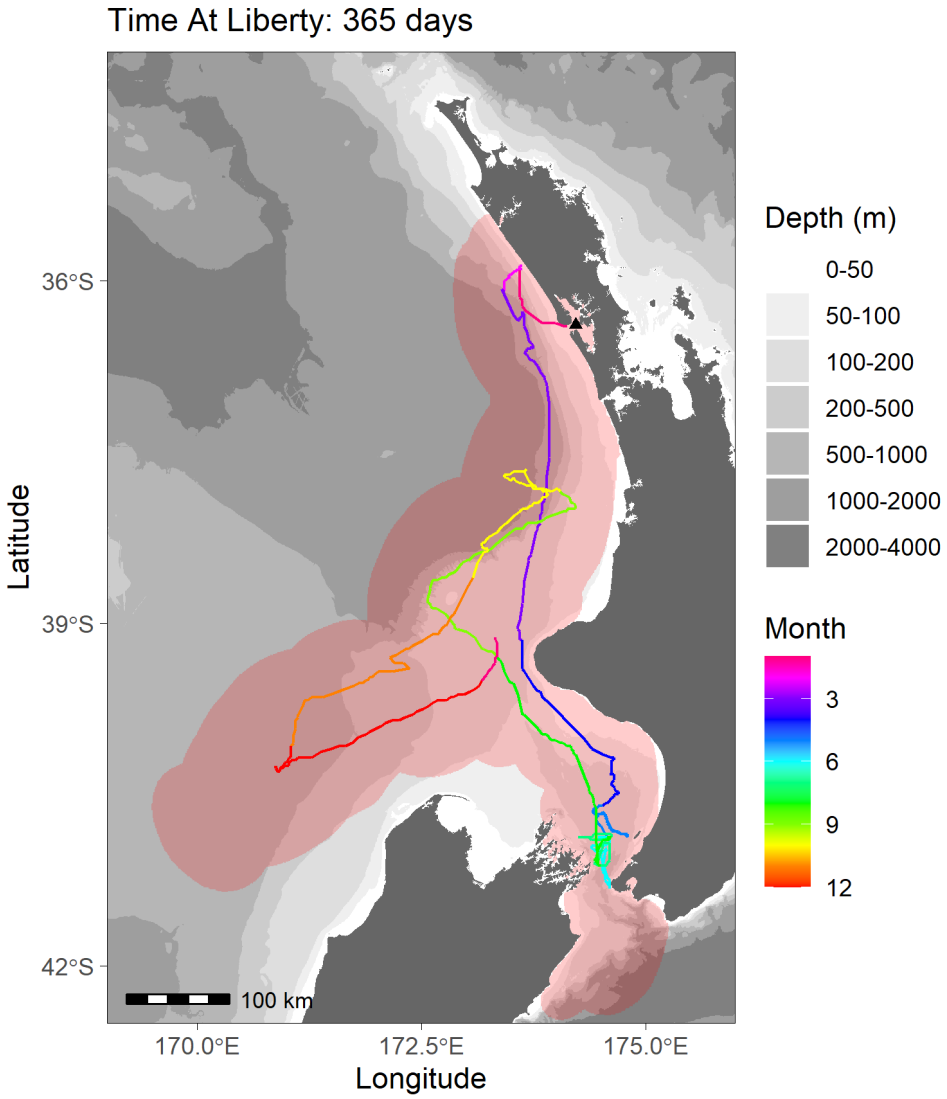


Figure A4.4.5: *The maximum likelihood track of Paula (21P0892). The black triangle is the release location. Month represents where the shark was at a given time. The red shaded area represents the 95% confidence interval of the track.*

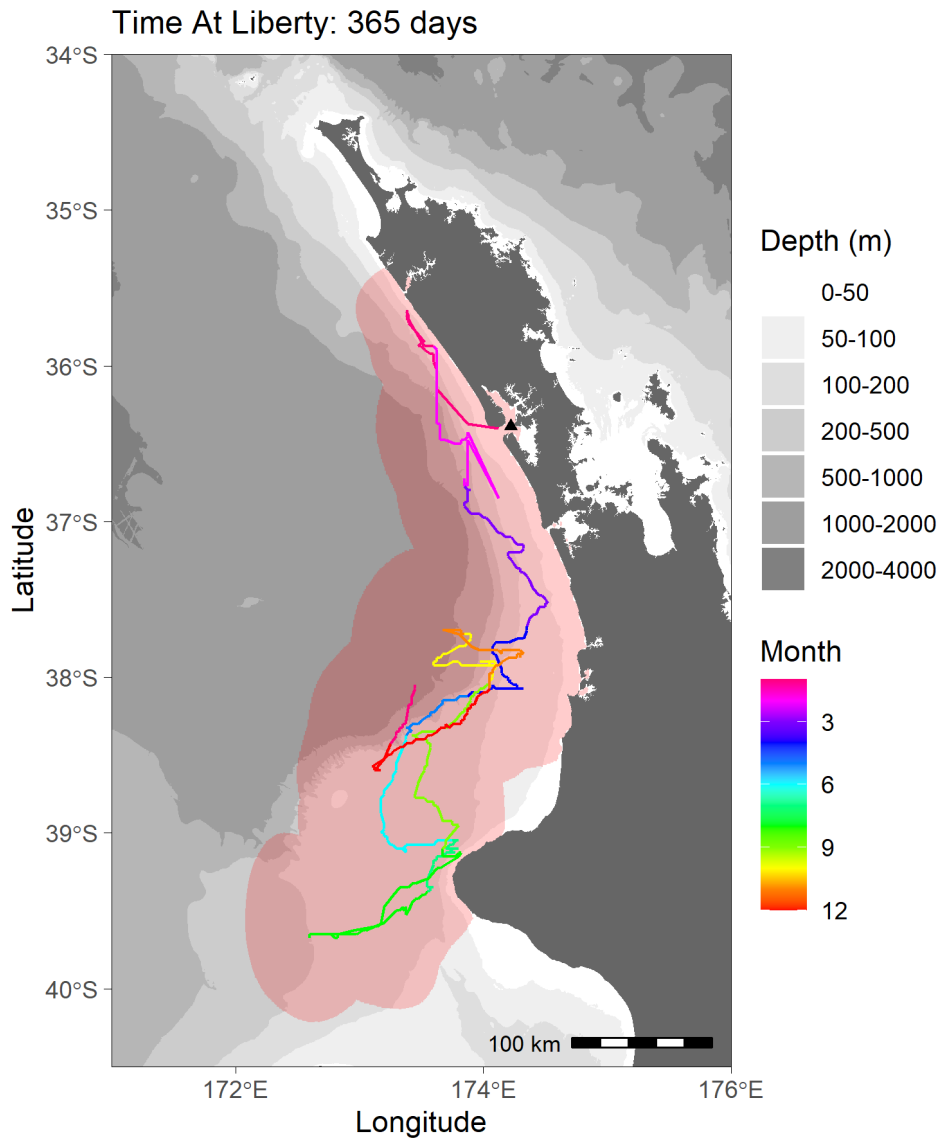


Figure A4.4.6: *The maximum likelihood track of Michelle (21P0899). The black triangle is the release location. Month represents where the shark was at a given time. The red shaded area represents the 95% confidence interval of the track.*

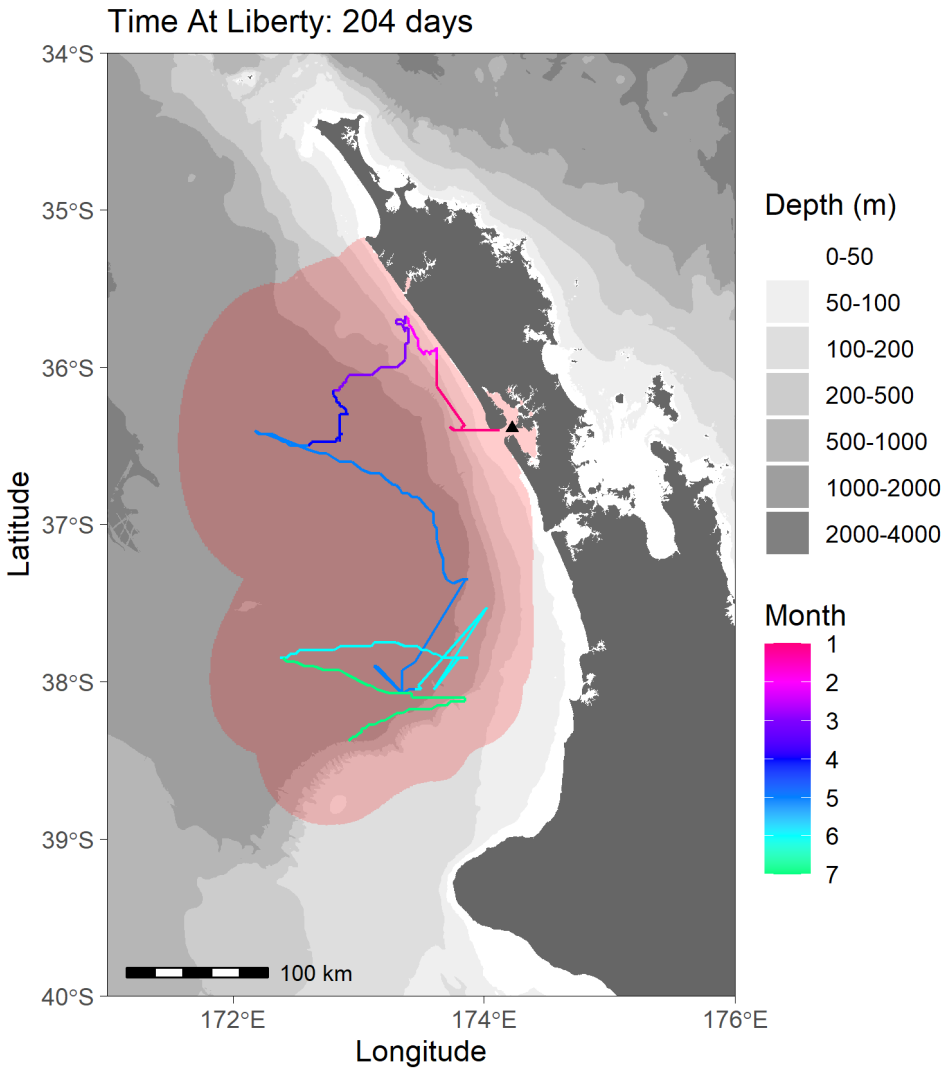


Figure A4.4.7: *The maximum likelihood track of Louie (21P0920). The black triangle is the release location. Month represents where the shark was at a given time. The red shaded area represents the 95% confidence interval of the track.*

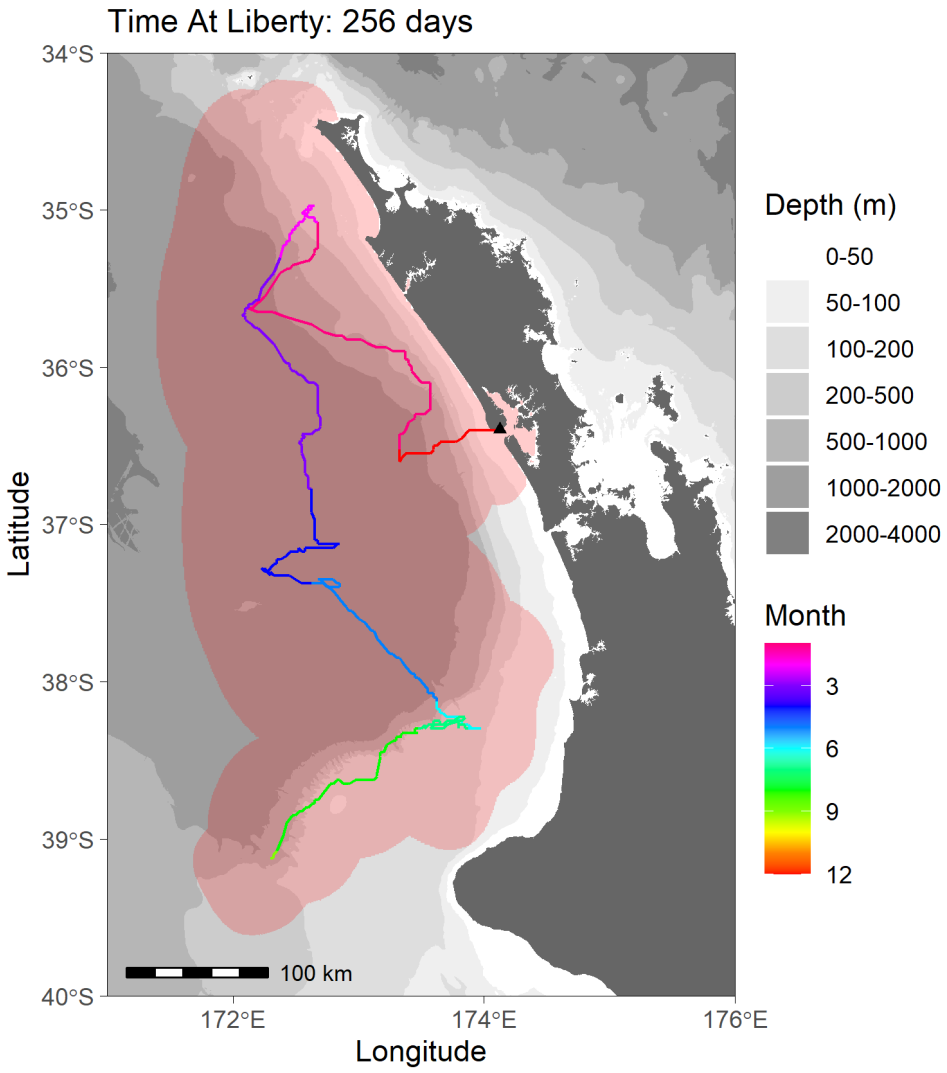


Figure A4.4.8: *The maximum likelihood track of Marie (21P0879). The black triangle is the release location. Month represents where the shark was at a given time. The red shaded area represents the 95% confidence interval of the track.*

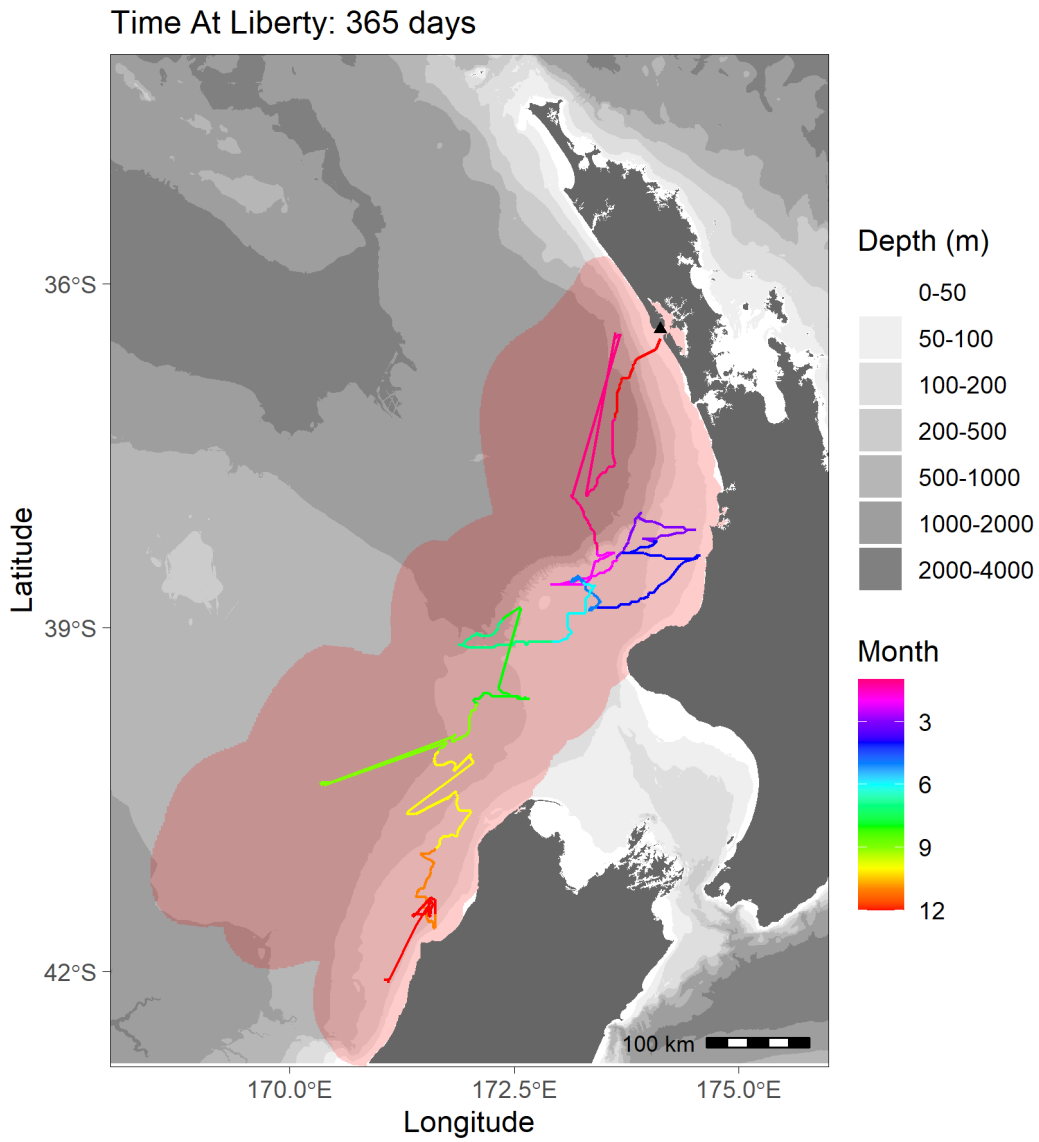


Figure A4.4.9: *The maximum likelihood track of Etoile (21P0880). The black triangle is the release location. Month represents where the shark was at a given time. The red shaded area represents the 95% confidence interval of the track.*

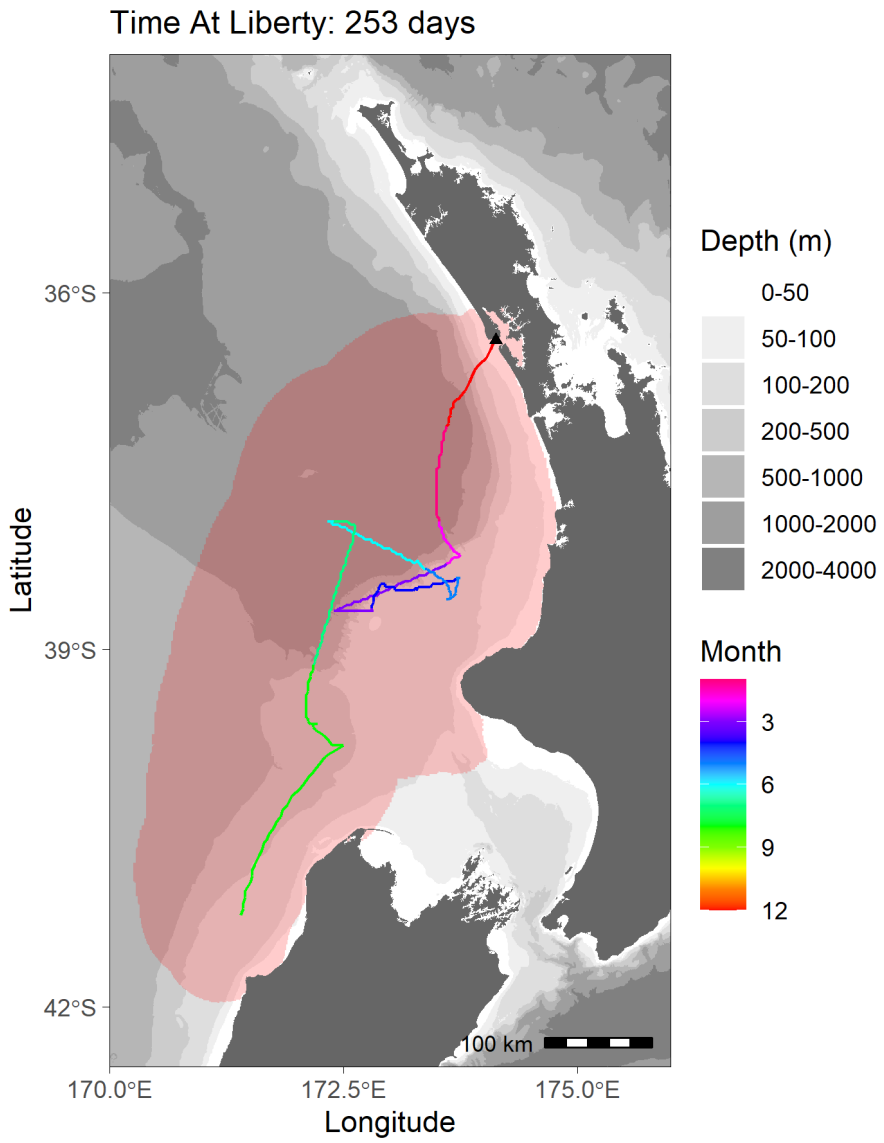


Figure A4.4.10: *The maximum likelihood track of Caitlyn (21P0896). The black triangle is the release location. Month represents where the shark was at a given time. The red shaded area represents the 95% confidence interval of the track.*

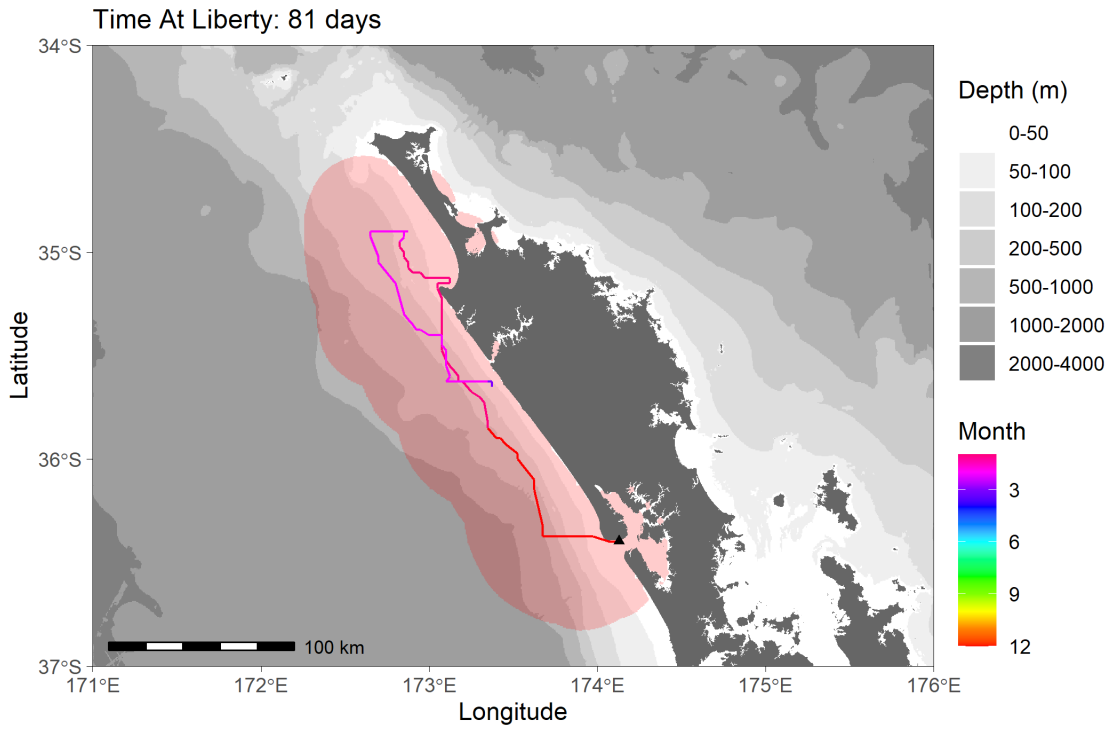


Figure A4.4.11: *The maximum likelihood track of Anna (21P0912). The black triangle is the release location. Month represents where the shark was at a given time. The red shaded area represents the 95% confidence interval of the track.*

A4.5: Modelled residency distributions of satellite tagged school sharks

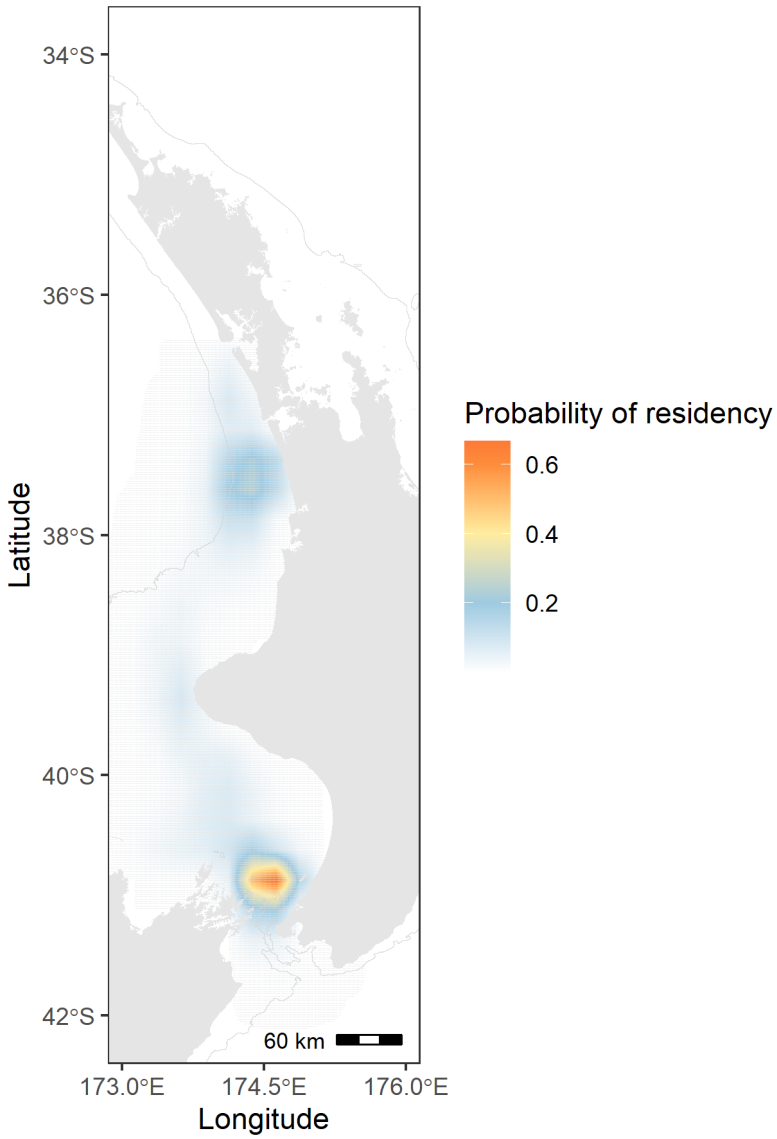


Figure A4.5.1: *The modelled residency distribution of Tindale-Marine (20P1825). Areas with a probability of modelled residency ≥ 0.2 are deemed temporary residency areas.*

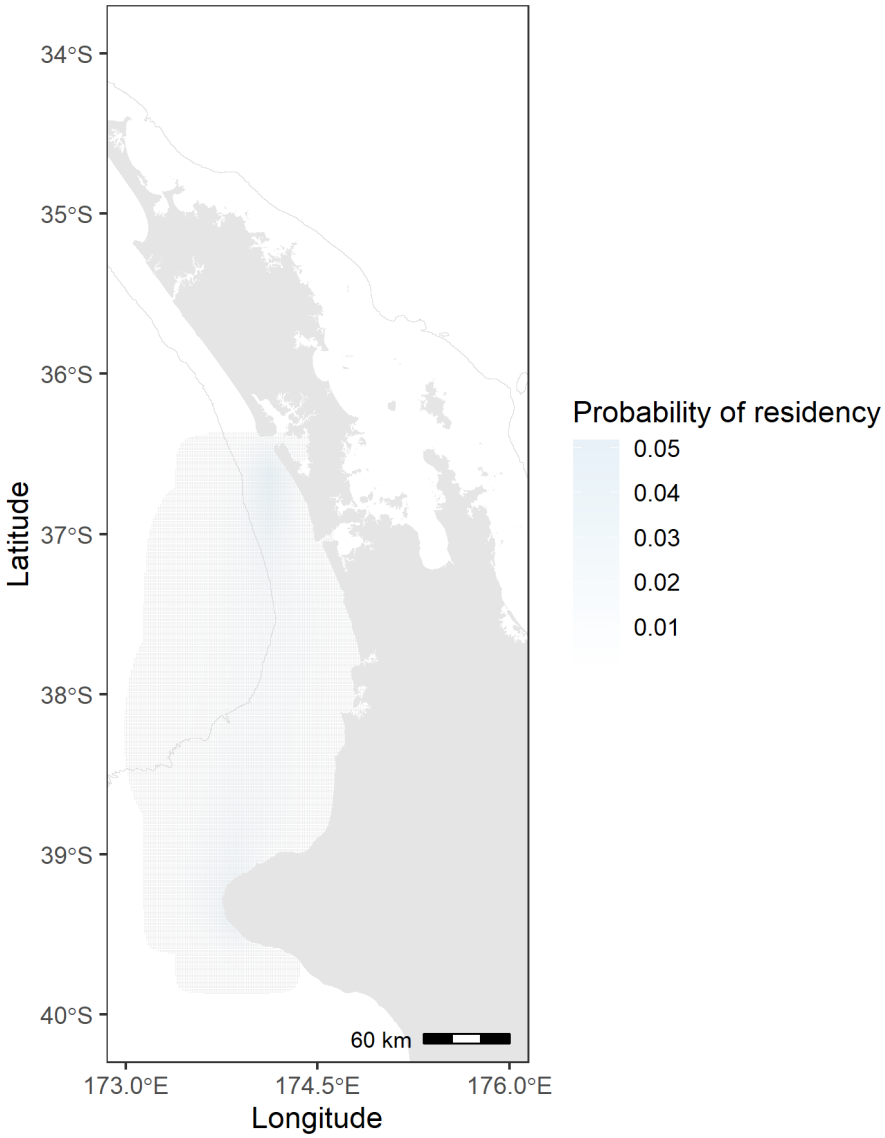


Figure A4.5.2: *The modelled residency distribution of Judy (20P1826). Areas with a probability of modelled residency ≥ 0.2 are deemed temporary residency areas.*

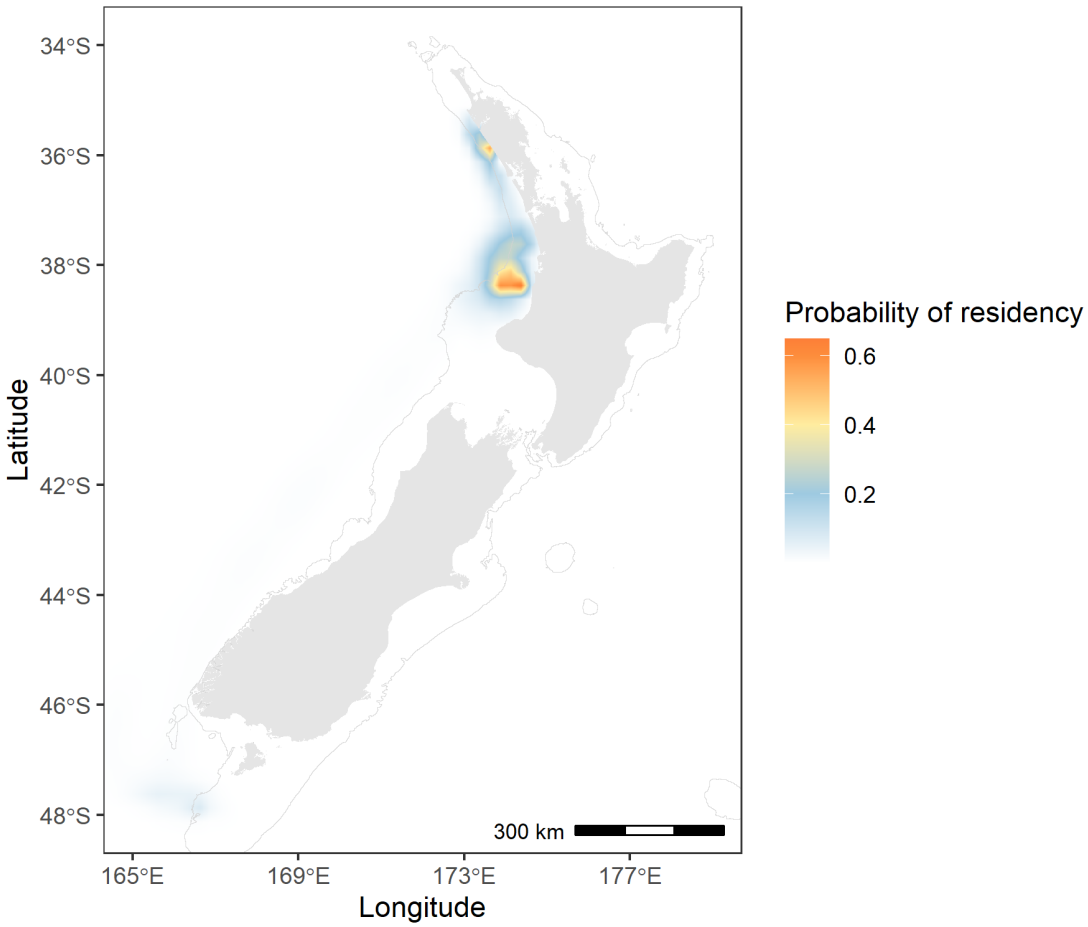


Figure A4.5.3: *The modelled residency distribution of Zoe (21P0882). Areas with a probability of modelled residency ≥ 0.2 are deemed temporary residency areas.*

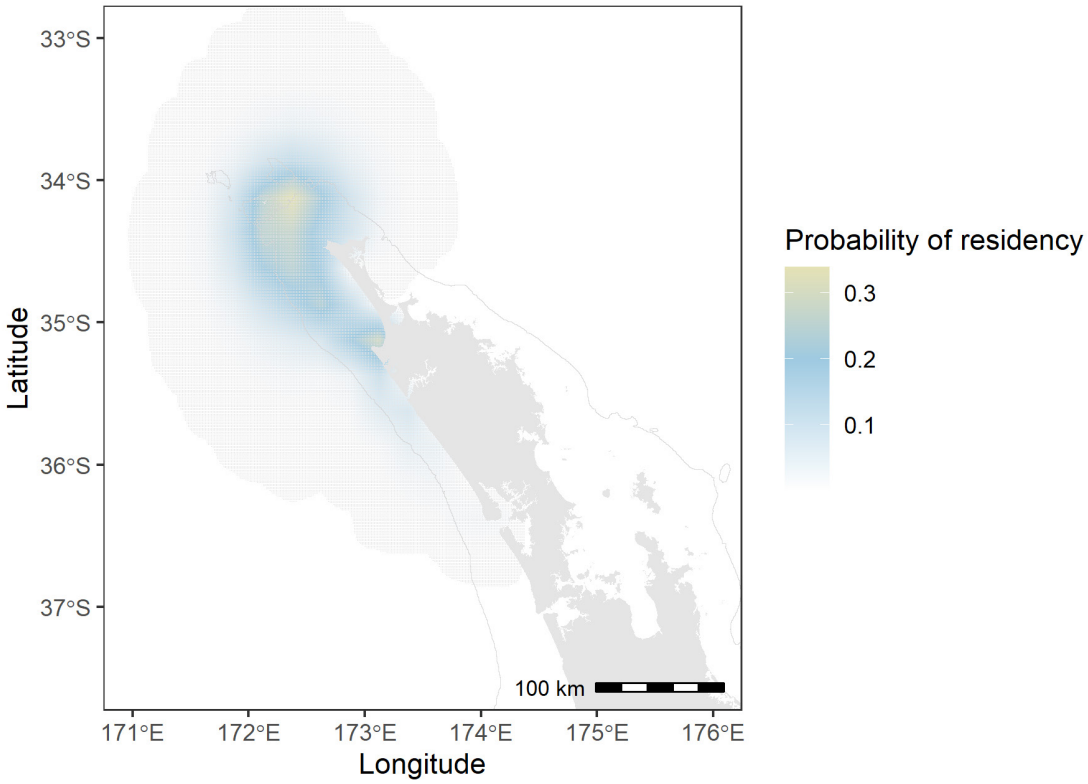


Figure A4.5.4: *The modelled residency distribution of Sharky (21P0890). Areas with a probability of modelled residency ≥ 0.2 are deemed temporary residency areas.*

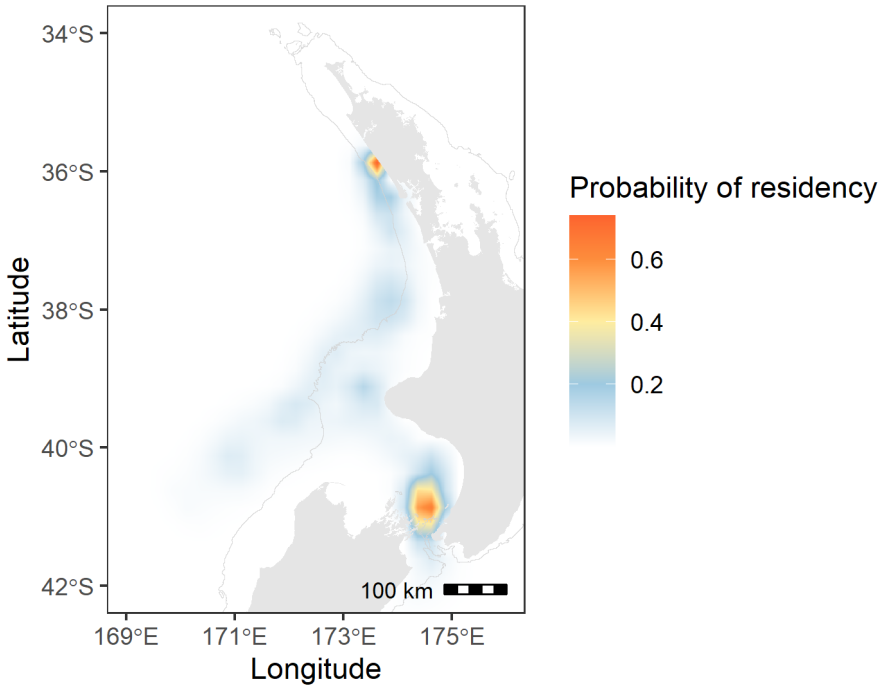


Figure A4.5.5: *The modelled residency distribution of Paula (21P0892). Areas with a probability of modelled residency ≥ 0.2 are deemed temporary residency areas.*

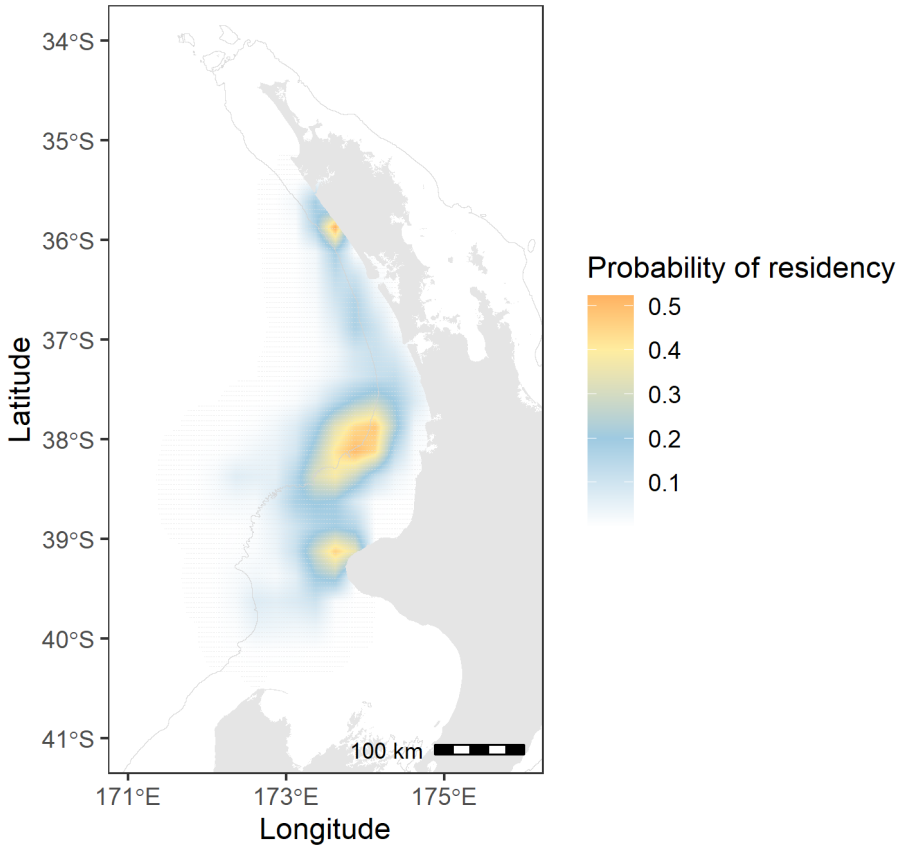


Figure A4.5.6: *The modelled residency distribution of Michelle (21P0899). Areas with a probability of modelled residency ≥ 0.2 are deemed temporary residency areas.*

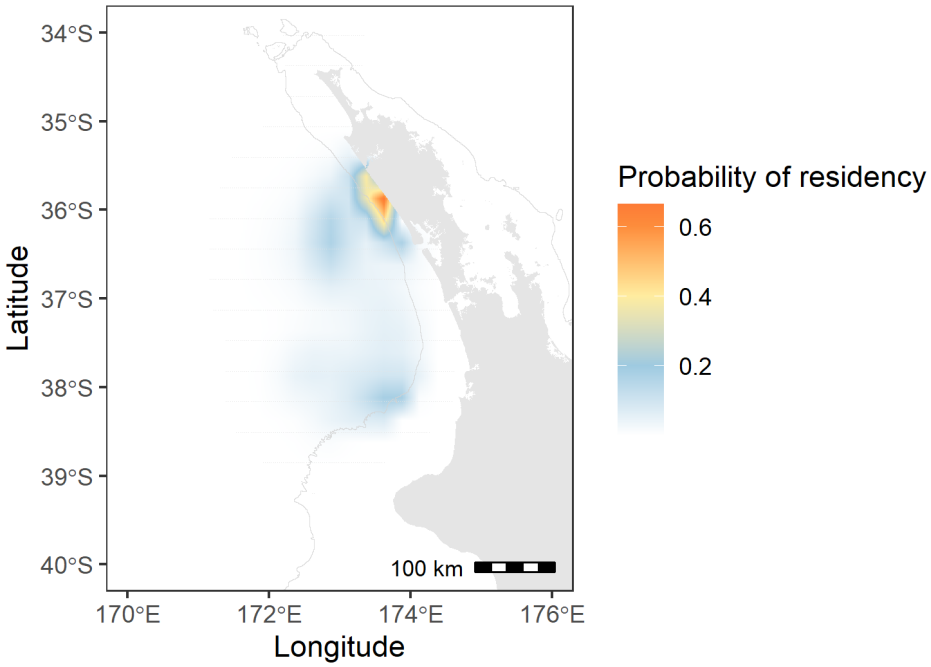


Figure A4.5.7: *The modelled residency distribution of Louie (21P0920). Areas with a probability of modelled residency ≥ 0.2 are deemed temporary residency areas.*

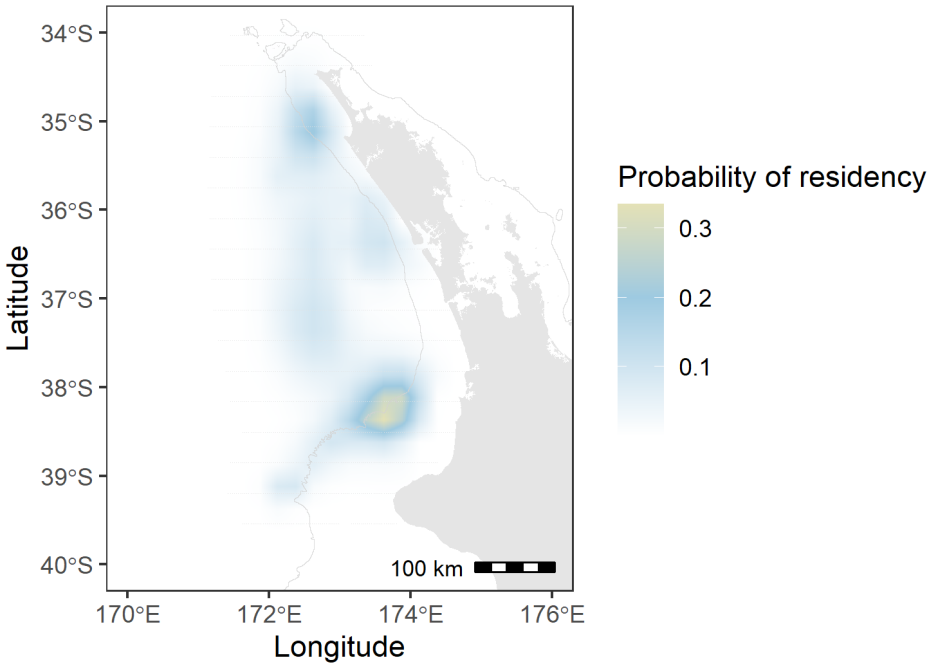


Figure A4.5.8: *The modelled residency distribution of Marie (21P0879). Areas with a probability of modelled residency ≥ 0.2 are deemed temporary residency areas.*

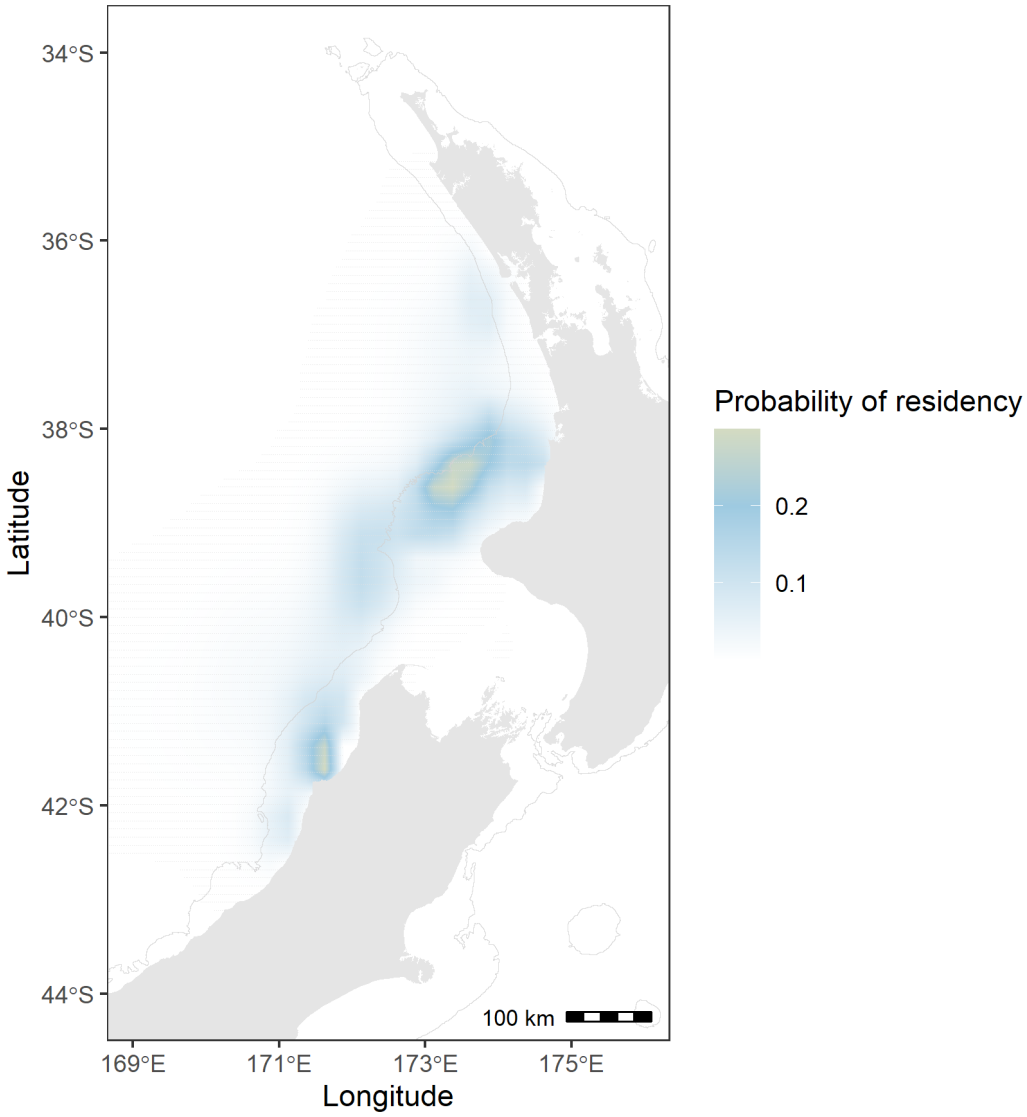


Figure A4.5.9: *The modelled residency distribution of Etoile (21P0880). Areas with a probability of modelled residency ≥ 0.2 are deemed temporary residency areas.*

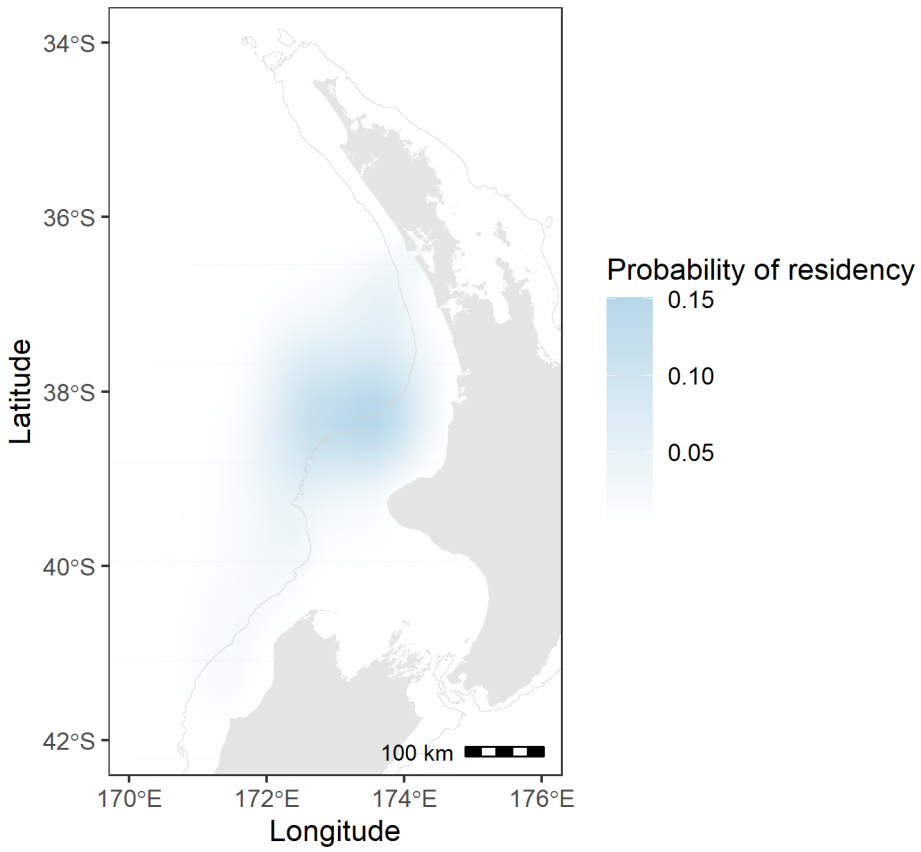


Figure A4.5.10: *The modelled residency distribution of Caitlyn (21P0896). Areas with a probability of modelled residency ≥ 0.2 are deemed temporary residency areas.*

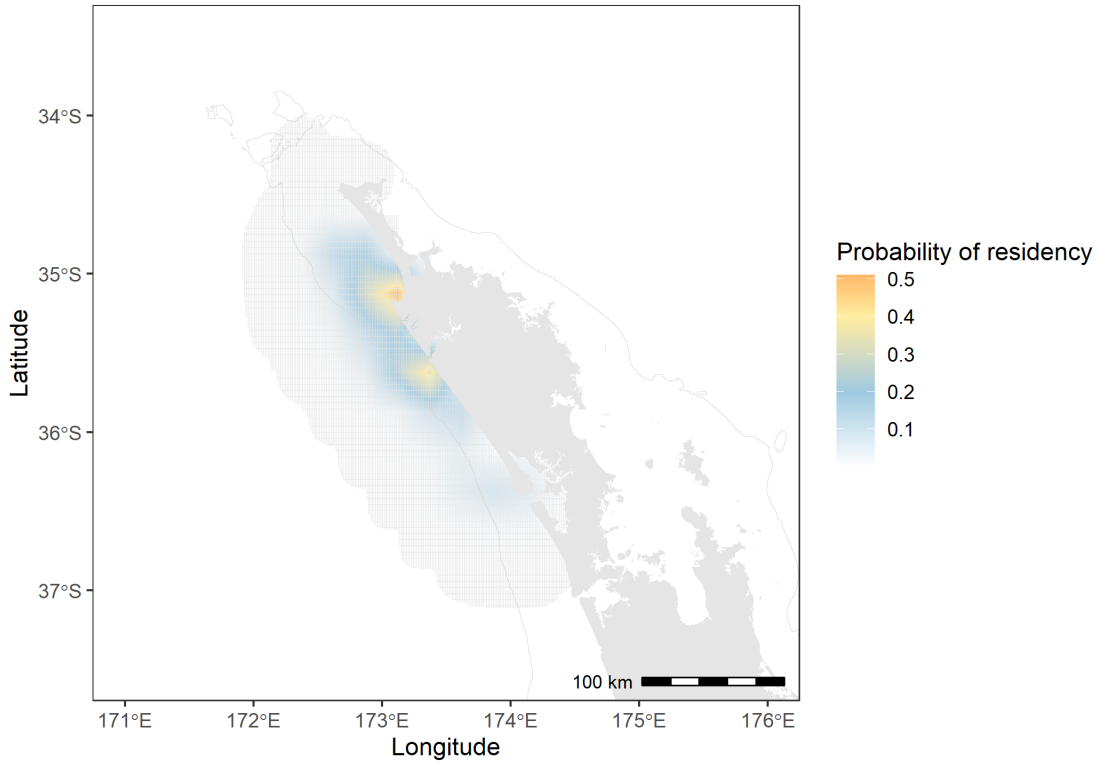


Figure A4.5.11: *The modelled residency distribution of Anna (21P0912). Areas with a probability of modelled residency ≥ 0.2 are deemed temporary residency areas.*

A4.6: Depth and temperature time series of satellite tagged school sharks

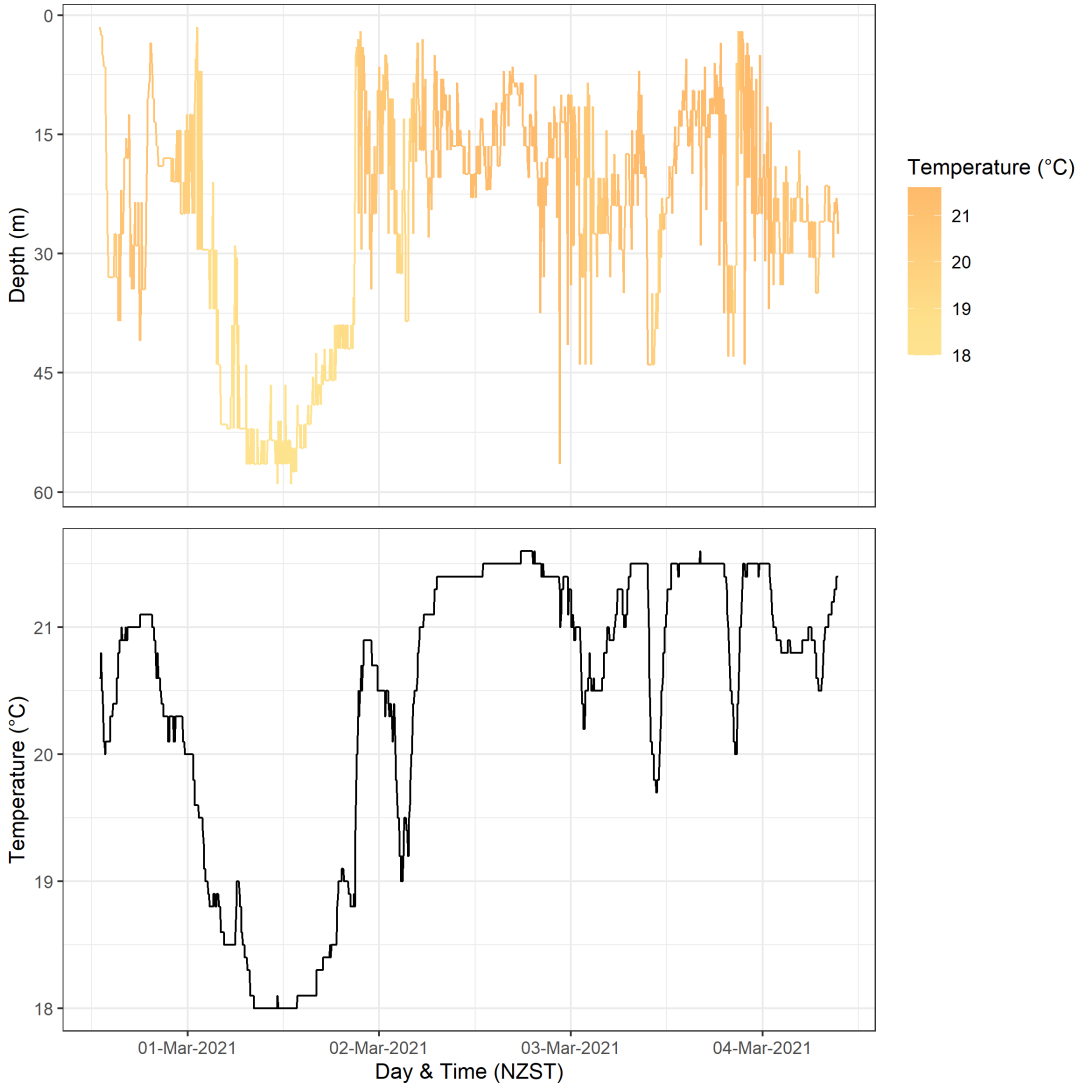


Figure A4.6.1: *Time series of depths and temperatures used by Sue (20P1813).*

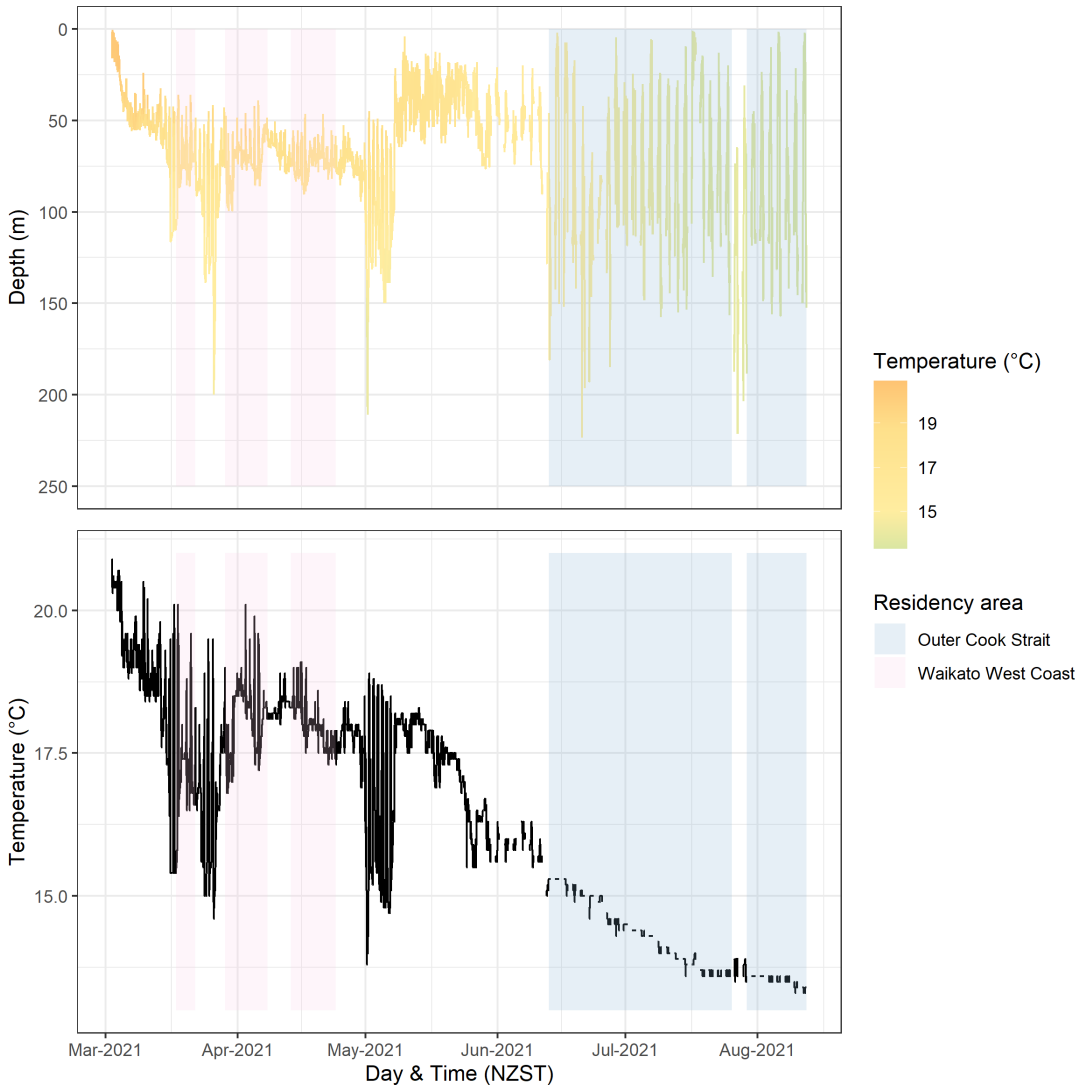


Figure A4.6.2: *Time series of depths and temperatures used by Tindale-Marine (20P1825).*

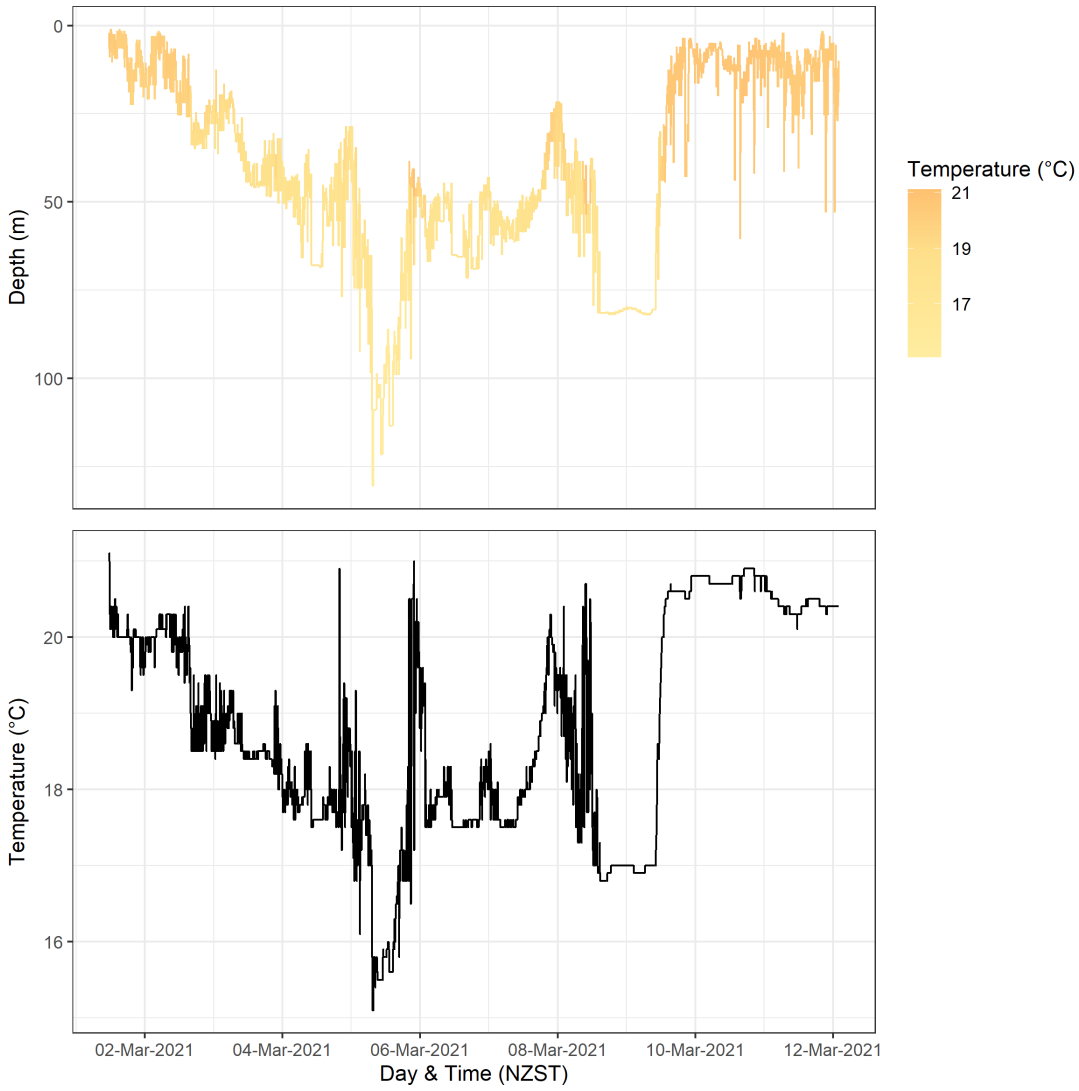


Figure A4.6.3: *Time series of depths and temperatures used by Judy (20P1826).*

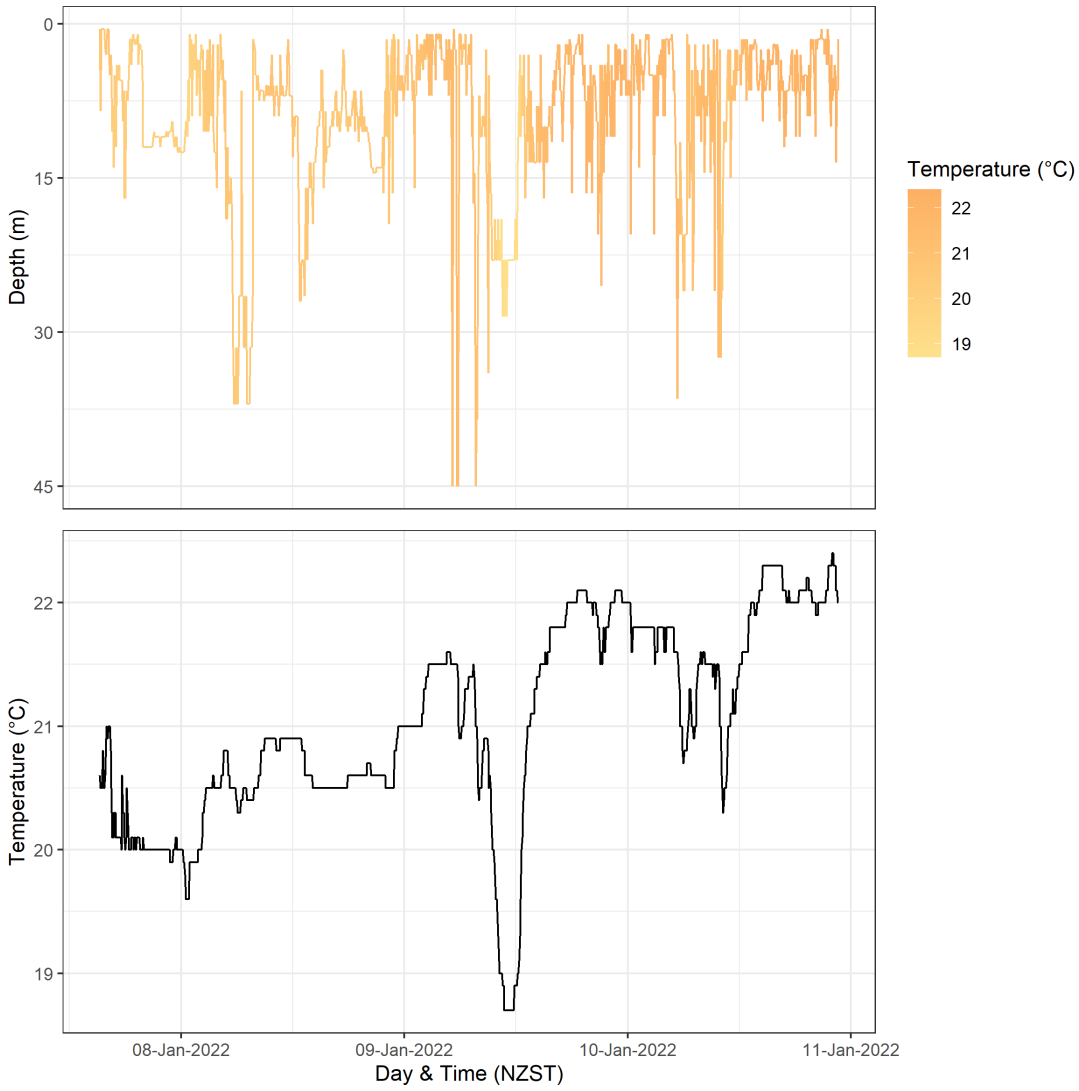


Figure A4.6.4: *Time series of depths and temperatures used by Karla (21P0578).*

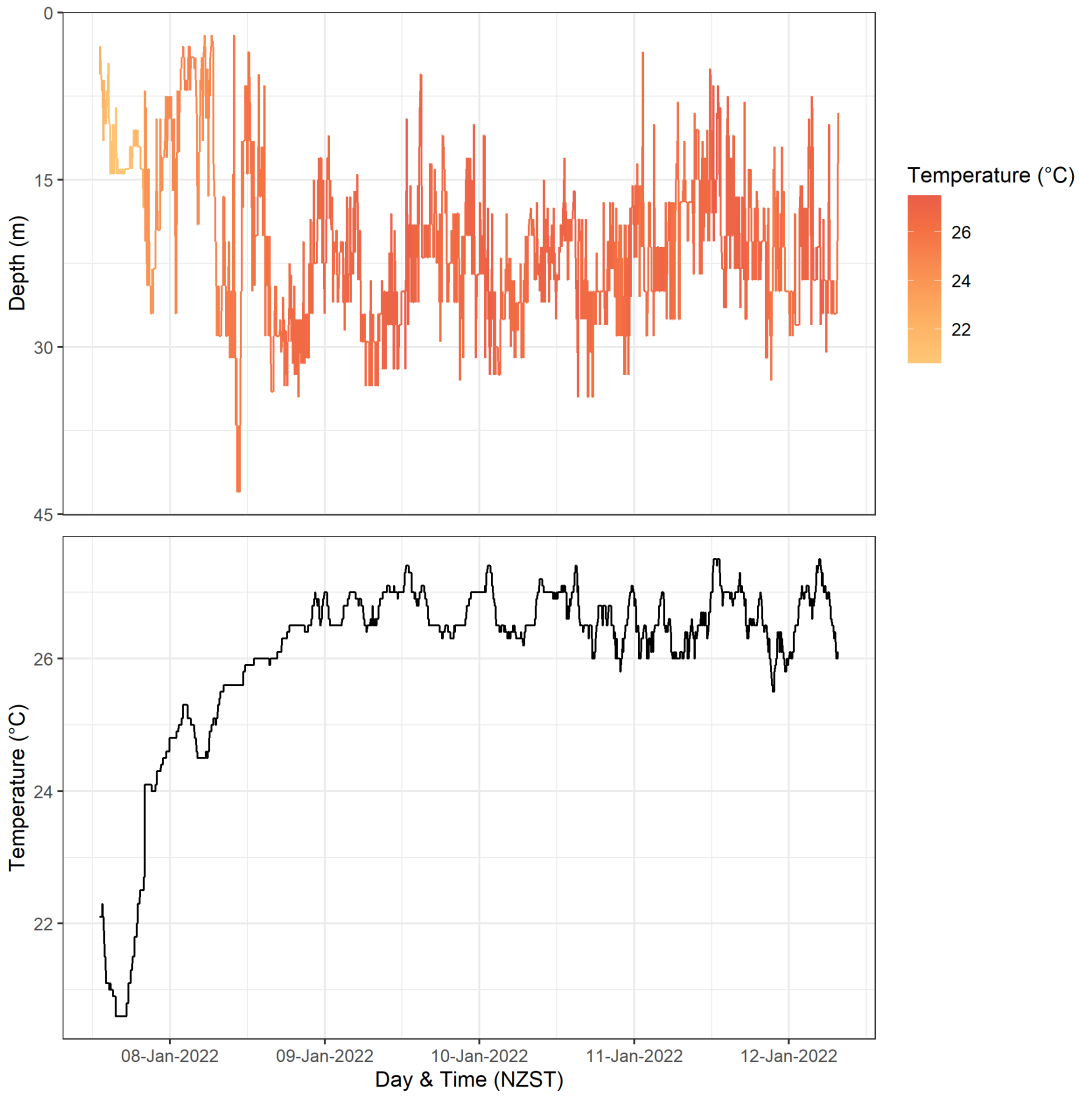


Figure A4.6.5: *Time series of depths and temperatures used by Alison (21P0881).*

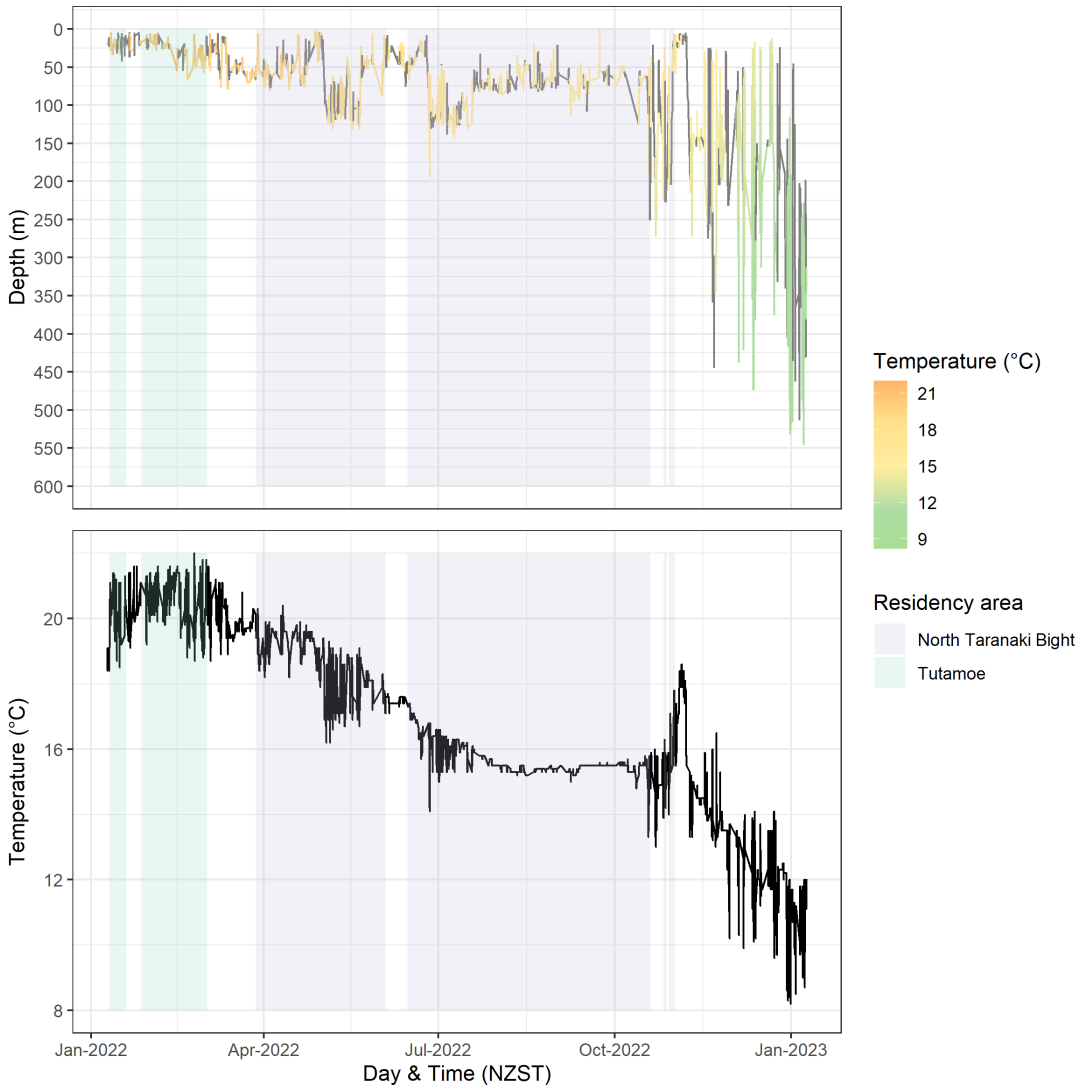


Figure A4.6.6: *Time series of depths and temperatures used by Zoe (21P0882).*

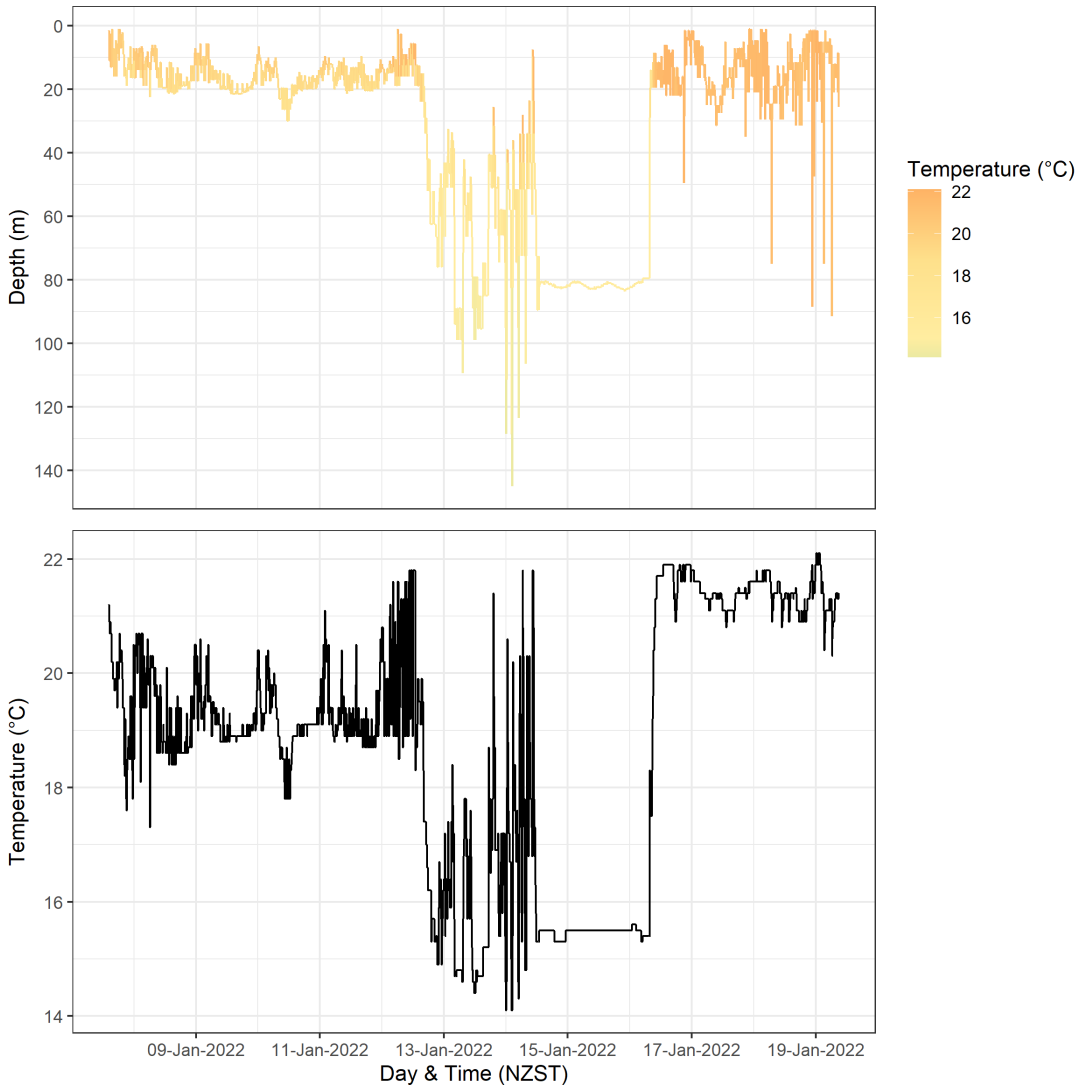


Figure A4.6.7: *Time series of depths and temperatures used by Emily (21P0888).*

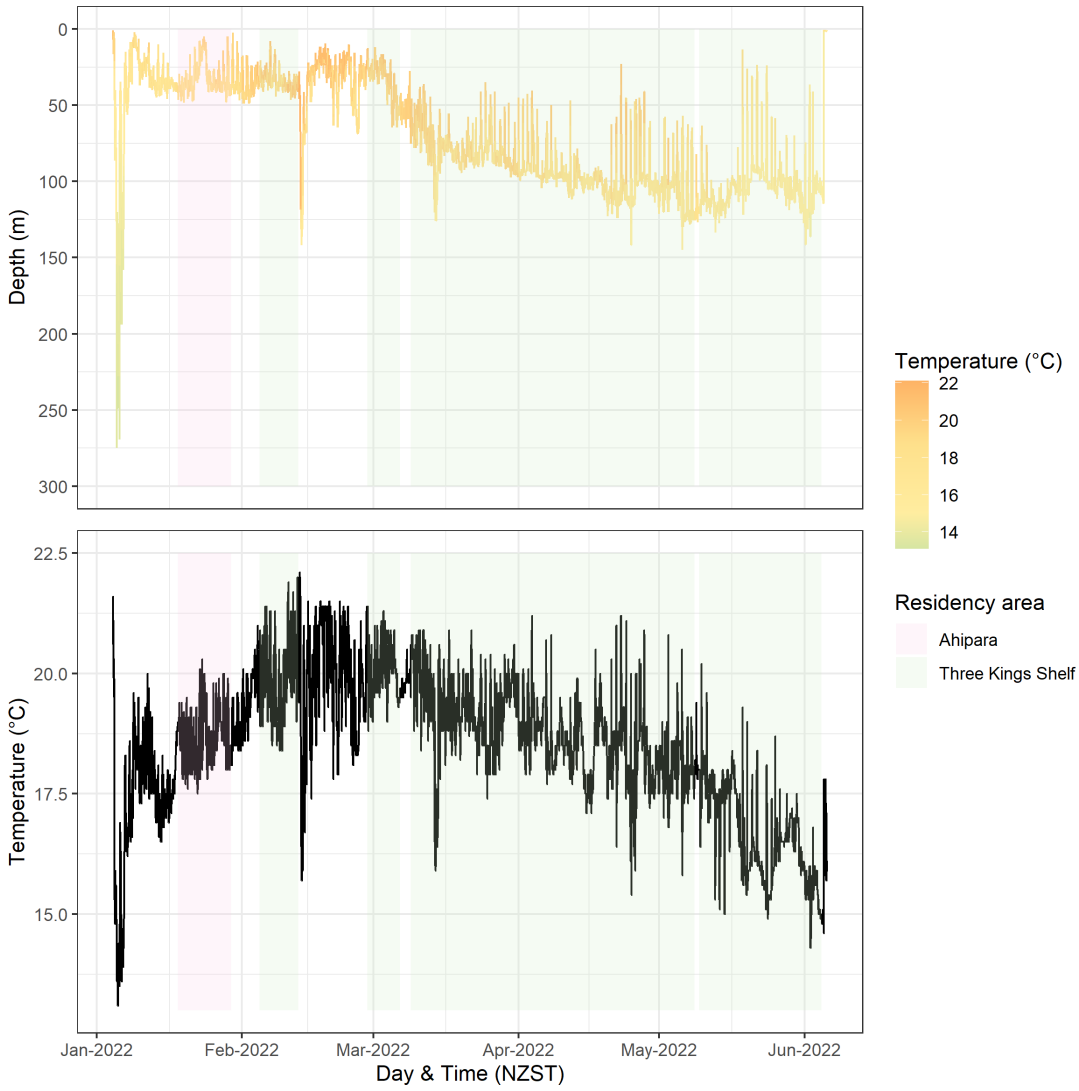


Figure A4.6.8: *Time series of depths and temperatures used by Sharky (21P0890).*

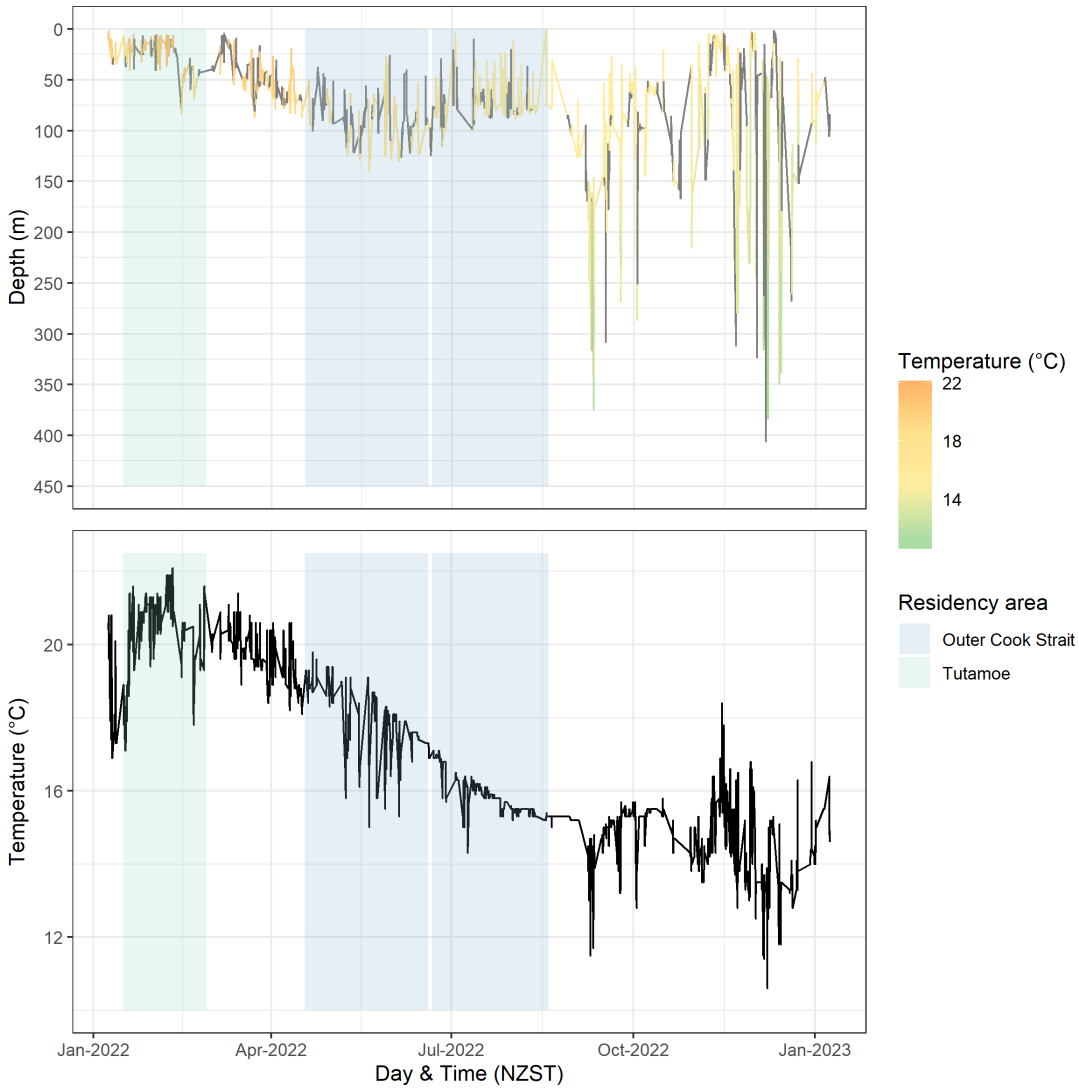


Figure A4.6.9: *Time series of depths and temperatures used by Paula (21P0892).*

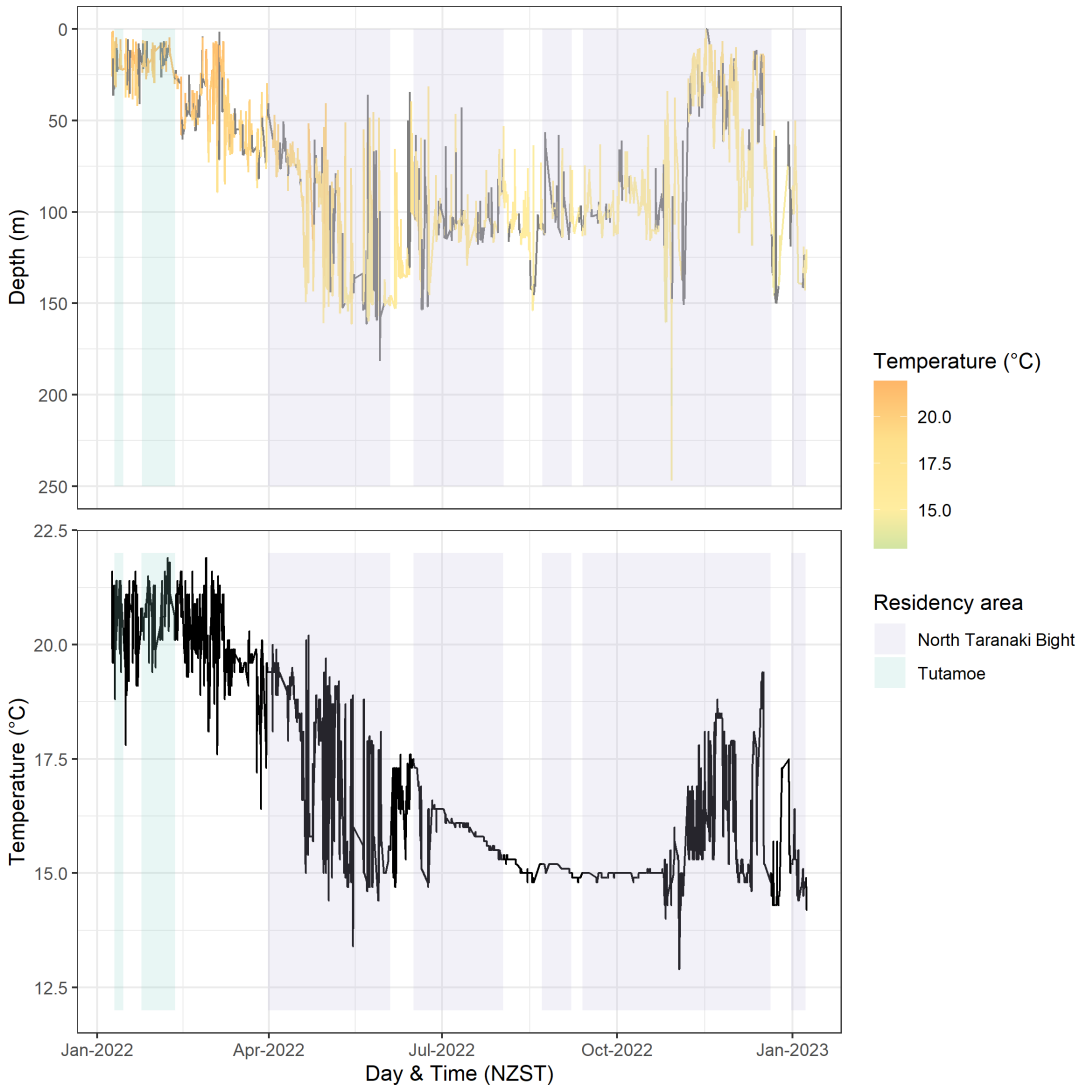


Figure A4.6.10: *Time series of depths and temperatures used by Michelle (21P0899).*

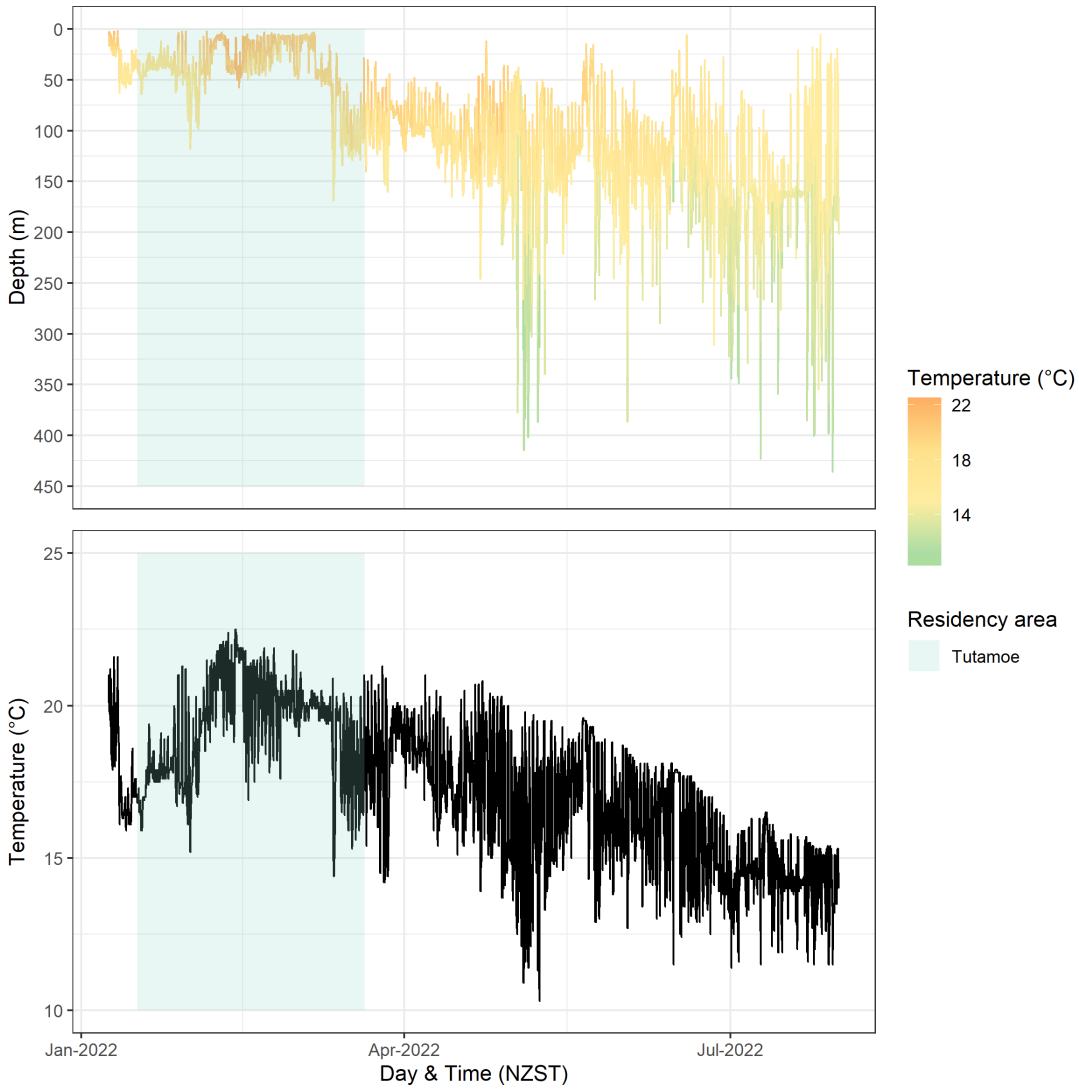


Figure A4.6.11: *Time series of depths and temperatures used by Louie (21P0920).*

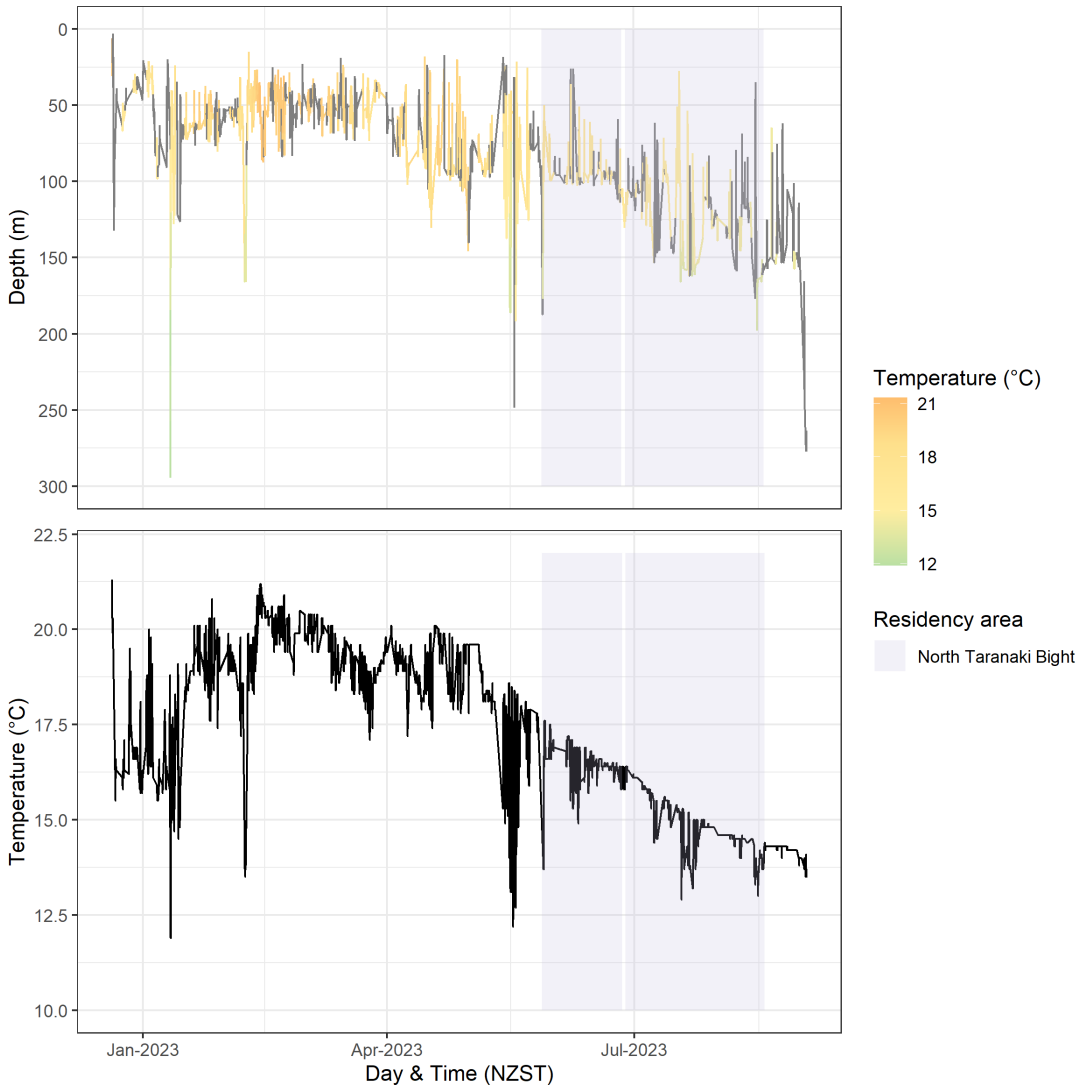


Figure A4.6.12: *Time series of depths and temperatures used by Marie (21P0879).*

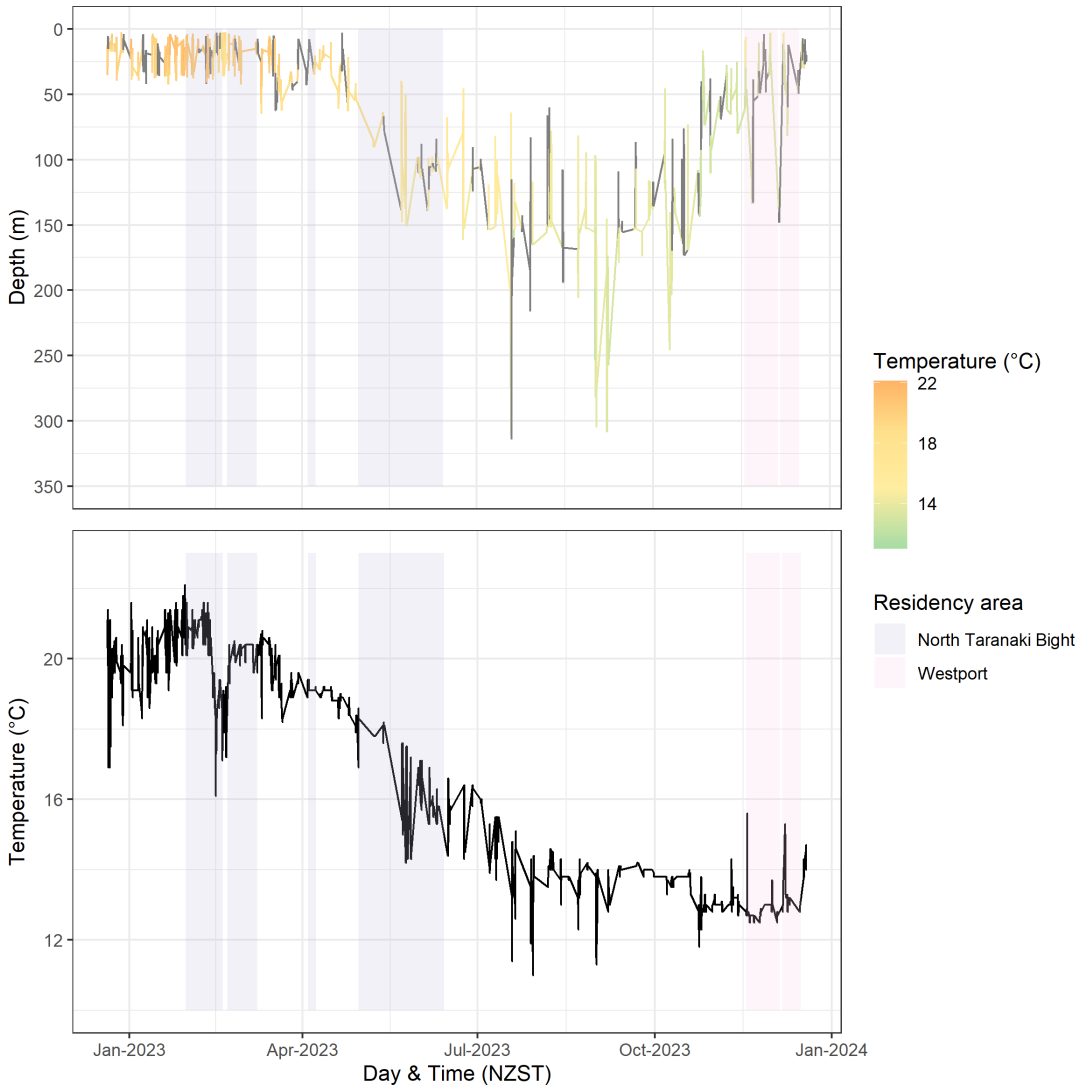


Figure A4.6.13: *Time series of depths and temperatures used by Etoile (21P0880).*

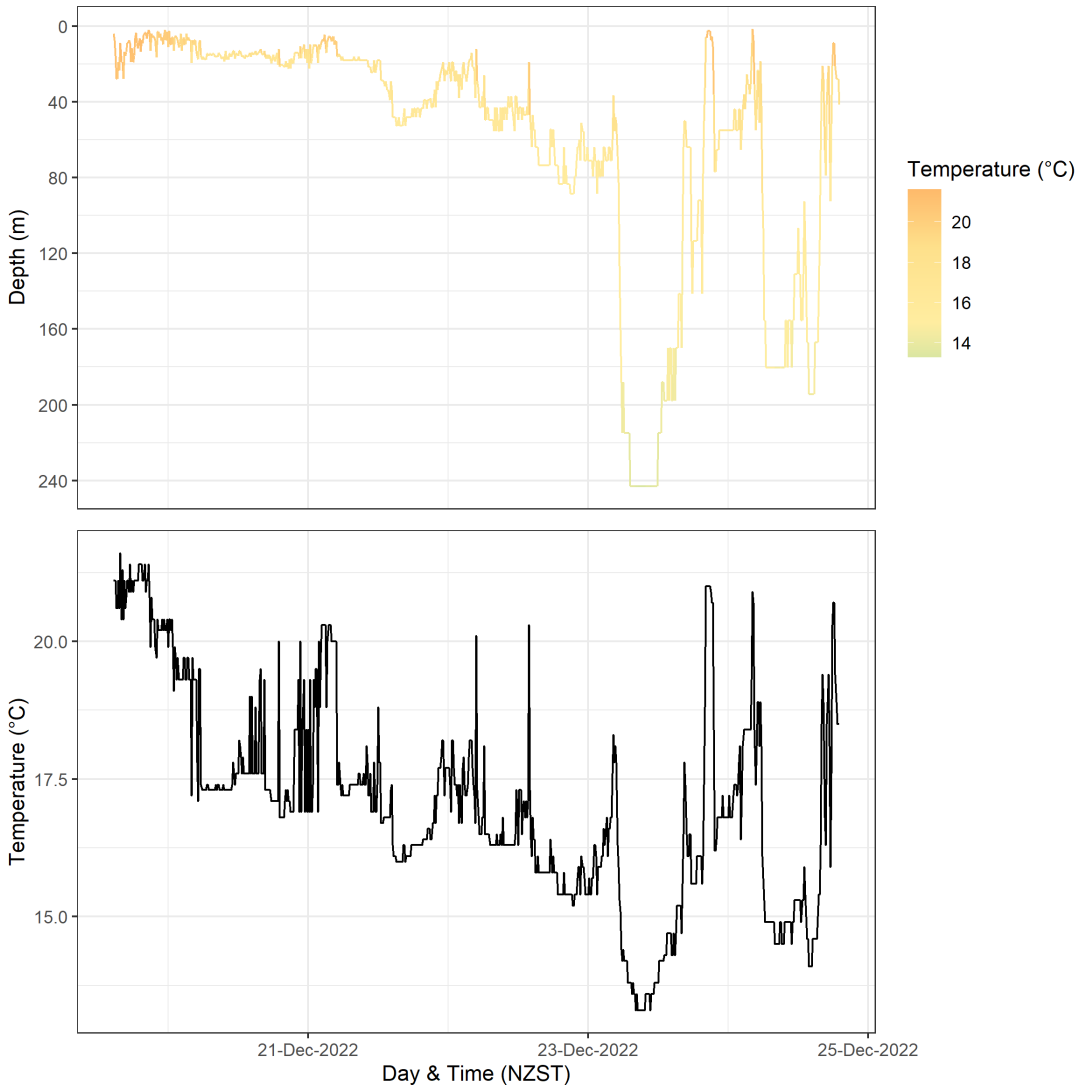


Figure A4.6.14: *Time series of depths and temperatures used by Kelly (21P0887).*

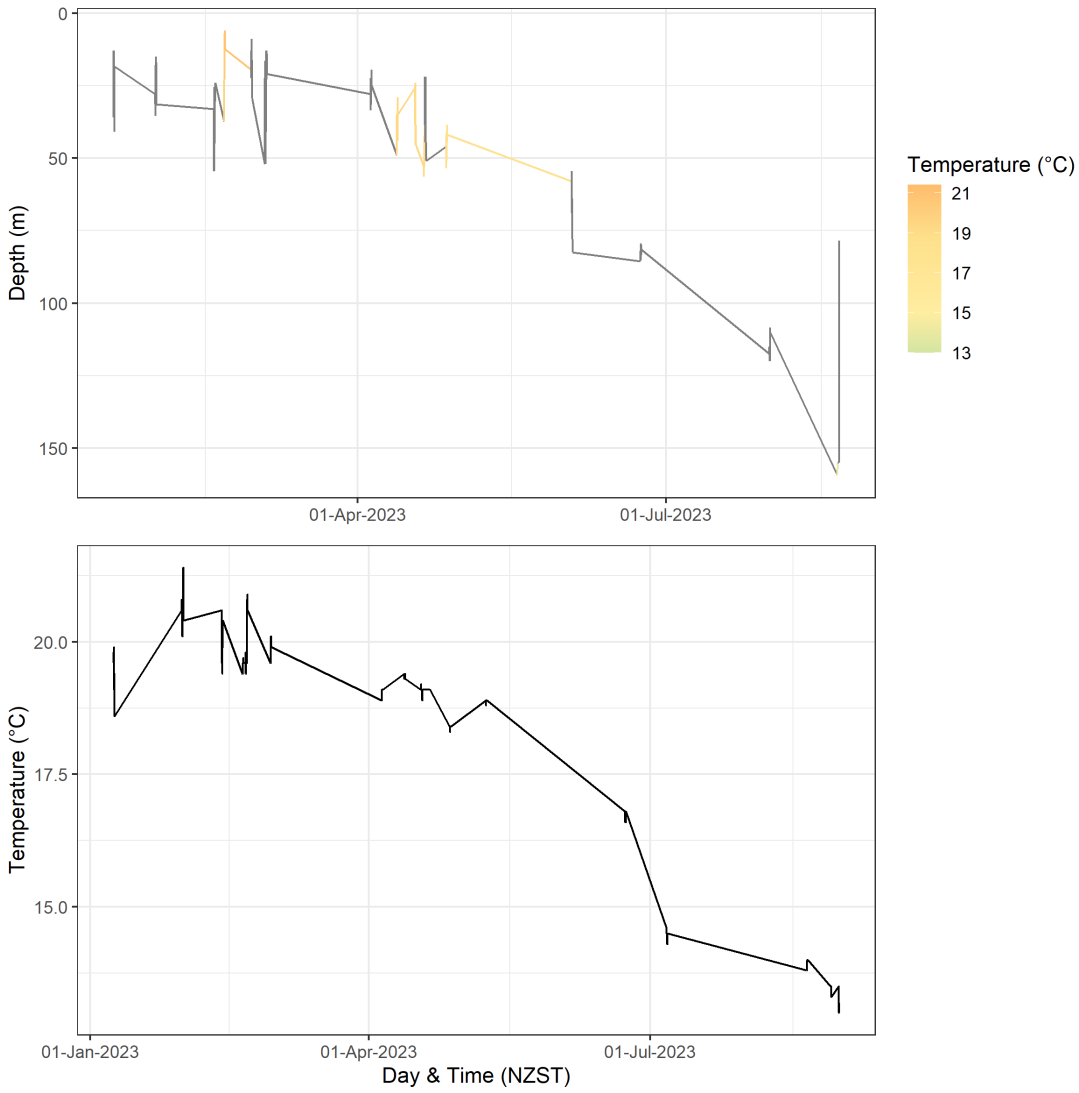


Figure A4.6.15: *Time series of depths and temperatures used by Caitlyn (21P0896).*

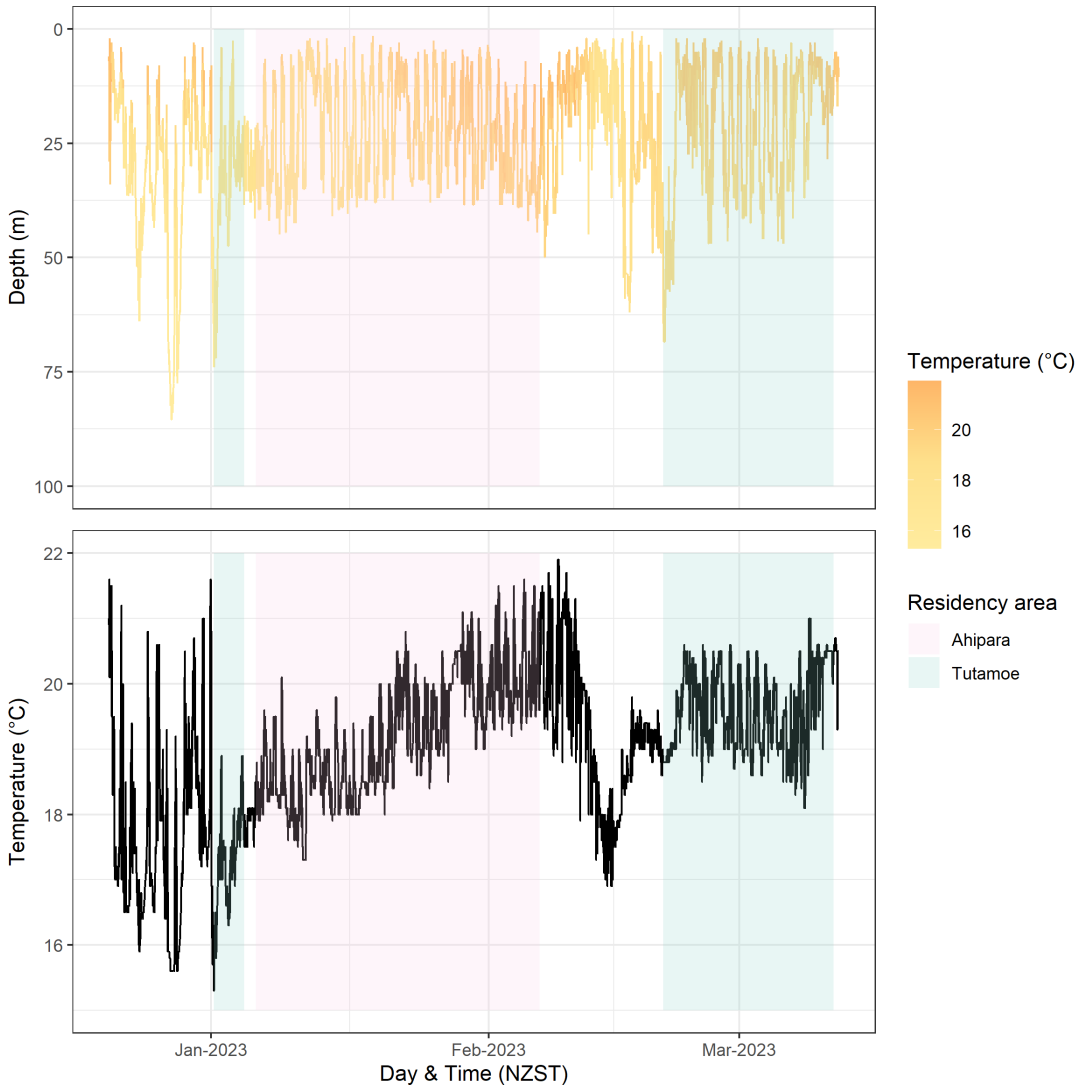
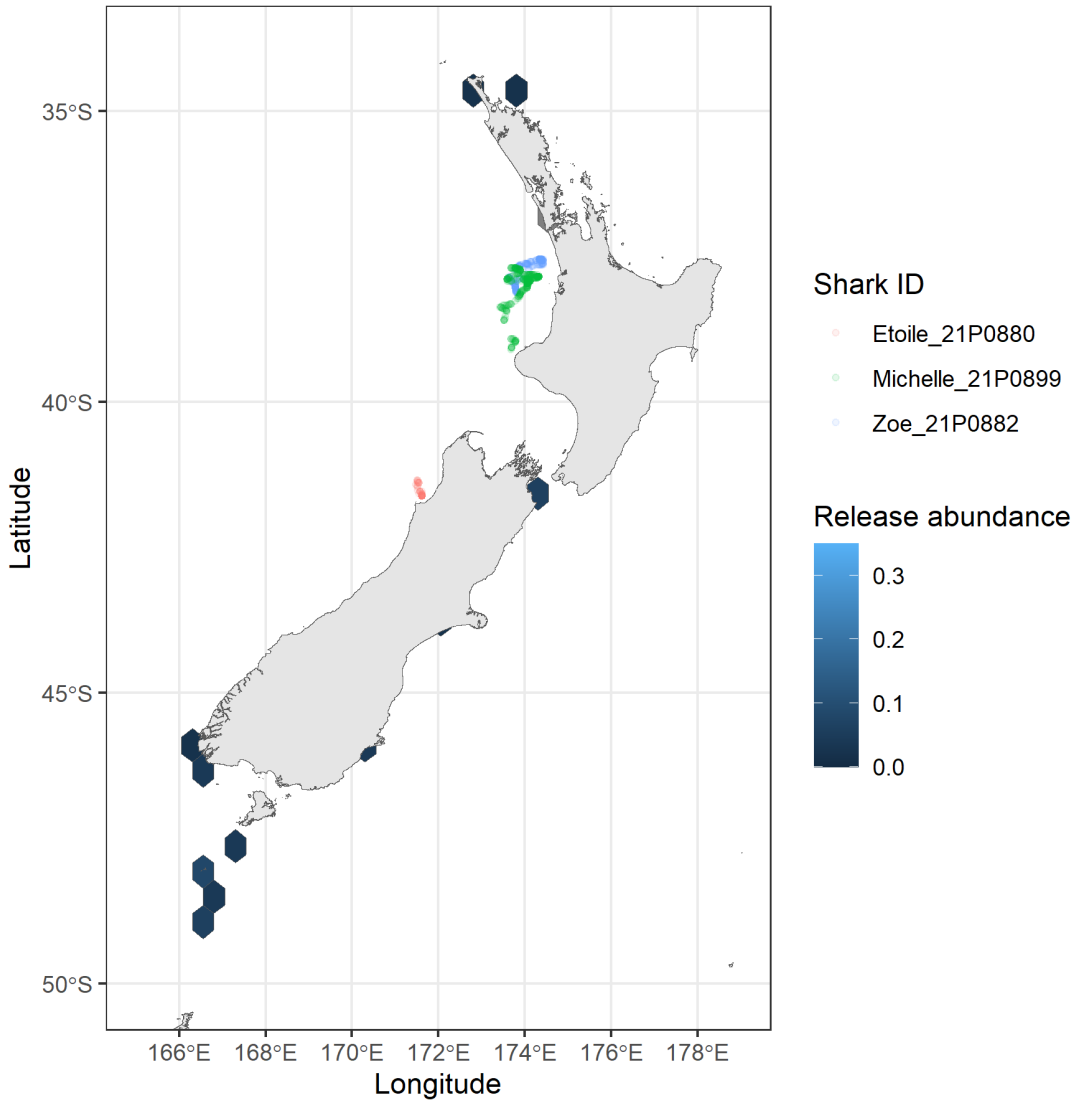
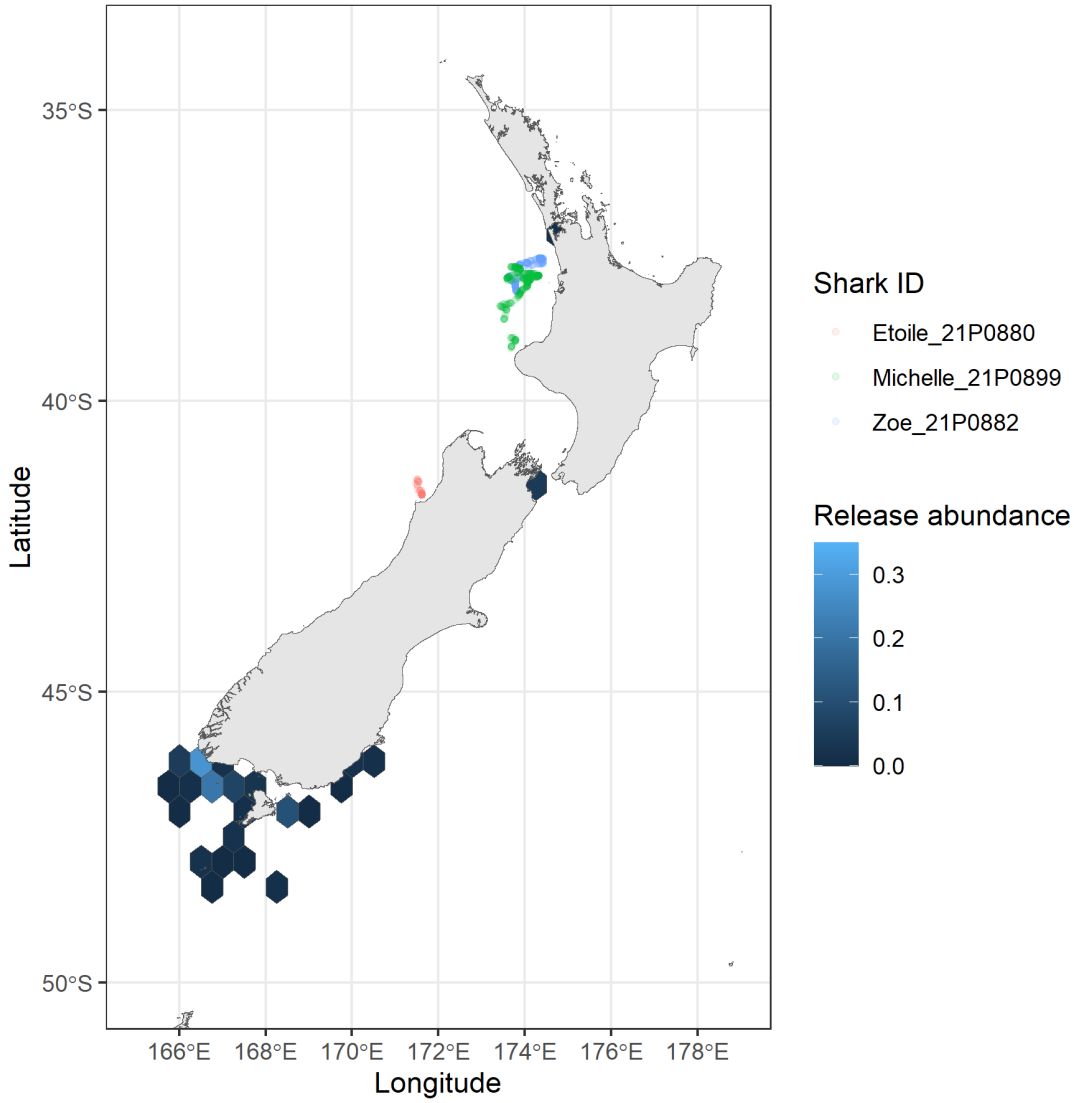


Figure A4.6.16: *Time series of depths and temperatures used by Anna (21P0912).*

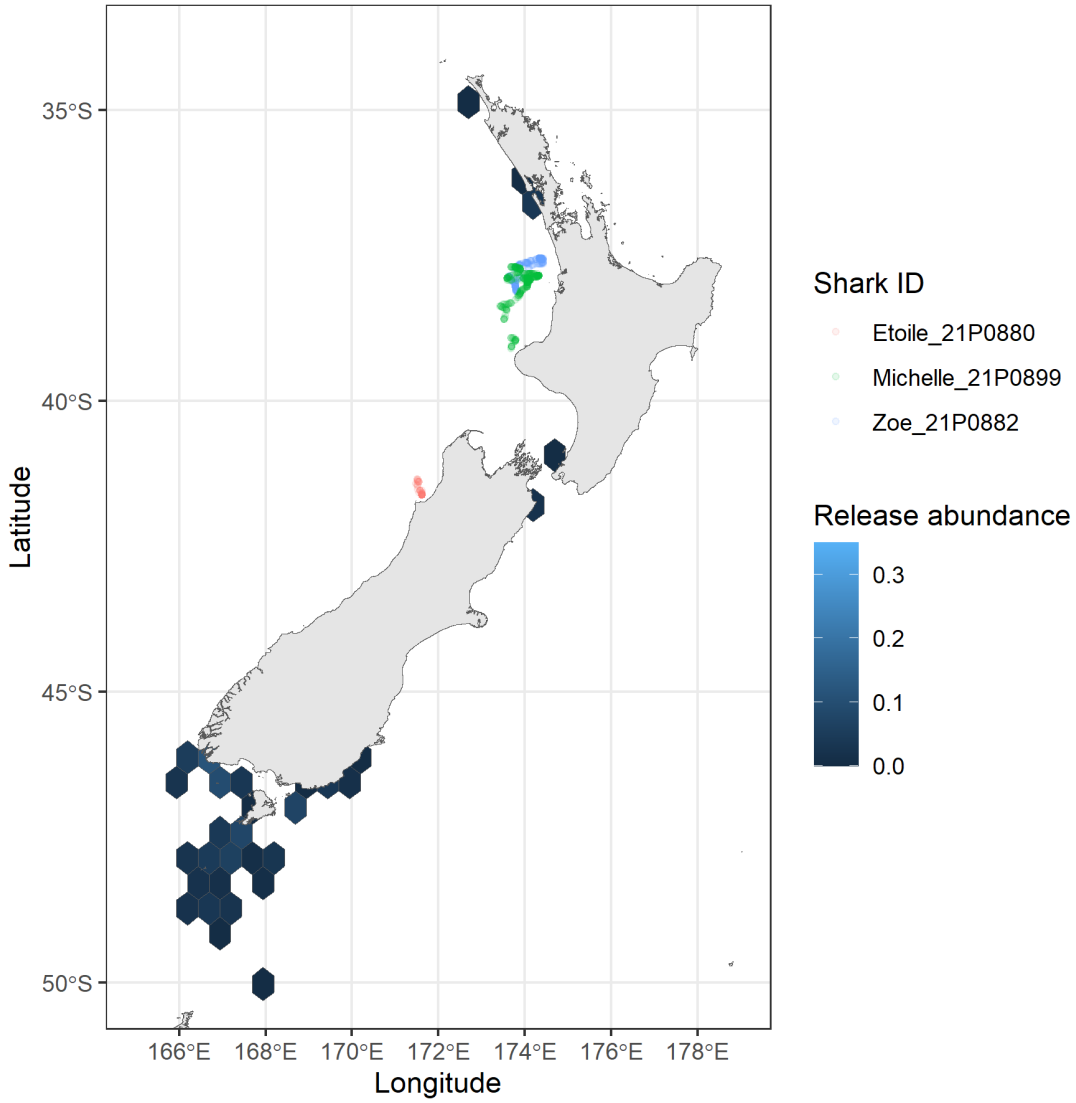
A4.7: Seasonal school shark abundance vs school shark residency



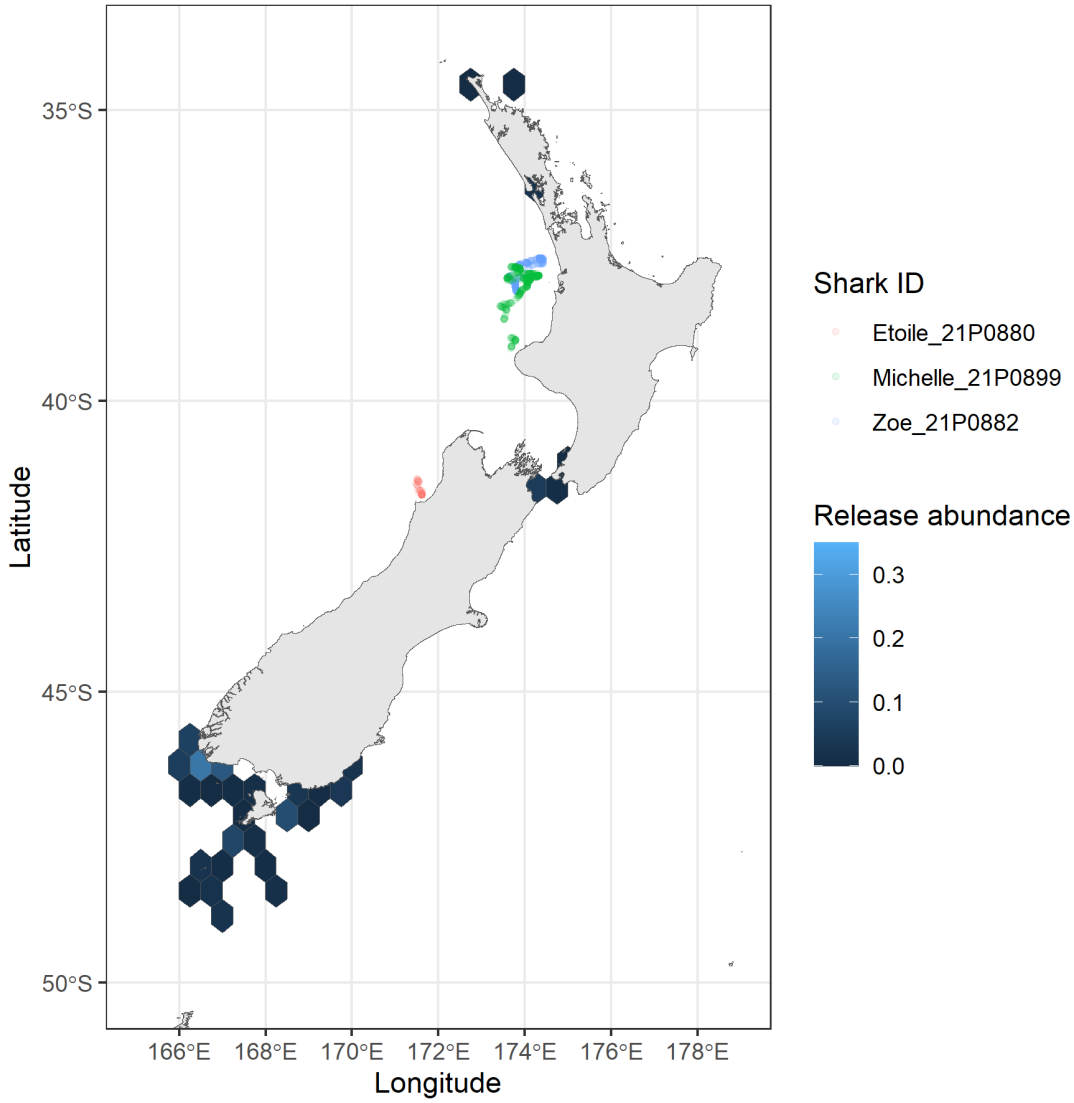
a) Adult females



b) Adult males

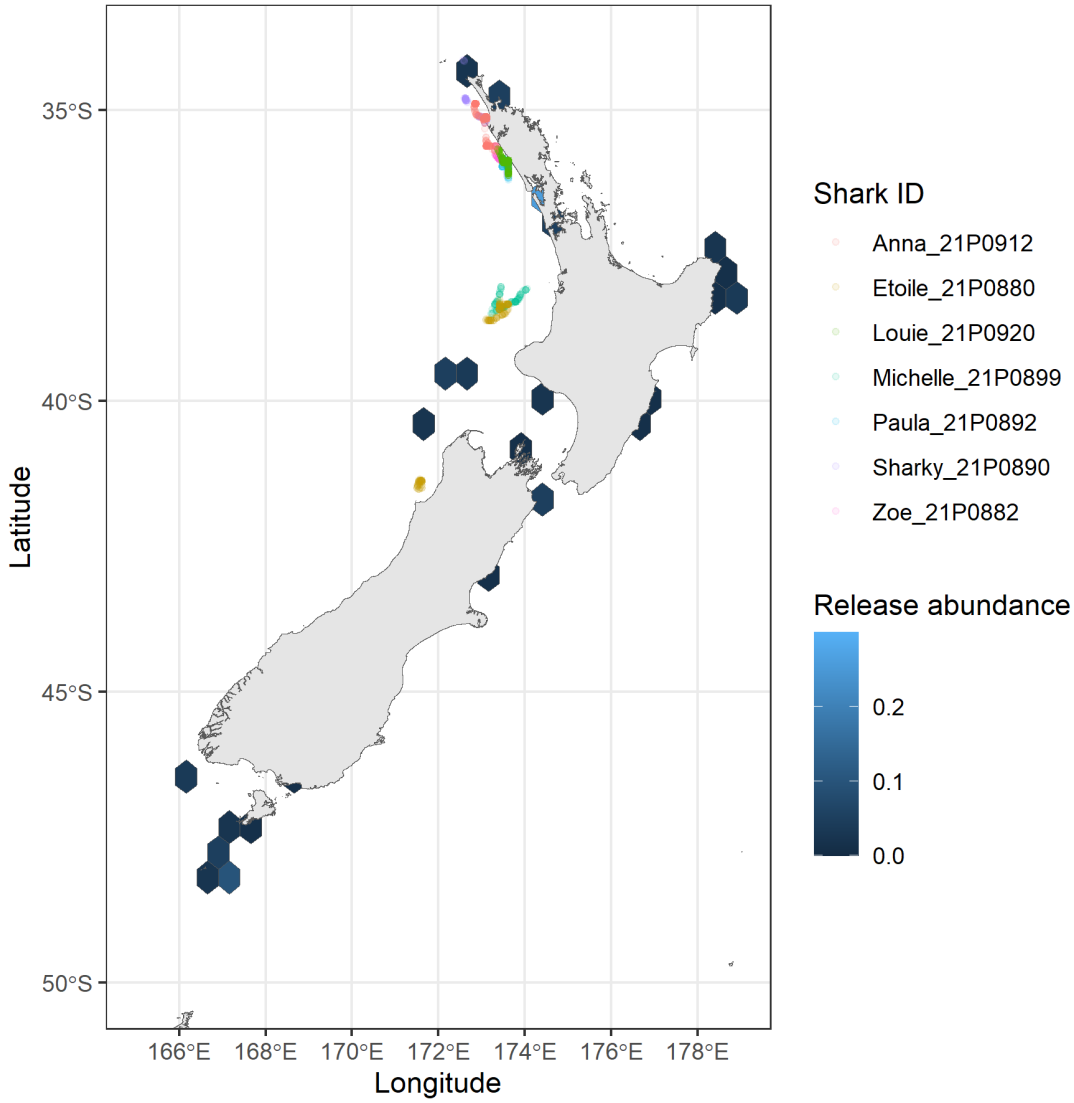


c) Juvenile females

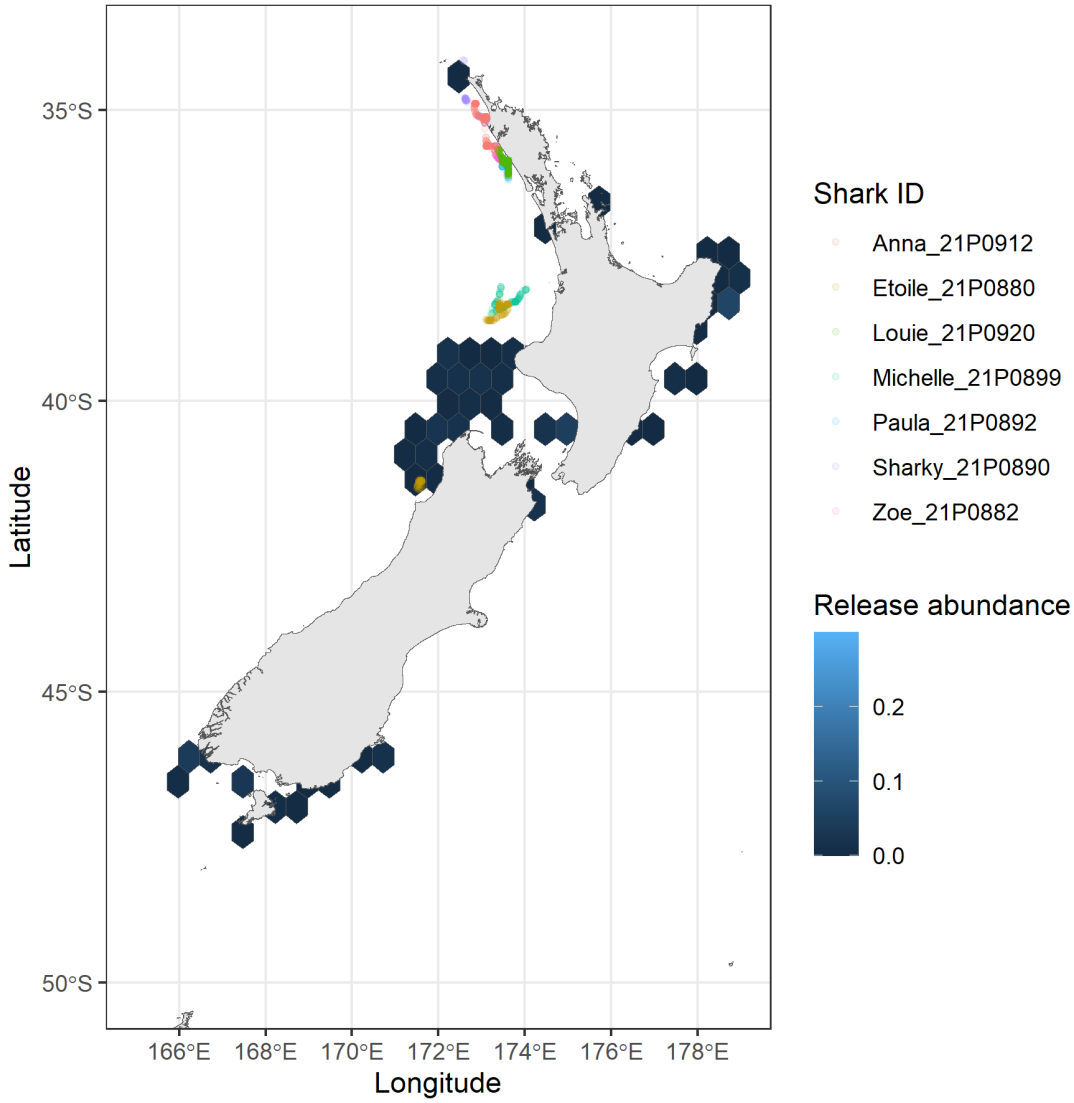


d) Juvenile males

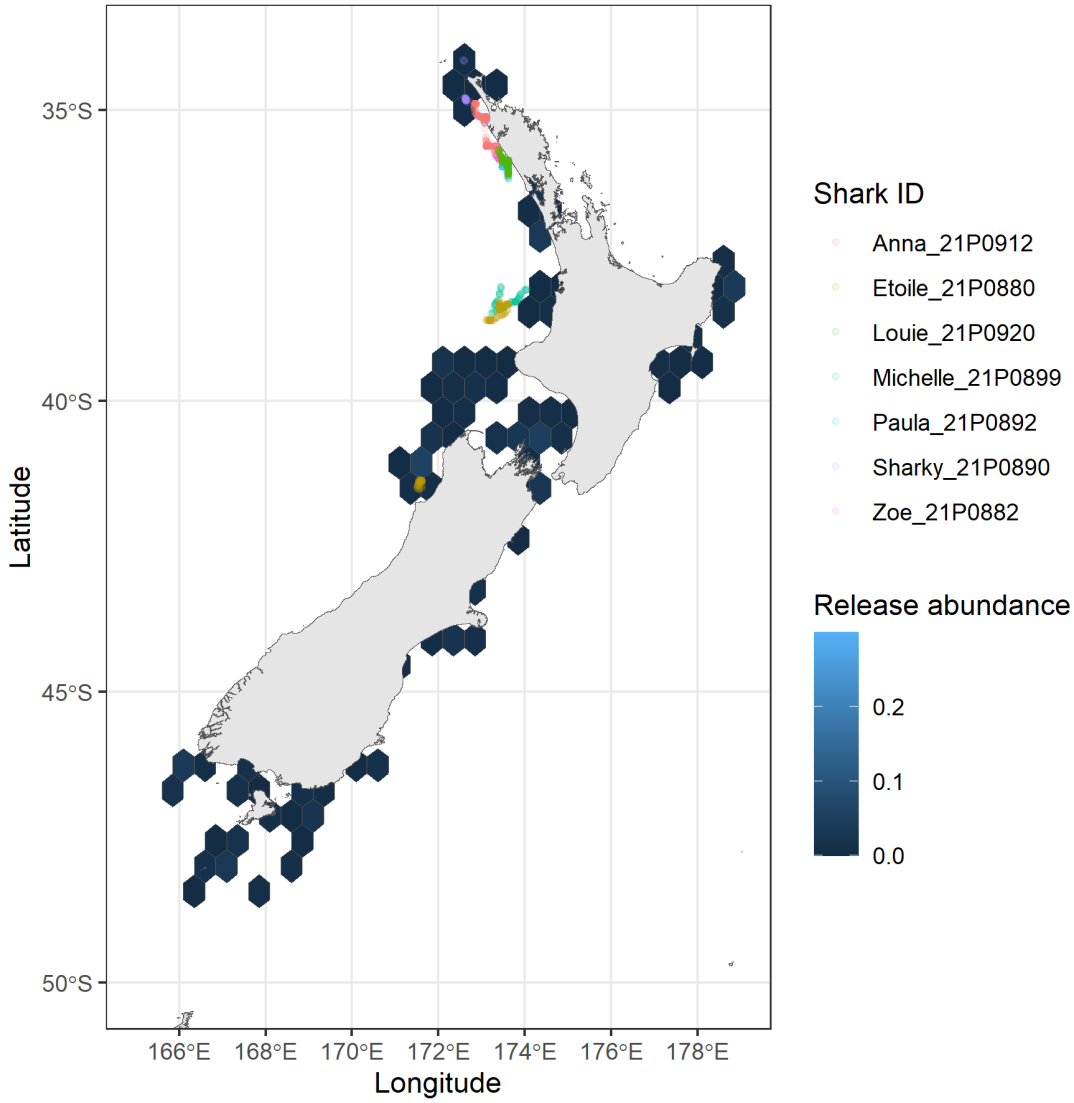
Figure A4.7.1: *Distribution of tagged school sharks released in spring vs temporary residency behaviours of satellite tagged school sharks. Points represent locations where satellite tagged school sharks were estimated to be temporarily residing. Shark ID is the ID of satellite tagged school sharks. Release abundance is the number of sharks released in an area divided by the total number of sharks released.*



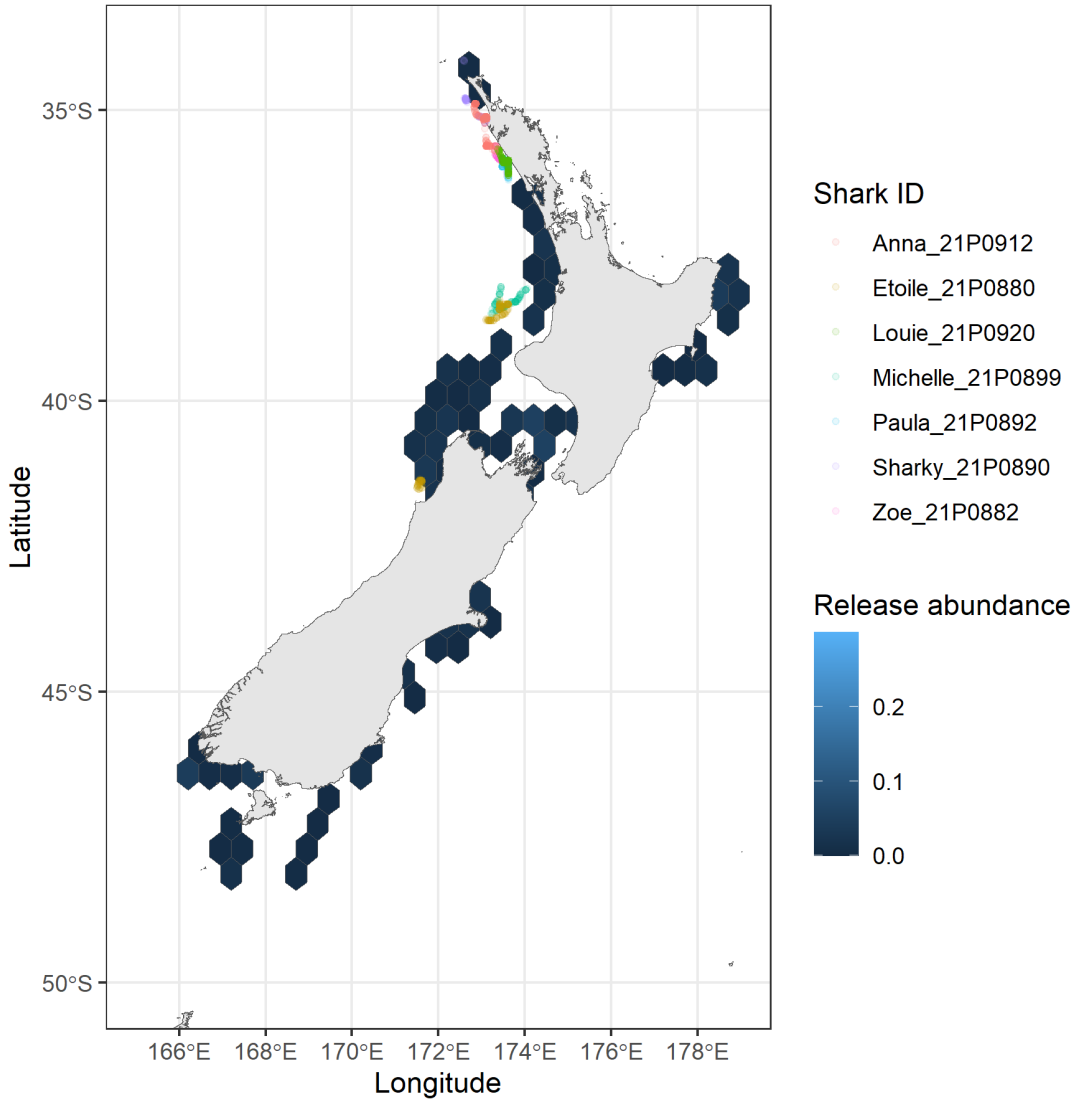
a) Adult females



b) Adult males

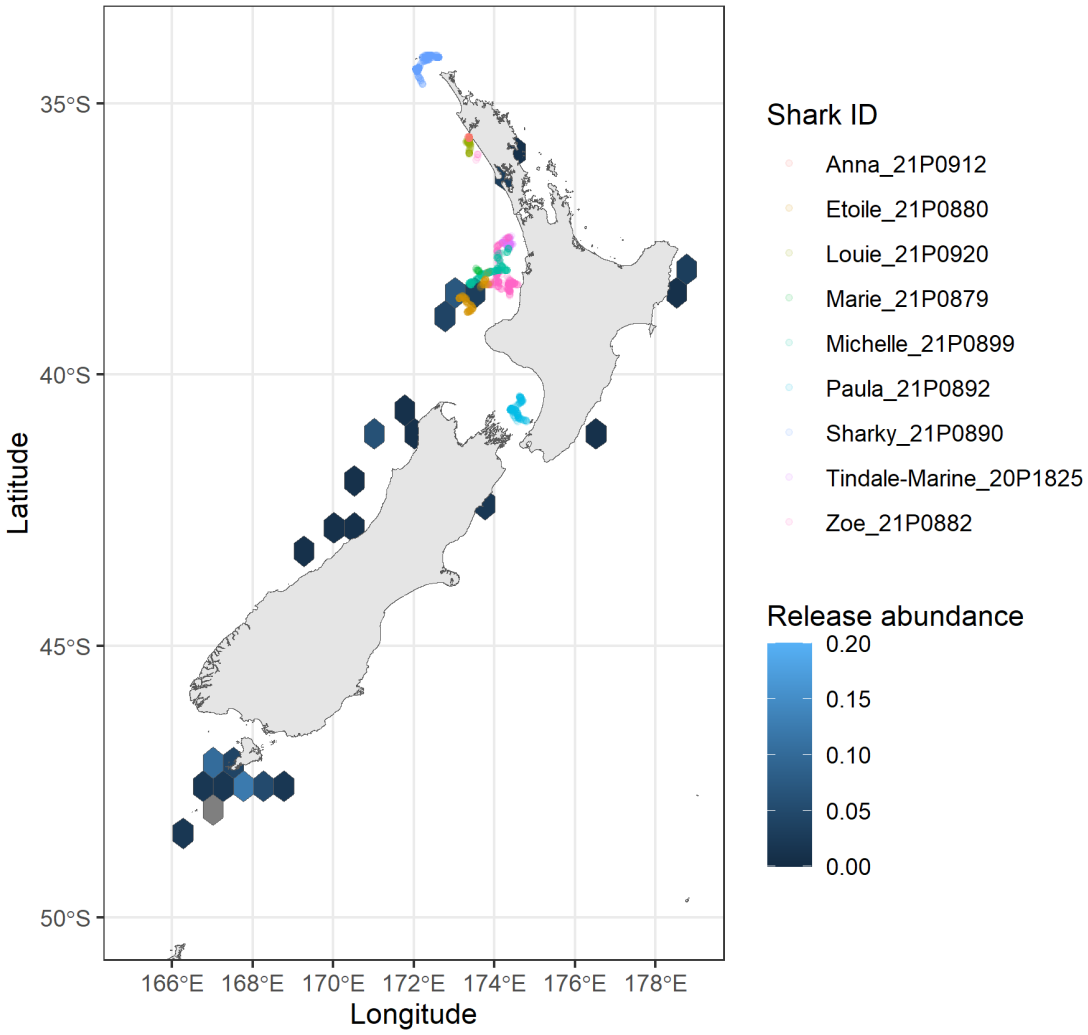


c) Juvenile females

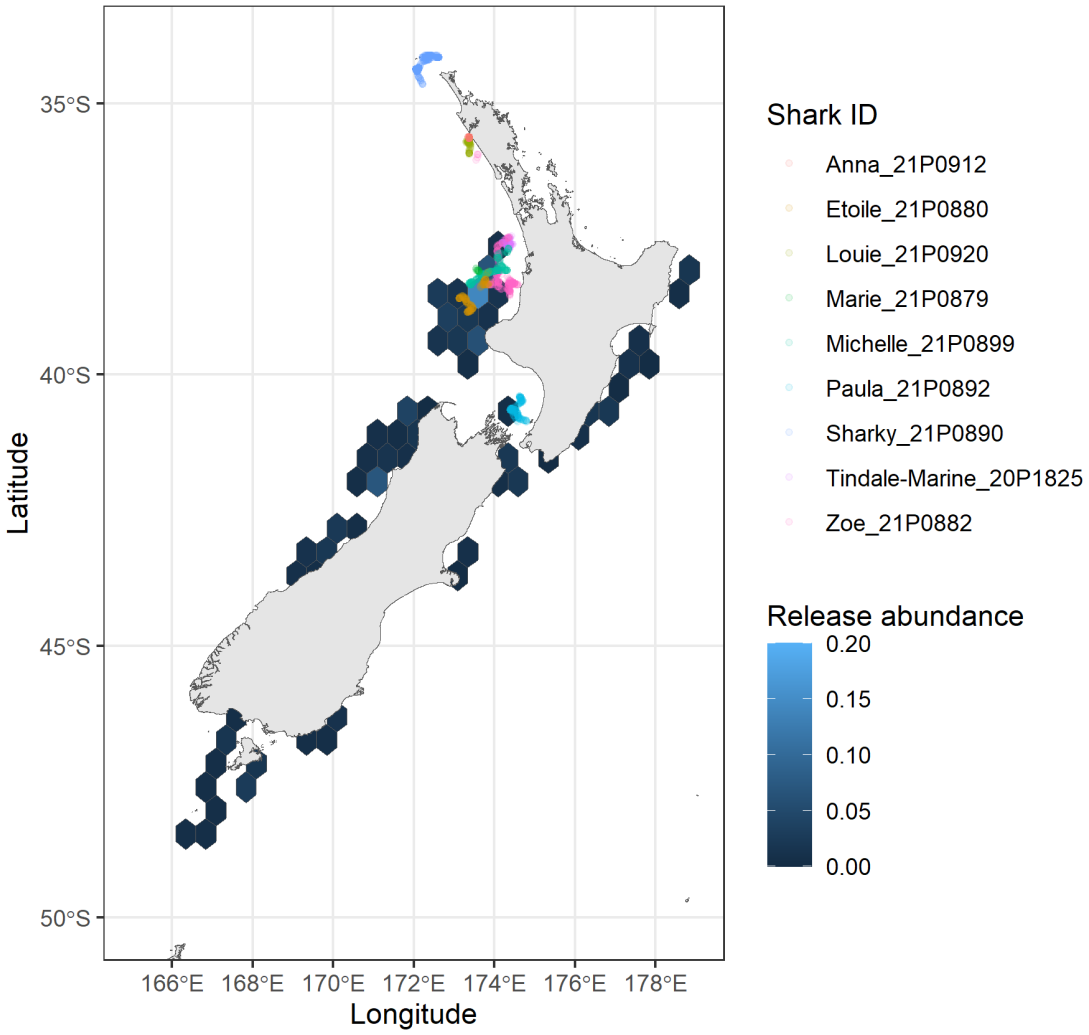


d) Juvenile males

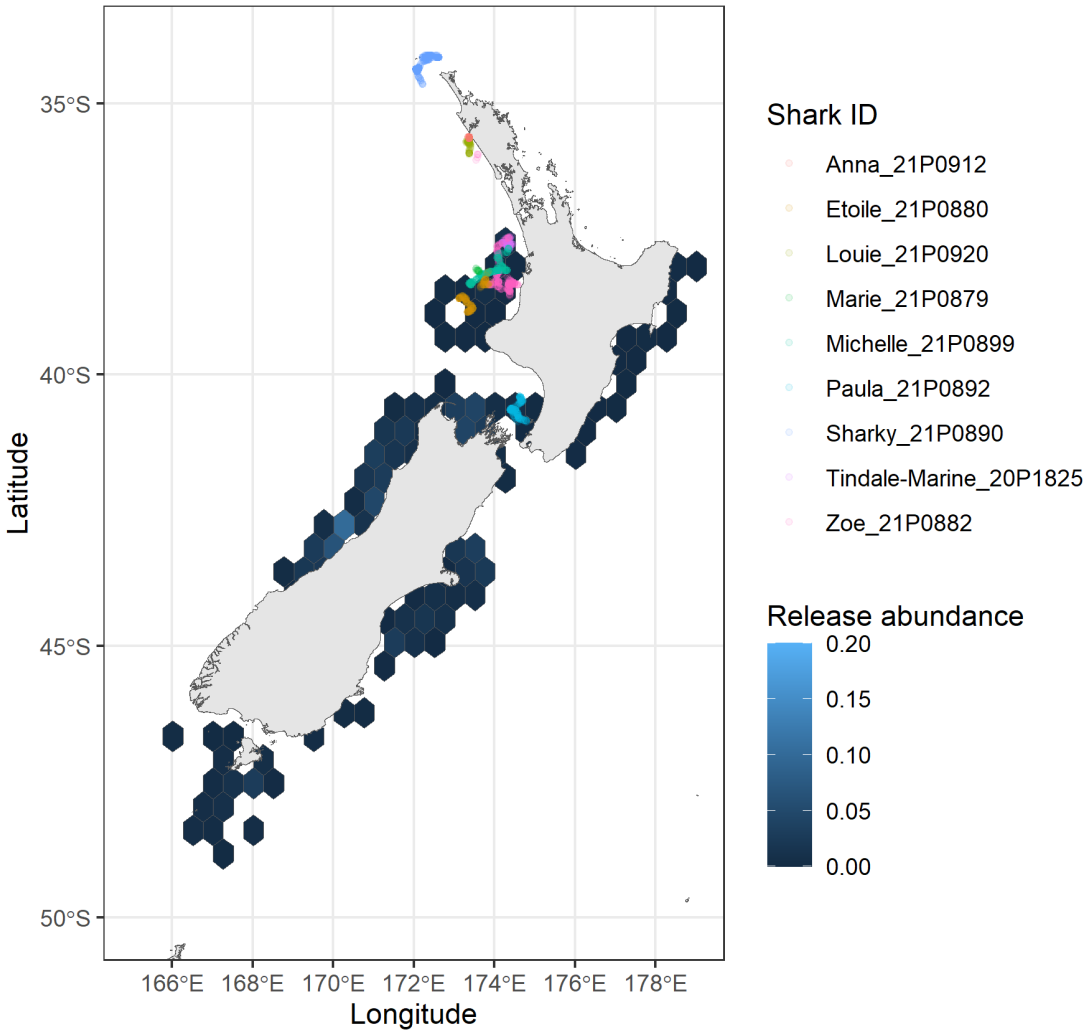
Figure A4.7.2: *Distribution of tagged school sharks released in summer vs temporary residency behaviours of satellite tagged school sharks. Points represent locations where satellite tagged school sharks were estimated to be temporarily residing. Shark ID is the ID of satellite tagged school sharks. Release abundance is the number of sharks released in an area divided the by total number of sharks released.*



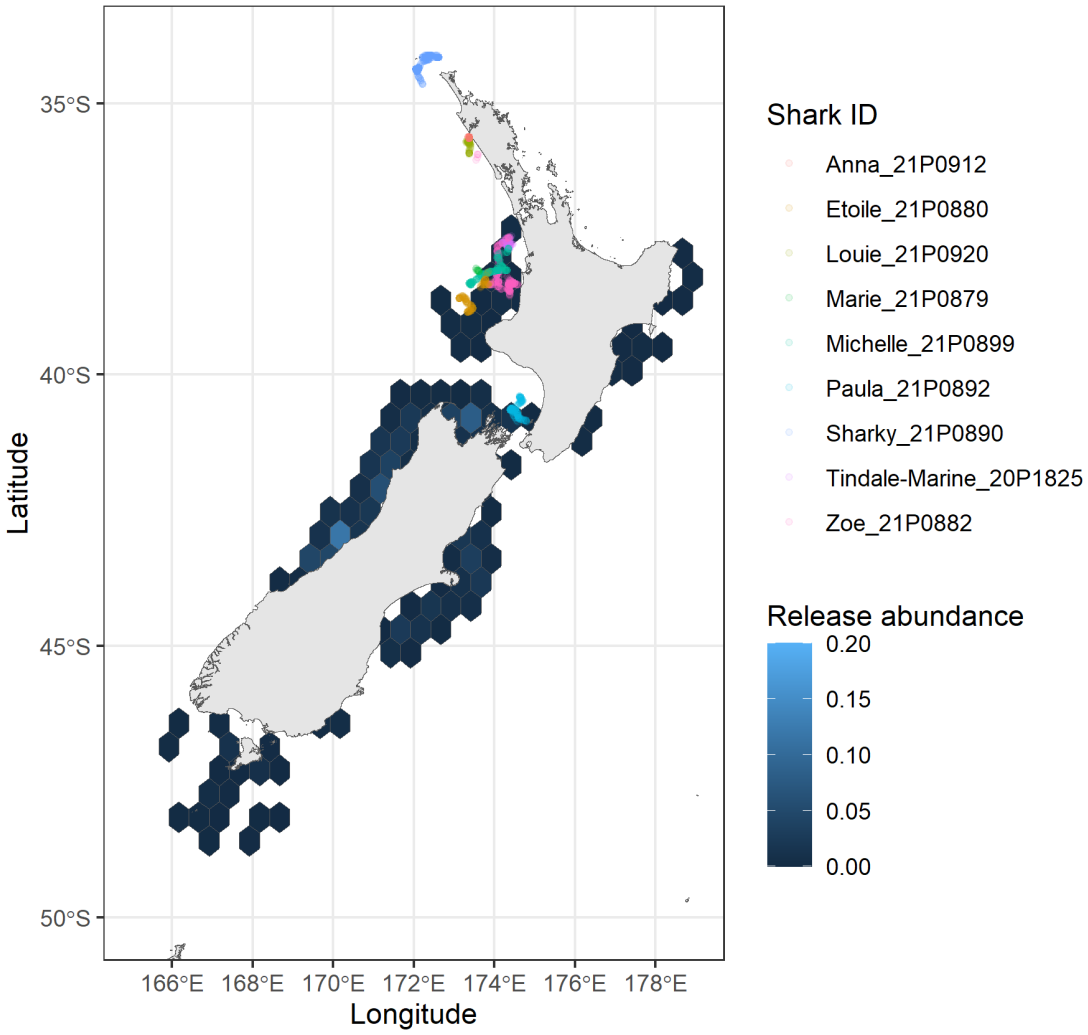
a) Adult females



b) Adult males

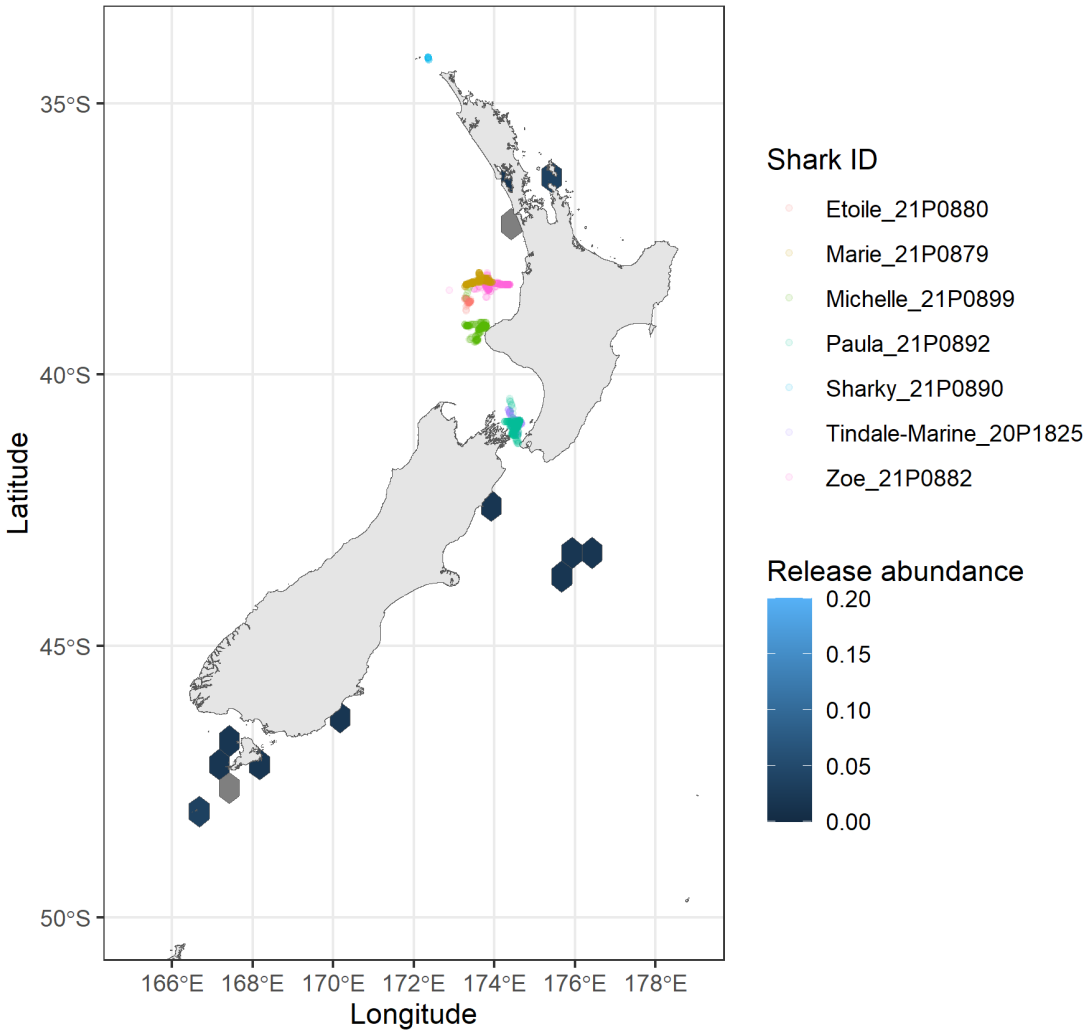


c) Juvenile females

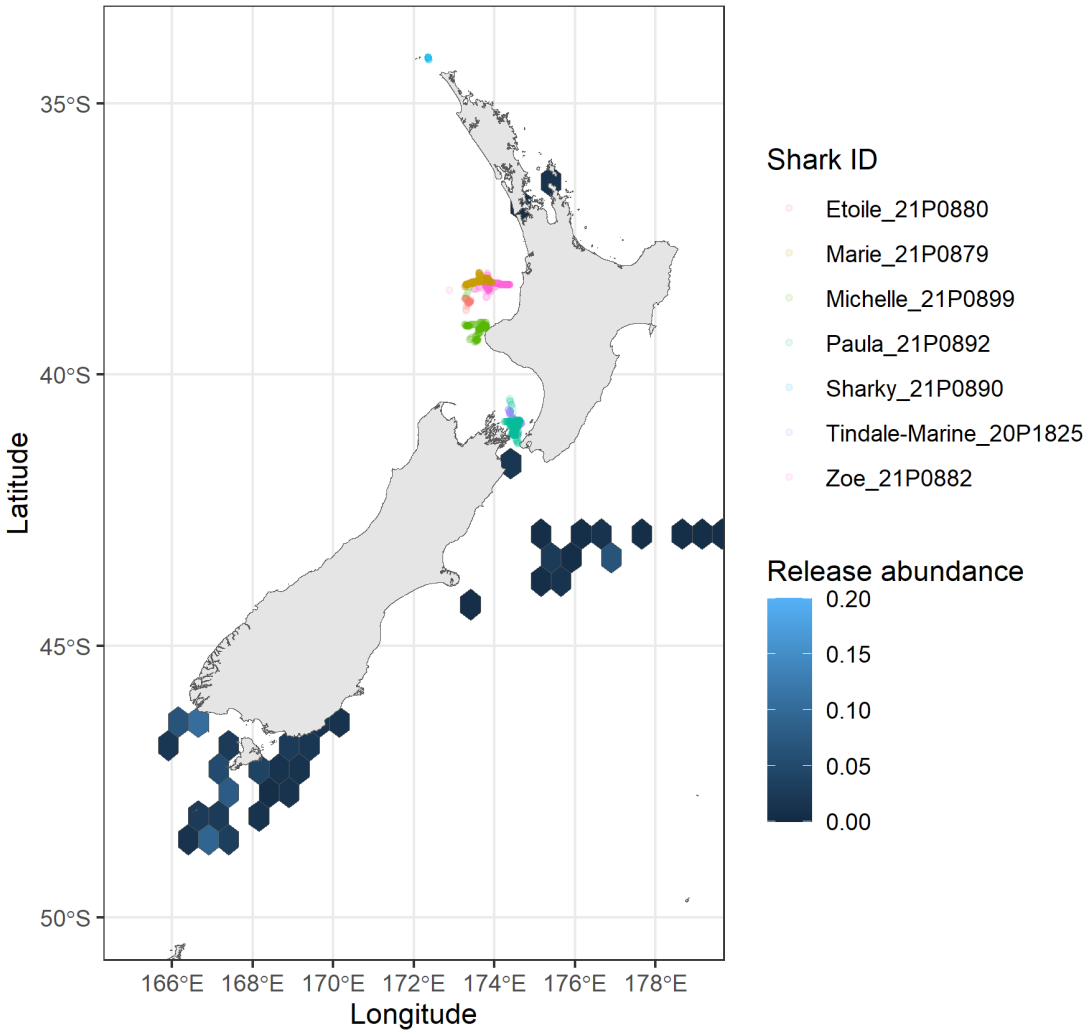


d) Juvenile males

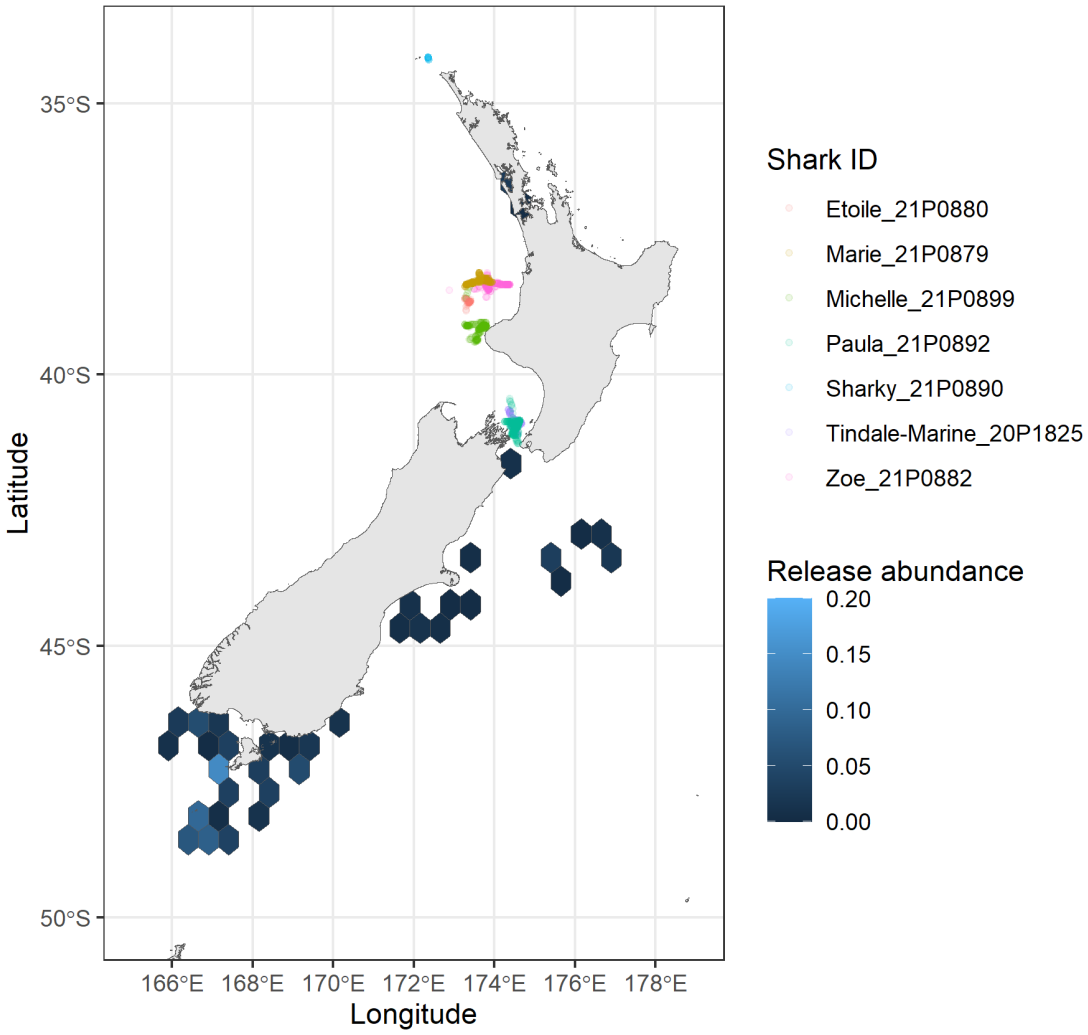
Figure A4.7.3: *Distribution of tagged school sharks released in autumn vs temporary residency behaviours of satellite tagged school sharks. Points represent locations where satellite tagged school sharks were estimated to be temporarily residing. Shark ID is the ID of satellite tagged school sharks. Release abundance is the number of sharks released in an area divided the by total number of sharks released.*



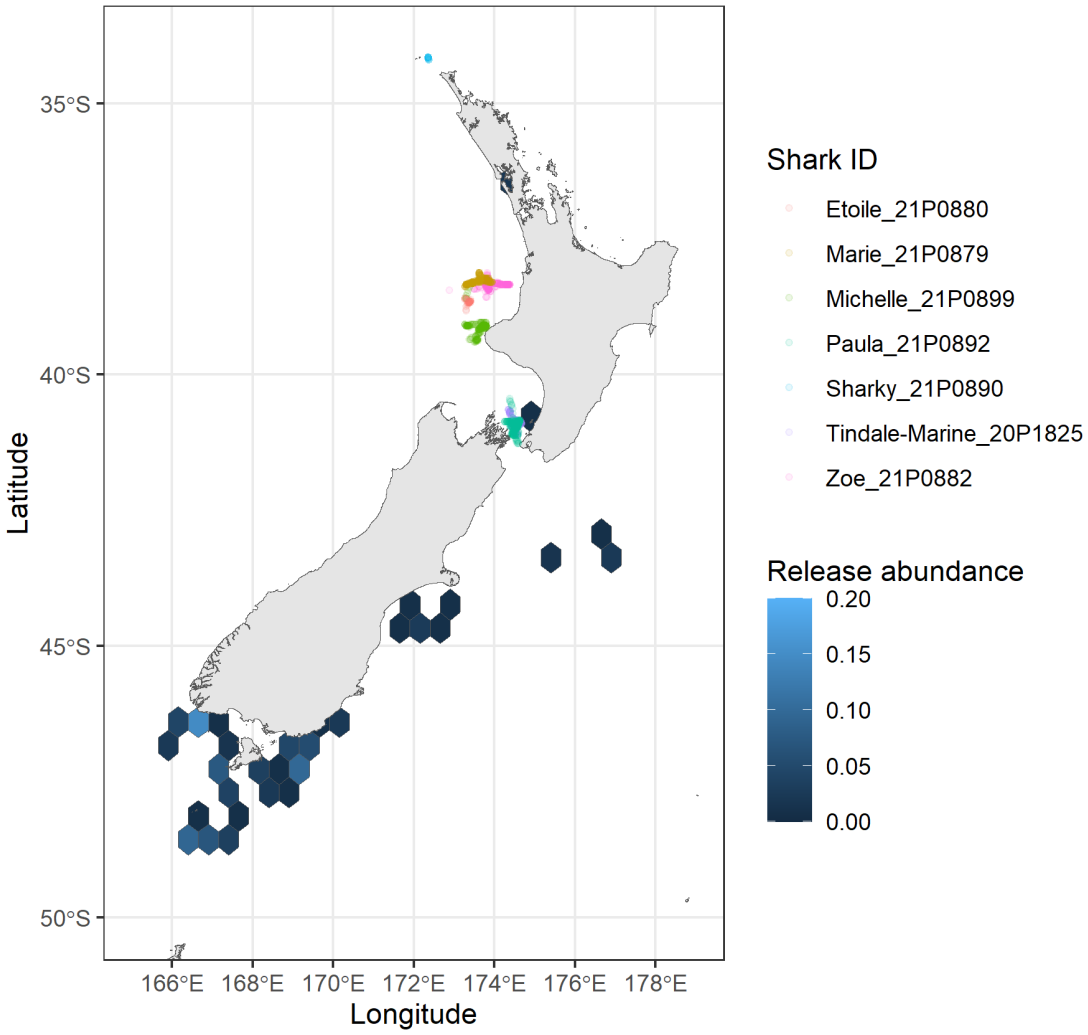
a) Adult females



b) Adult males

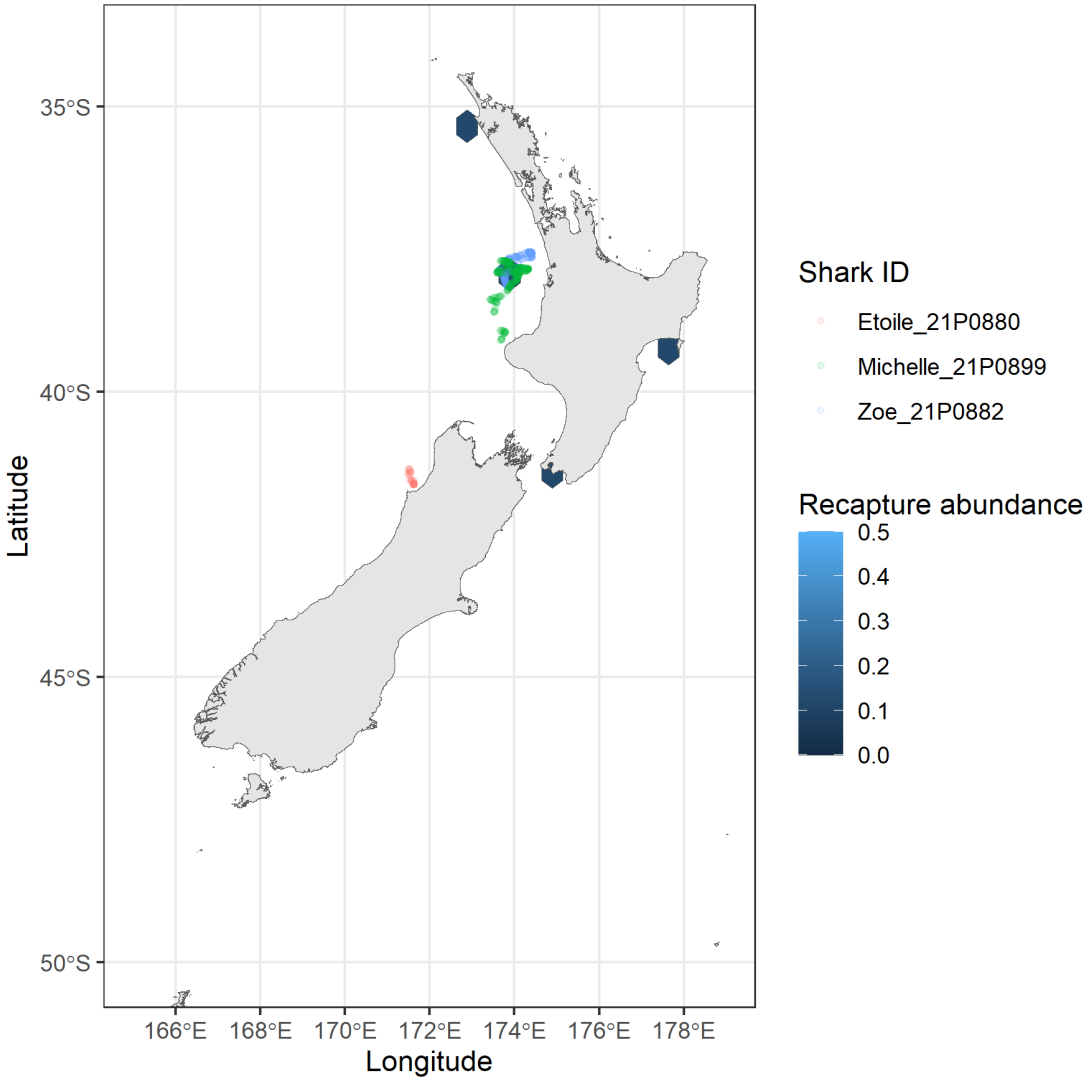


c) Juvenile females

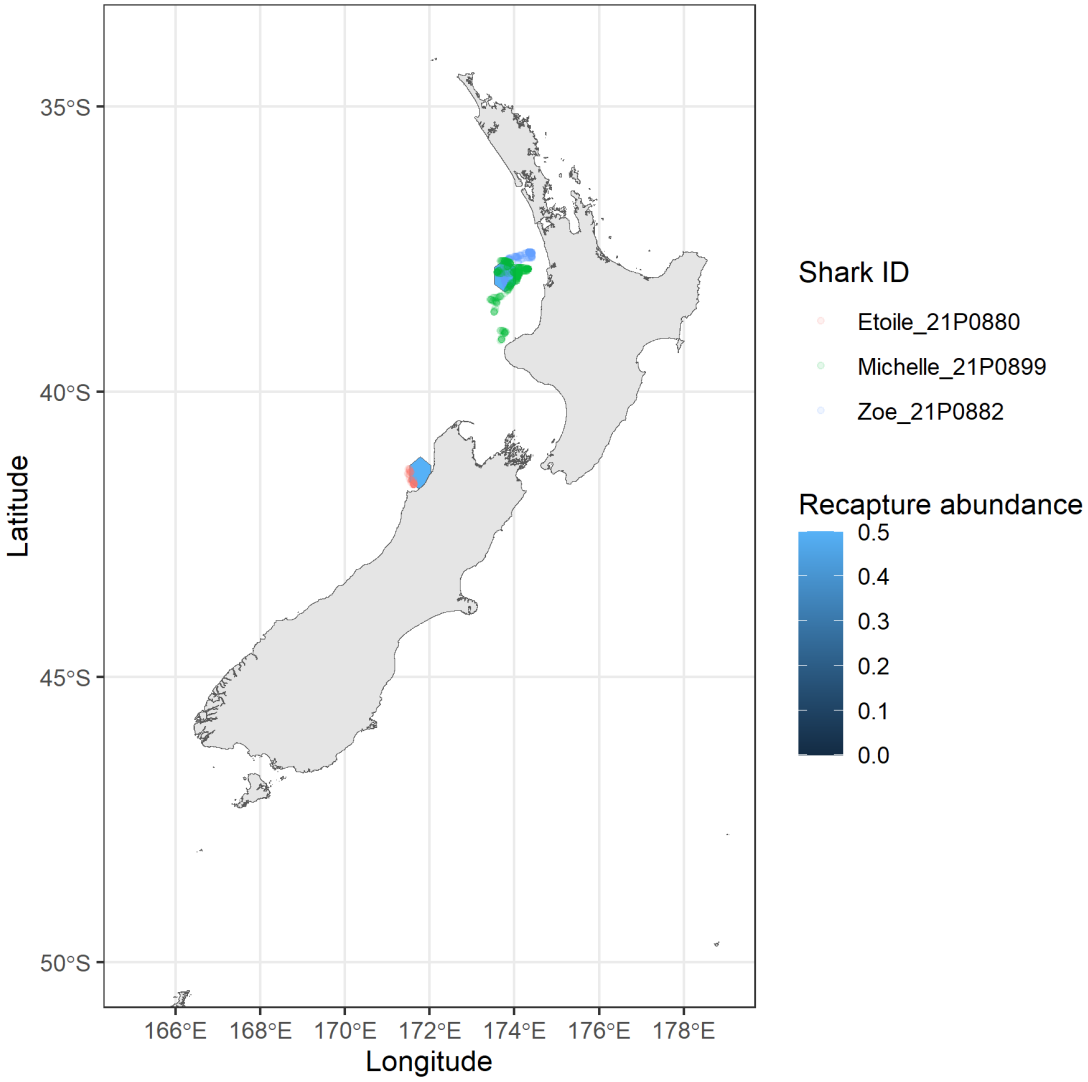


d) Juvenile males

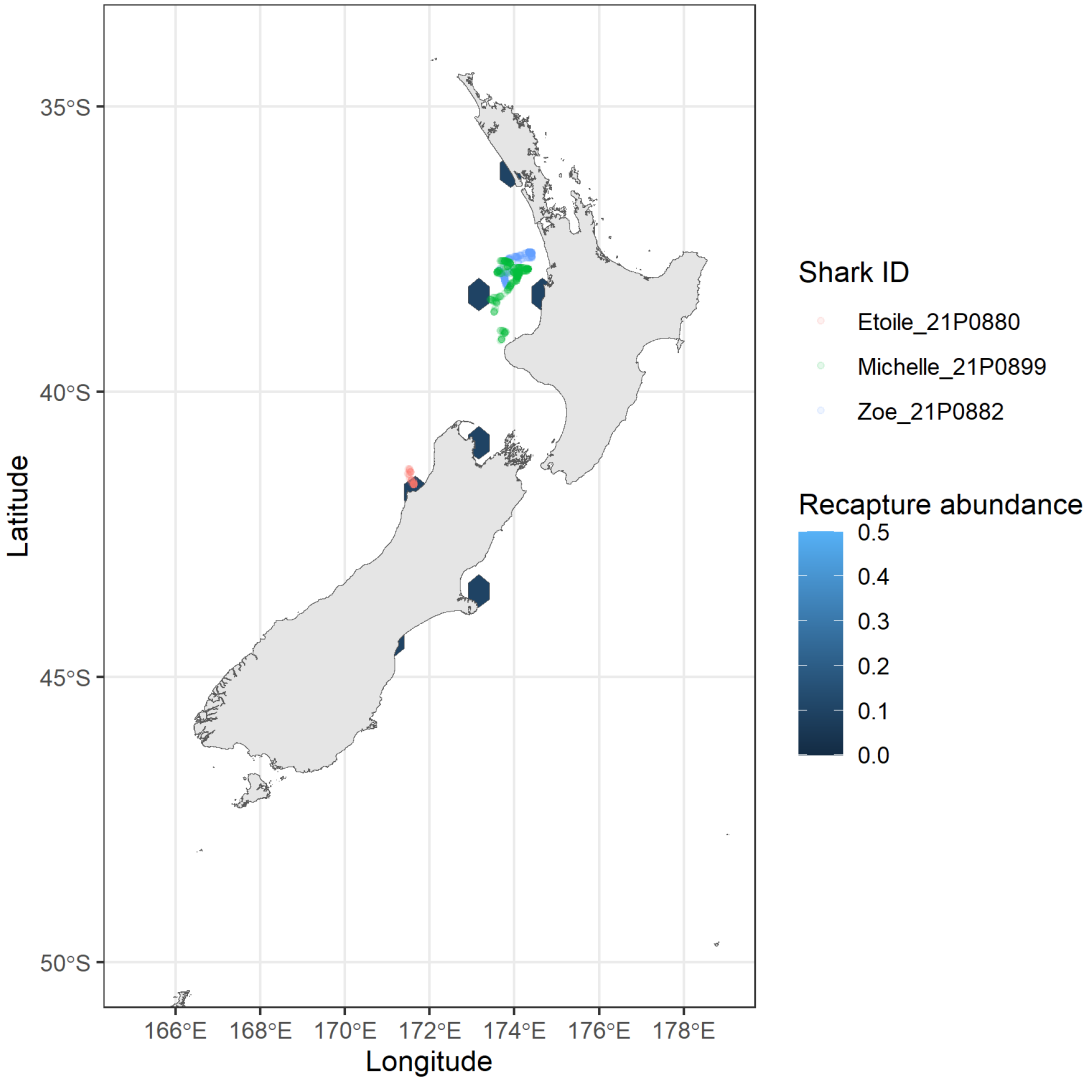
Figure A4.7.4: *Distribution of tagged school sharks released in winter vs temporary residency behaviours of satellite tagged school sharks. Points represent locations where satellite tagged school sharks were estimated to be temporarily residing. Shark ID is the ID of satellite tagged school sharks. Release abundance is the number of sharks released in an area divided by the total number of sharks released.*



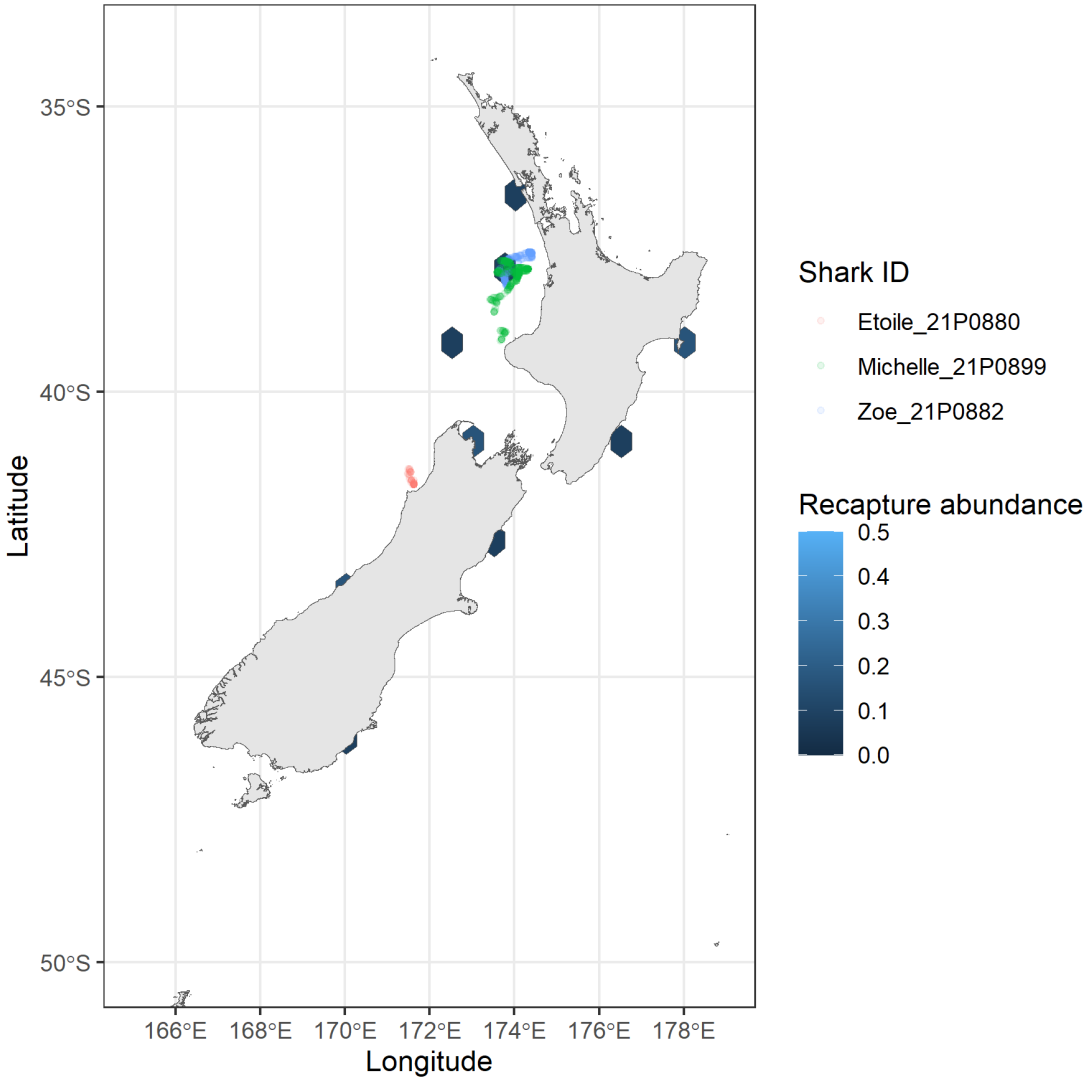
a) Adult females



b) Adult males

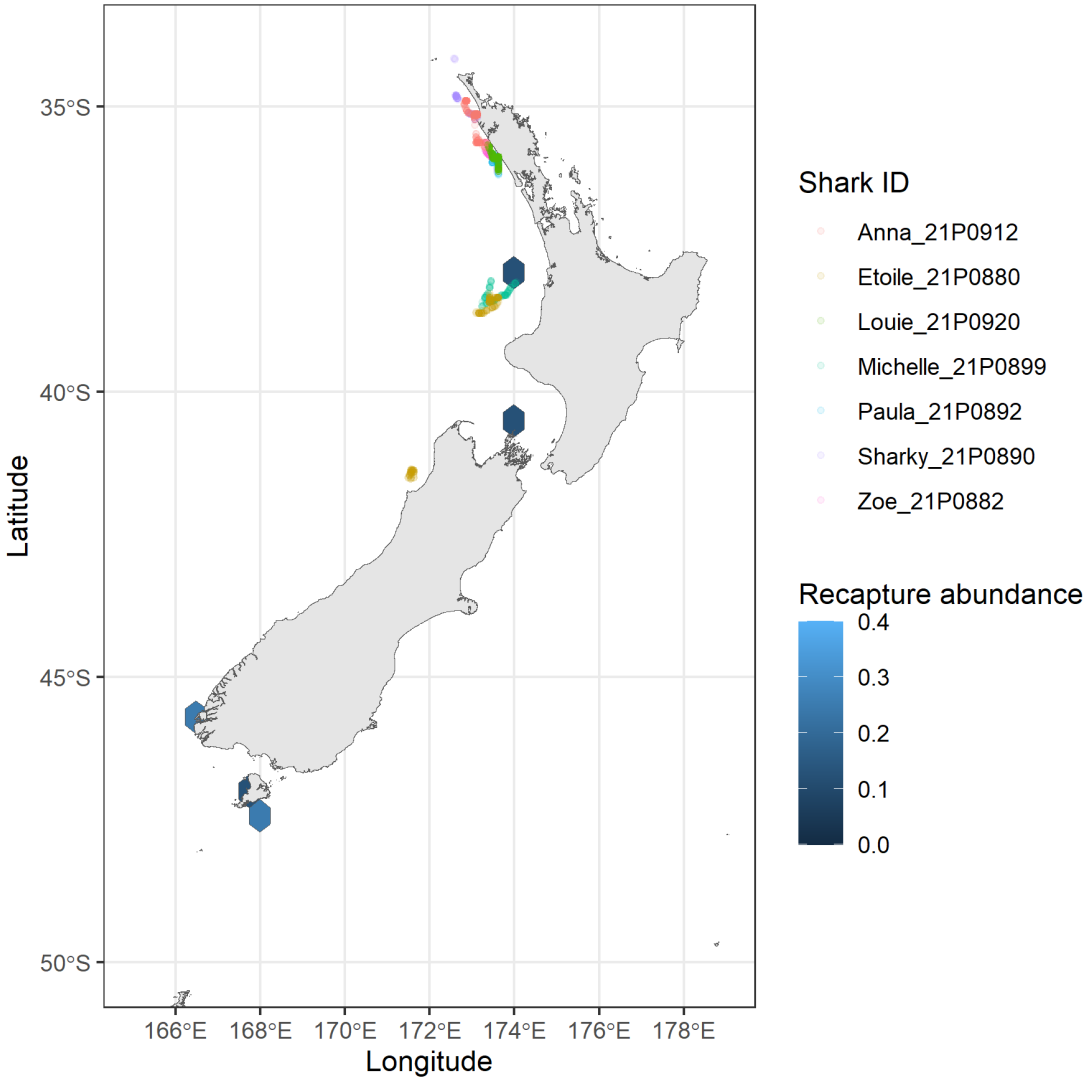


c) Juvenile females

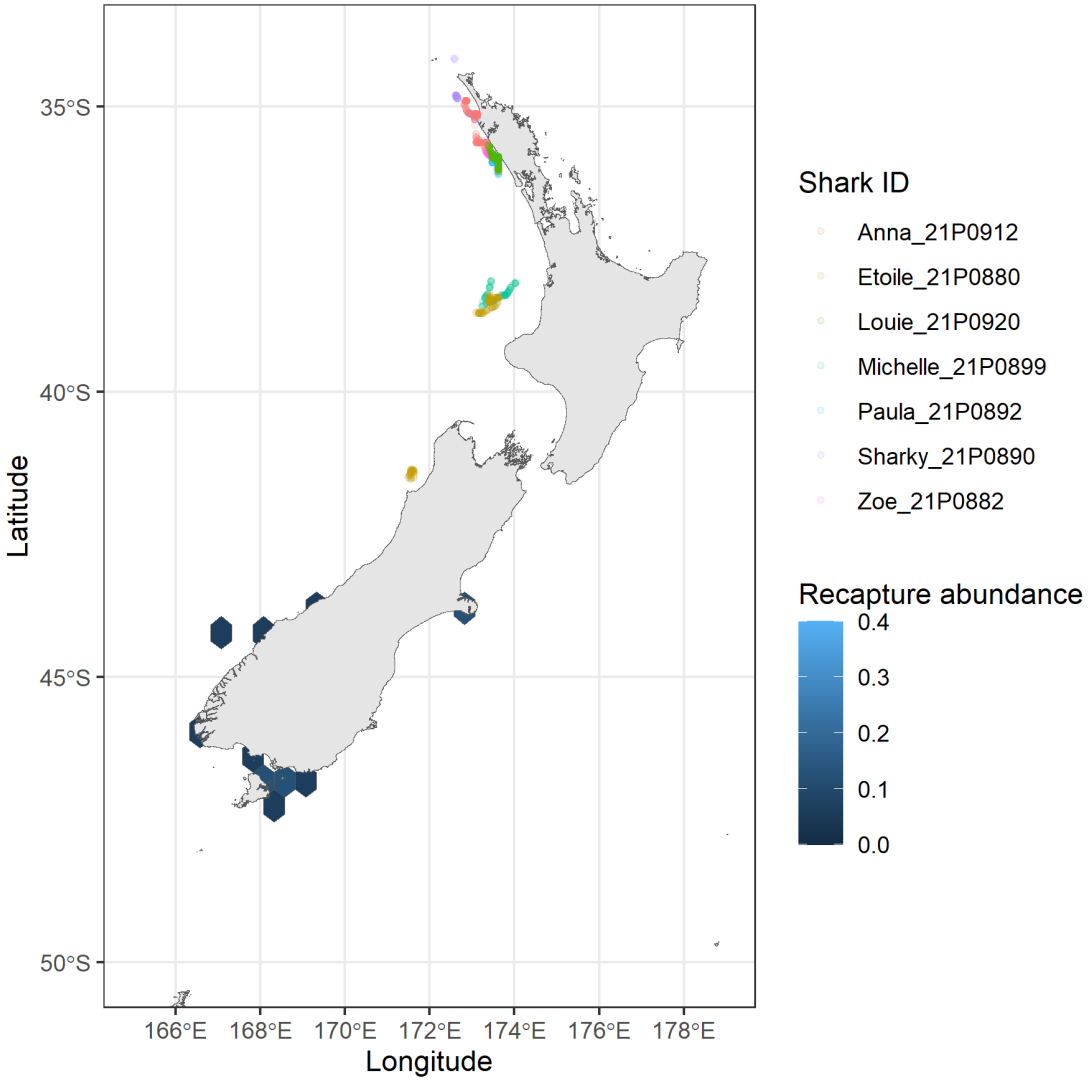


d) Juvenile males

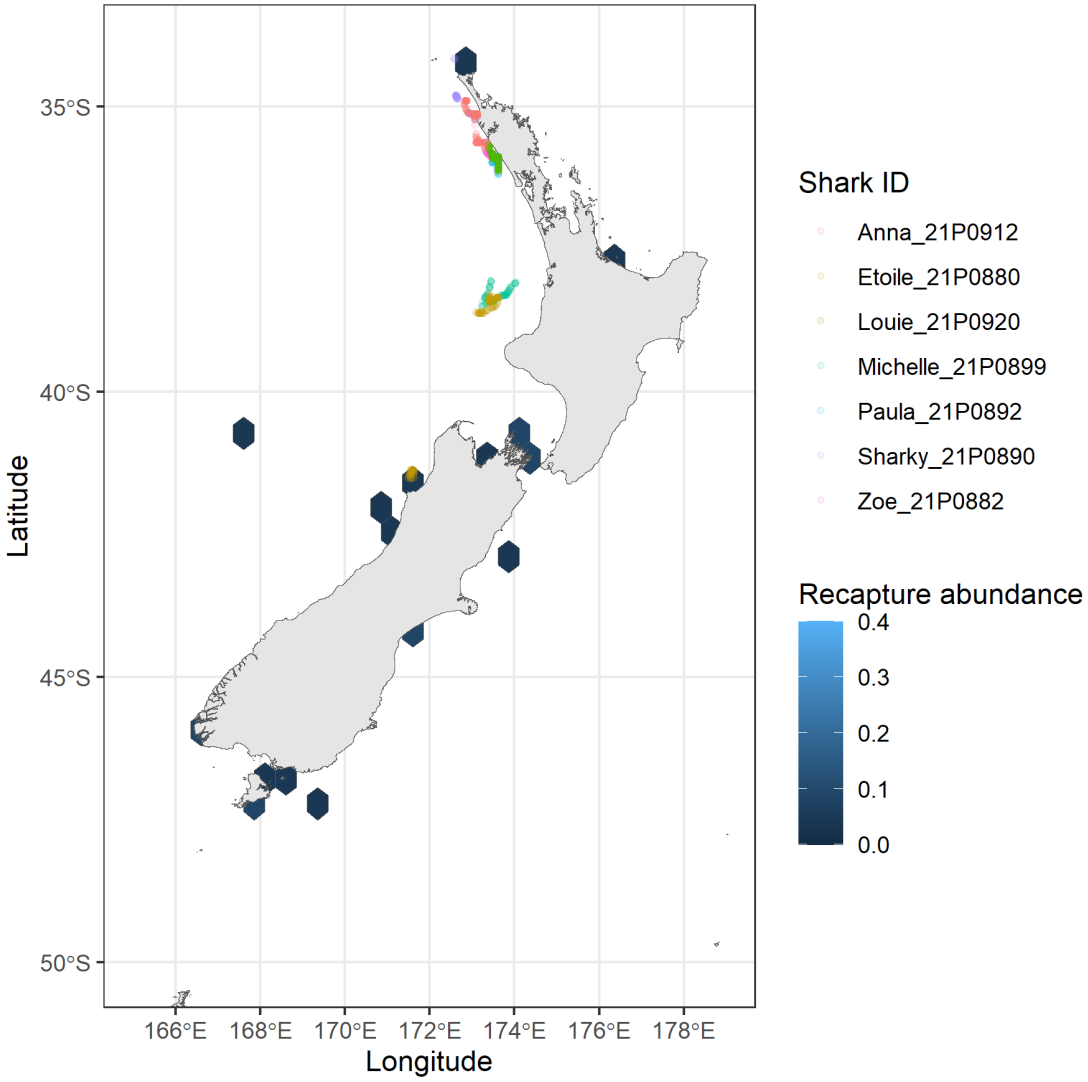
Figure A4.7.5: *Distribution of tagged school sharks recaptured in spring vs temporary residency behaviours of satellite tagged school sharks. Points represent locations where satellite tagged school sharks were estimated to be temporarily residing. Shark ID is the ID of satellite tagged school sharks. Recapture abundance is the number of sharks recaptured in an area divided by the total number of sharks recaptured.*



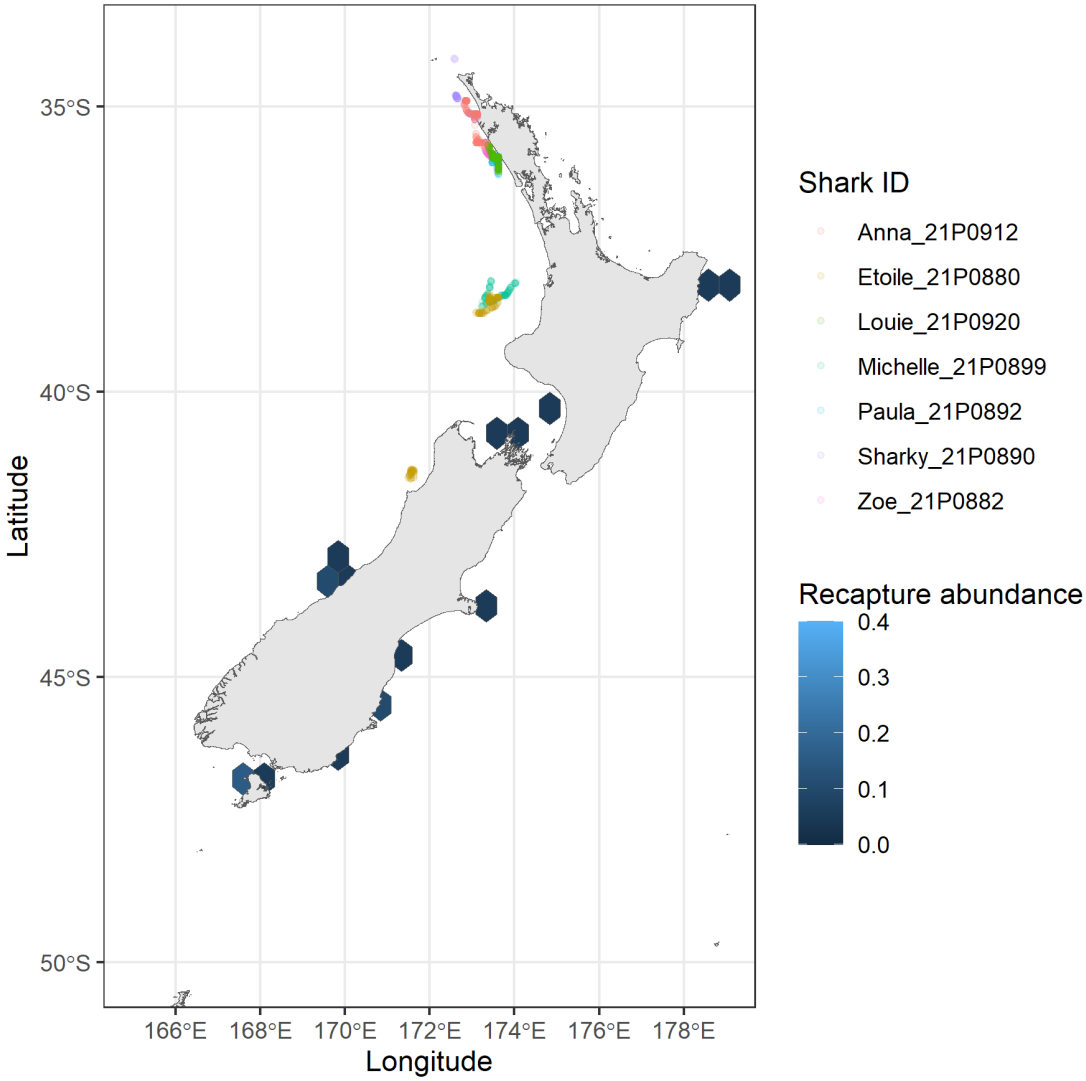
a) Adult females



b) Adult males

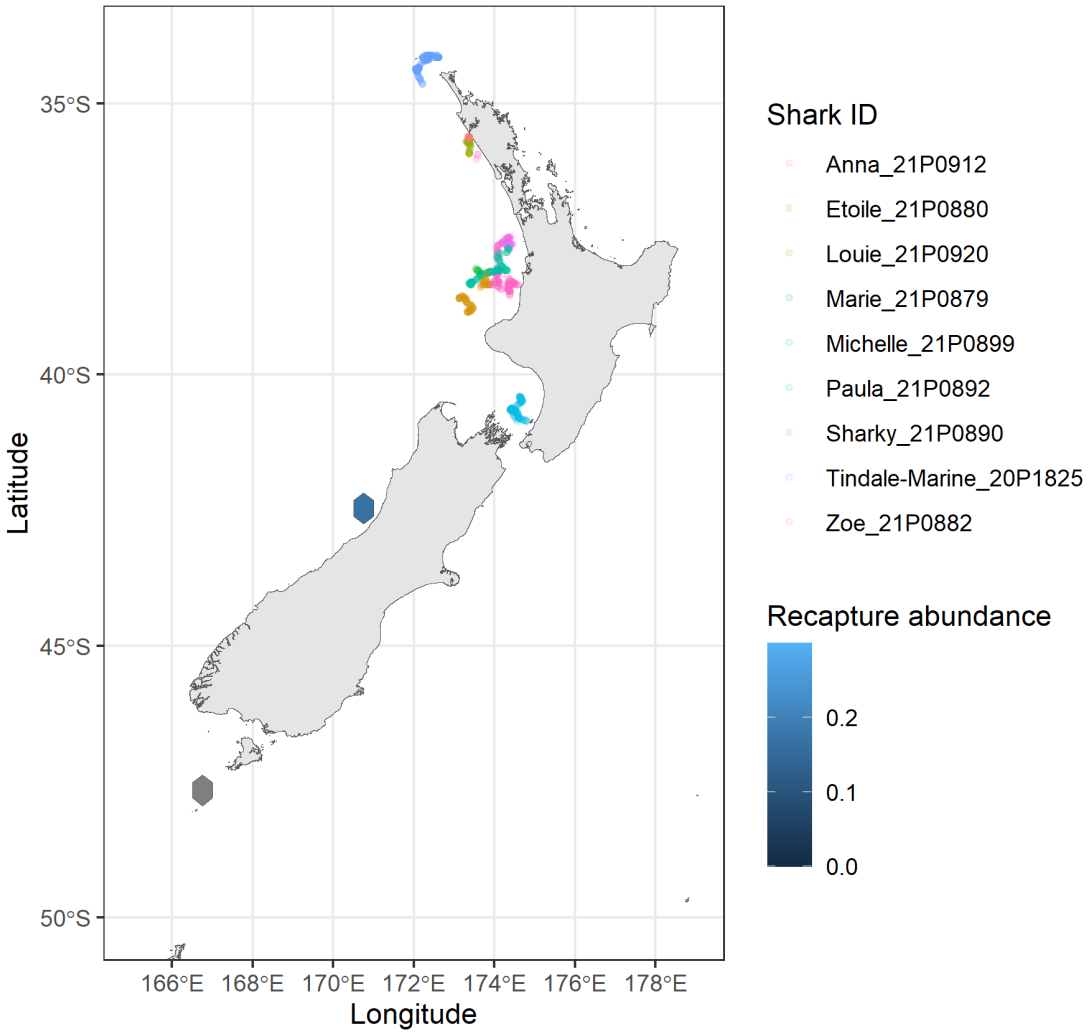


c) Juvenile females

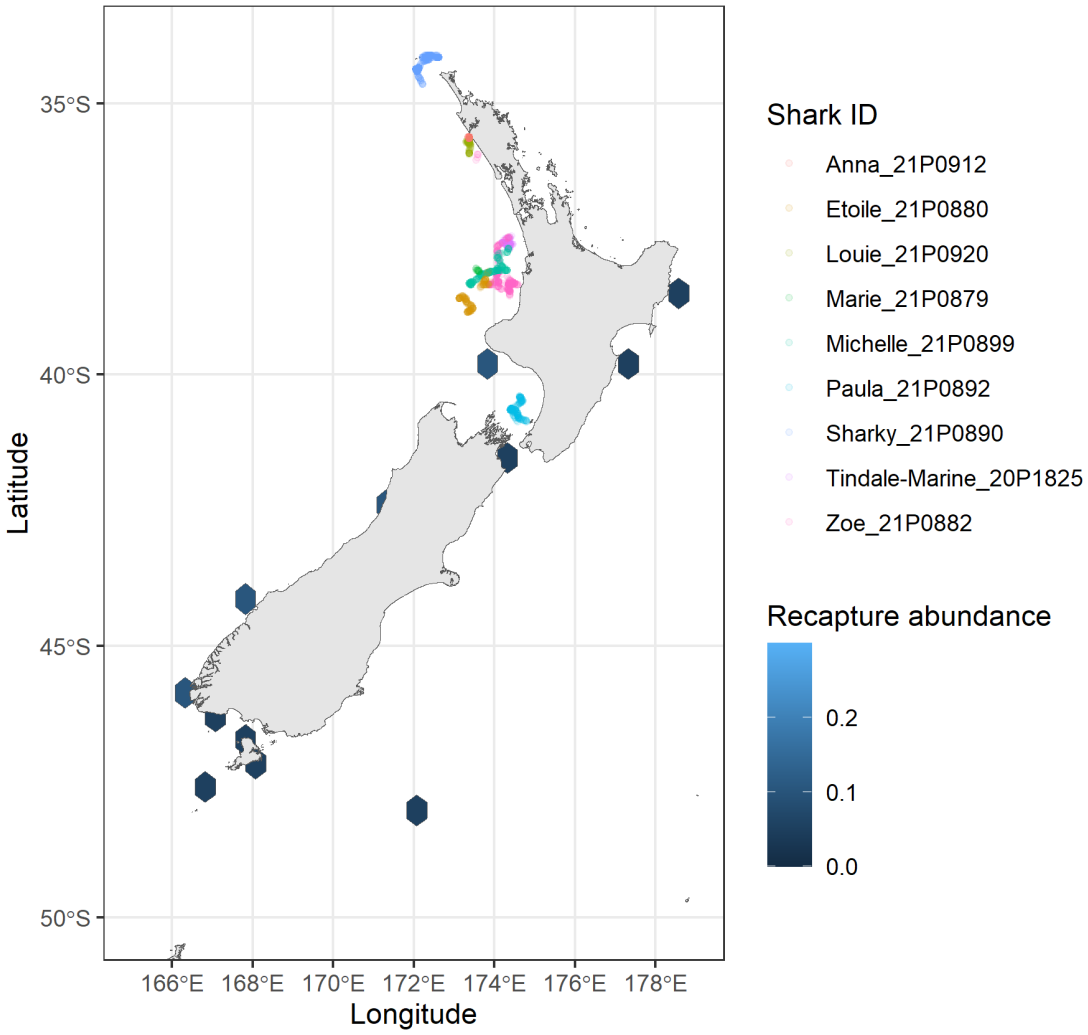


d) Juvenile males

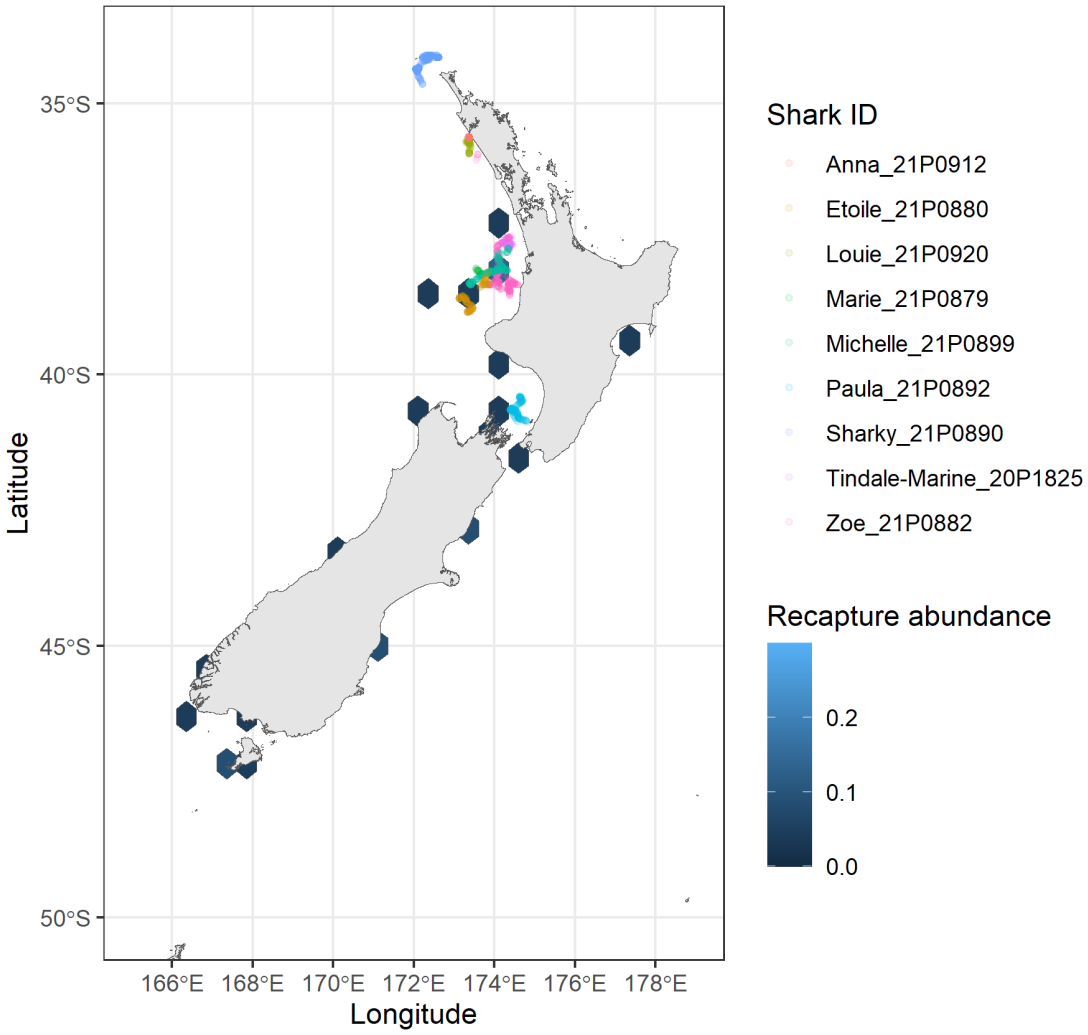
Figure A4.7.6: *Distribution of tagged school sharks recaptured in summer vs temporary residency behaviours of satellite tagged school sharks. Points represent locations where satellite tagged school sharks were estimated to be temporarily residing. Shark ID is the ID of satellite tagged school sharks. Recapture abundance is the number of sharks recaptured in an area divided by the total number of sharks recaptured.*



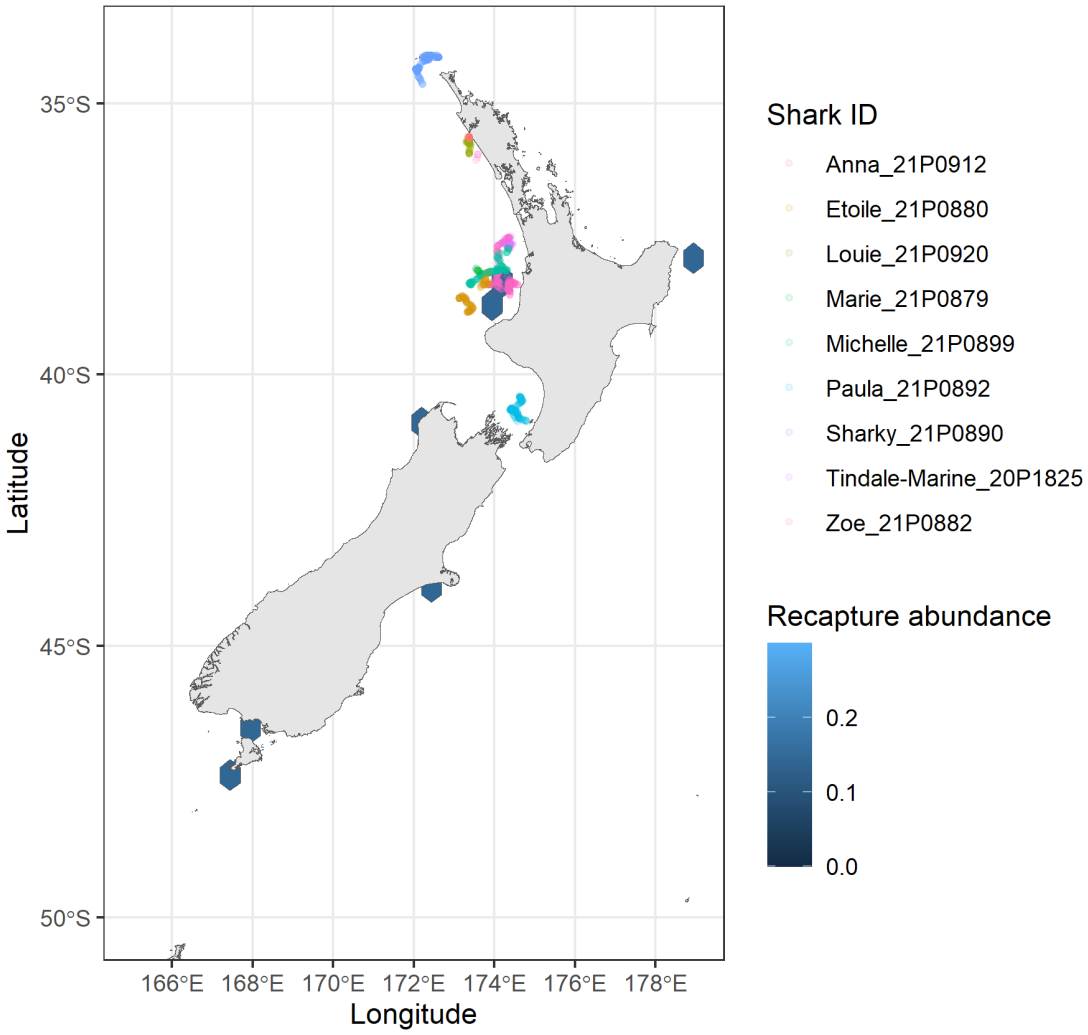
a) Adult females



b) Adult males

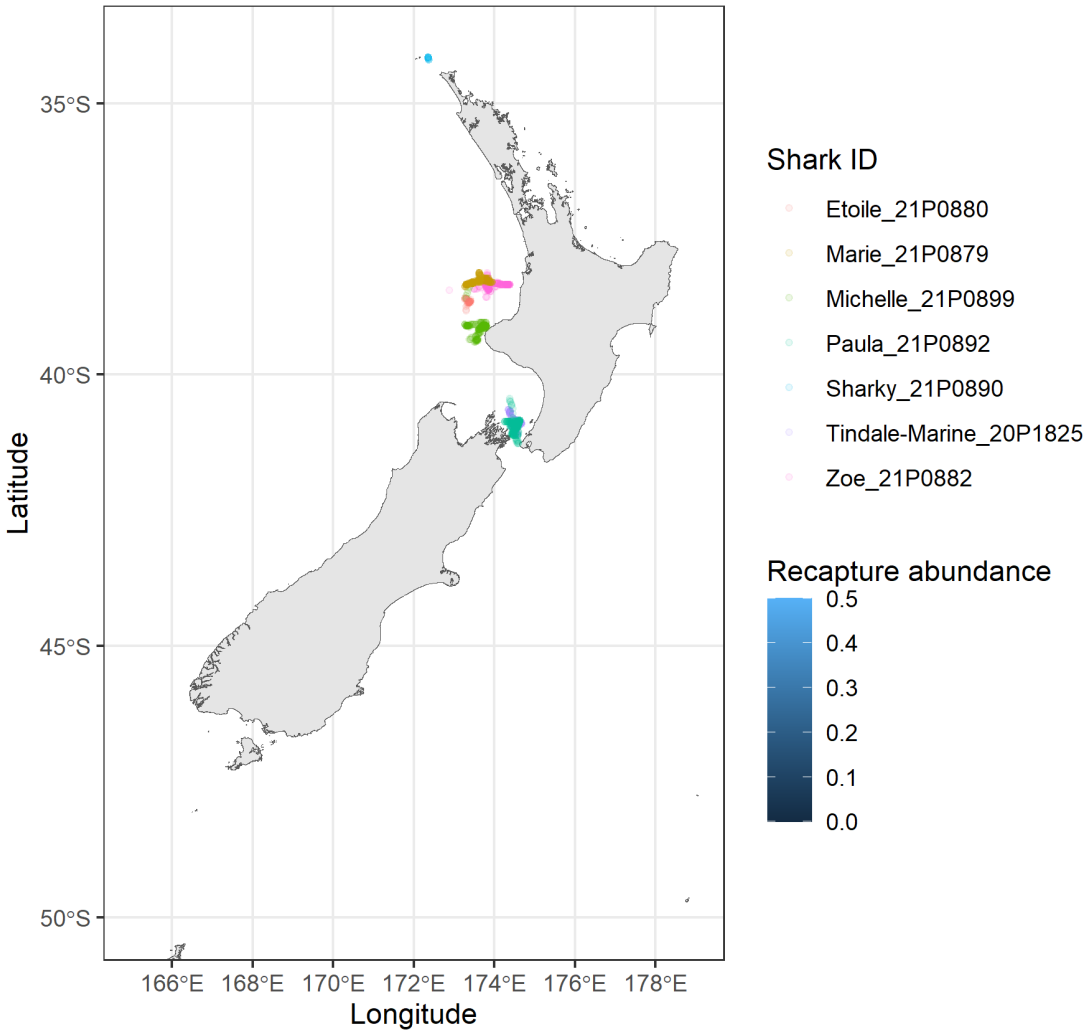


c) Juvenile females

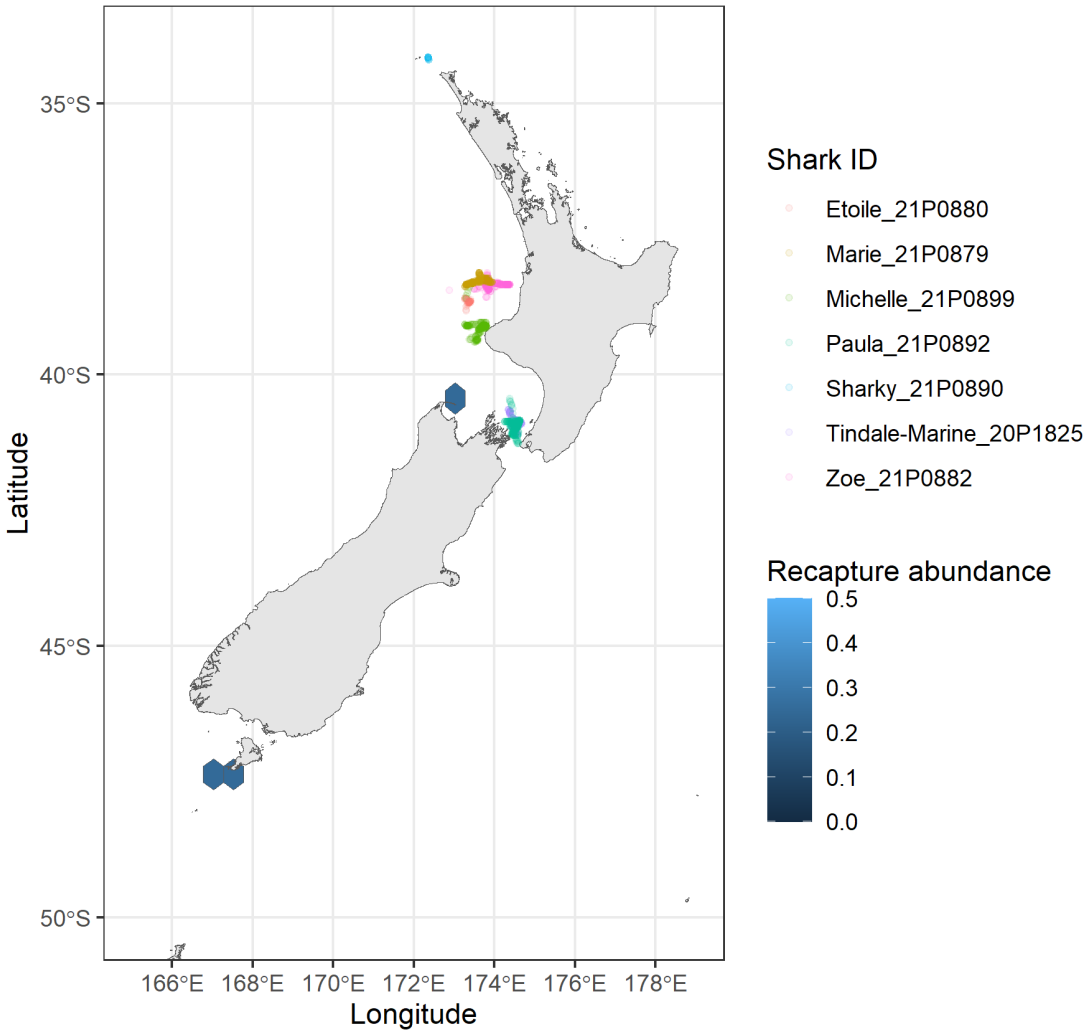


d) Juvenile males

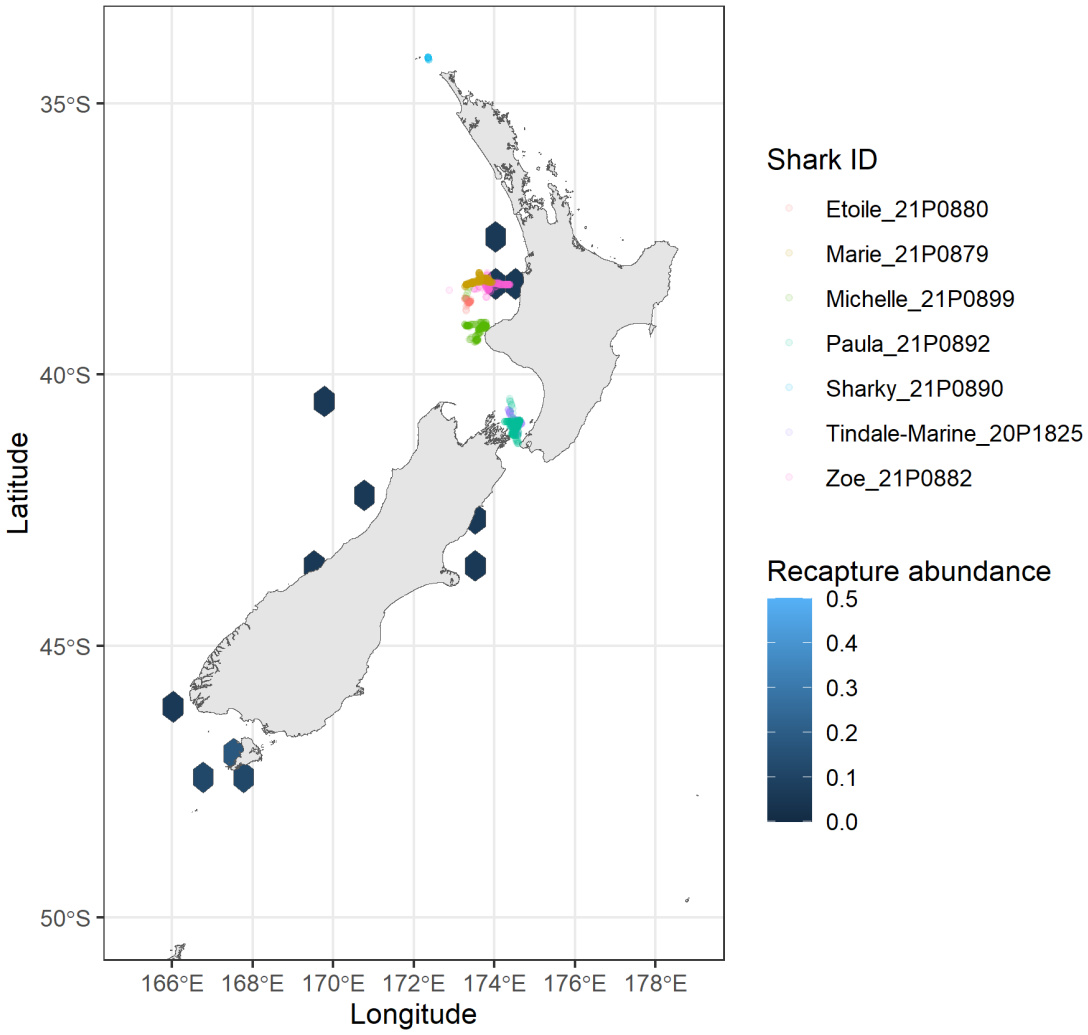
Figure A4.7.7: *Distribution of tagged school sharks recaptured in autumn vs temporary residency behaviours of satellite tagged school sharks. Points represent locations where satellite tagged school sharks were estimated to be temporarily residing. Shark ID is the ID of satellite tagged school sharks. Recapture abundance is the number of sharks recaptured in an area divided by the total number of sharks recaptured.*



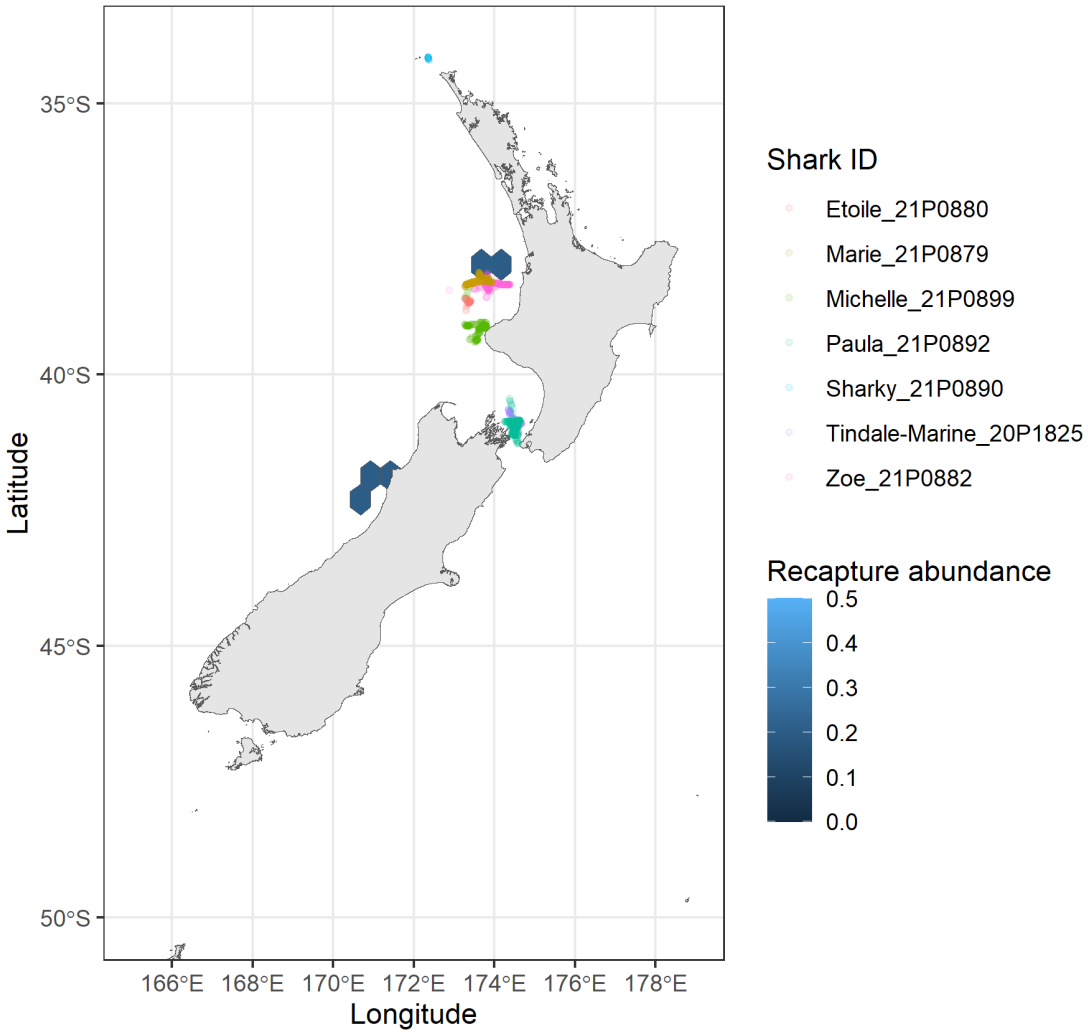
a) Adult females



b) Adult males



c) Juvenile females



d) Juvenile males

Figure A4.7.8: *Distribution of tagged school sharks recaptured in winter vs temporary residency behaviours of satellite tagged school sharks. Points represent locations where satellite tagged school sharks were estimated to be temporarily residing. Shark ID is the ID of satellite tagged school sharks. Recapture abundance is the number of sharks recaptured in an area divided by the total number of sharks recaptured.*

A4.8: Likely diet of New Zealand school sharks

Table A4.8.1: *Potential prey of school sharks in New Zealand. Based on literature (Biton-Porsmoguer, 2022; Coleman & Mobley, 1984; Dunn et al., 2010; Ellis et al., 1996; Freer, 1992; Gonzalez-Pestana et al., 2020; Graham, 1938; Henderson et al., 2003; Lucifora et al., 2006; McCord, 2005; Menni et al., 1982; Morato et al., 2003; Olsen, 1954; Poiesz et al., 2021; Ripley, 1946; Walker et al., 1989; York, 1970); C. Duffy unpublished data; P. Young personal observations; and A. Burton personal observations during school shark post-mortems. Confirmed diet is if a prey item was confirmed as part of the diet of New Zealand school sharks from Dunn et al. (2010); Graham, (1938); C. Duffy unpublished data, or A. Burton personal observations.*

Group	Common name	Scientific name(s)	Confirmed diet
Fish	Pilchard	*Sprattus* sp., *Sardinops* sp.	Y
	Anchovy	*Engraulis australis*	
	Ahuru	*Auchenoceros punctatus*	Y
	Red cod	*Pseudophycis bachus*	Y
	Flatfish	*Rhombosolea* sp., *Pelotretis* sp., *Peltorhamphus* sp., *Colistium* sp.	
	Barracouta	*Thyrsites atun*	
	Jack mackerel	*Trachurus novaezelandiae*, *T. declivis*, *T. murphyi*	Y
	Blue mackerel	*Scomber australasicus*	
	Hoki	*Macruronus novazelandiae*	Y
	Gurnard	*Pterygotrigla andertoni*, *Chelidonichthys kumu*, *Lepidotrigla brachyoptera*	
	Ray's bream	*Brama brama*	Y
	Silverside	*Argentia elongata*	
	Rattail	*Coelorinchus bollonsi*	Y
	Javelin fish	*Coelorinchus australis*	
	Sea perch	*Helicolenus percoides*	Y
	Warehou	*Seriolella brama*, *S. caerulea*, *S. punctata*	
	Snapper	*Pagrus auratus*	Y
	Blue cod	*Parapercis colias*	
	Southern Hake	*Merluccius australis*	
	Redbait	*Emmelichthys nitidus*	
	Scorpion fish	*Scorpaena papillosa*	

Group	Common name	Scientific name(s)	Confirmed diet
	Leatherjacket	*Meuschenia scabra*	
	Barracuda	*Sphyraena waitii*	
	Grey mullet	*Mugil cephalus*	
	Kahawai	*Arripis* sp.	
	Drummer	*Girella* sp.	
	Tarakihi	*Nemadactylus macropterus*	
	Flyingfish	*Cheilopogon pinnatibarbatus*	
	Goatfish	*Upeneichthys lineatus*	
	Conger eel	*Conger* sp.	
Chondrichthyes	Elephant fish	*Callorhinchus milii*	Y
	Spiny dogfish	*Squalus* sp.	Y
	Chimera	*Hydrolagus* sp.	
	Rig	*Mustelus lenticulatus*	
	Skate (eggs)	*Zearaja nasuta*, *Dipturus innominatus*	
Cephalopoda	Squid	*Ancistrocheirus* sp., *Doryteuthis* sp., *Nototodarus* sp., *Sepioteuthis* sp., *Onykia ingens*	Y
	Paper Nautlis	*Argonauta argo*, *A. nodosa*	
	Octopus	*Macroctopus maroum*, *Octopus tericus*, *Octopus vulgaris*, *Robsonella* sp.	
Crustacea	Crabs	Family Brachyura	
	Squat lobster	*Grimothea gregaria*	
	Crayfish	*Jasus edwardsii* (in soft shell state)	

A4.9: Areas of known or suspected importance to school sharks

Table A4.9.1: *Areas of known or suspected importance to the life-history of school sharks in Australia and New Zealand used by, or linked to habitats used by, school sharks that dispersed from the Kaipara Harbour. "*" represents areas used by satellite tagged individuals in Chapter 5. Evidence is what evidence is available to suggest the habitat is important. Confirmed is whether the habitat has been confirmed to provide the suggested services.*

Country	Area	Habitats present	Evidence	Confirmed	References
New Zealand	Canterbury Bight	Pupping/nursery ground	0+ individuals, pregnant females with pups	N	Ministry for Primary Industries (2024a); Paul & Bradford (2000)
New Zealand	Golden and Tasman Bays	Pupping/nursery ground	Newborns, 0+ individuals, pregnant females with pups	N	Ministry for Primary Industries (2024a); Figure 6.1; A. Burton unpublished data; M. Cryer personal observations
New Zealand	Kapiti Coast	Pupping/nursery ground	Newborns, 0+ individuals, pregnant females with pups	N	Coxon (2018); Hernández Muñoz (2013); M. Griffiths personal observations
New Zealand	North Taranaki Bight*	Mating and gestation ground	Pregnant females with pups, mature males and females at the same time	N	Figure 5.3; Figure 6.1; Appendix 4.7; A. Burton personal observations
New Zealand	Otago Peninsula	Pupping/nursery ground	1+ individuals, pregnant females with pups	N	Boyd (2008); Francis et al. (2012); Paul & Bradford (2000); Figure 5.5b; C. Duffy unpublished data
New Zealand	Snares Islands*	Mating ground	Mature males and females at the same time	N	Figures A4.4.3 and A4.5.3; Appendix 4.7
New Zealand	Stewart Island	Mating and pupping/nursery ground	Pregnant females with pups, mature males and females at the same time	N	McMillan et al. (2019); Paul & Bradford (2000); Figure 5.5a-d; Appendix 4.7
New Zealand	Westport*	Mating and pupping/nursery grounds	Newborns, 0+ individuals, pregnant females with pups, mature males and females at the same time	N	Ministry for Primary Industries (2024a); Paul & Bradford (2000); Figures A4.4.9 and A4.5.9; Appendix 4.7
Australia	Bass Strait (incl. Victoria)	Pupping/nursery ground	Newborns, 0+ individuals, pregnant females with pups	Y	Stevens & West (1997)
Australia	Tasmania	Pupping/nursery ground	Newborns, 0+ individuals, pregnant females with pups	Y	McAllister et al. (2015); Stevens & West (1997)
Australia	South Australia	Pupping/nursery and gestation ground	Newborns, 0+ individuals, pregnant females with pups	N	McMillan et al. (2018); McMillan et al. (2019); Rogers et al. (2017)

Appendix 5 – Chapter 6: Maternal transfer potential

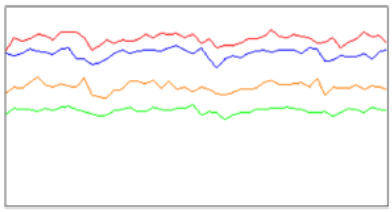
A5.1: Inductively Coupled Plasma – Mass Spectrometry instrument conditions

Tune Check Report

Operator Name	ICPMS-admin
Acq/Data Batch	C:\Agilent\ICPMH\1\DATA\ICP-MS Data\09-11-2023_Shark_Alex Burton_Massey_A.b
Acq. Date-Time	11/9/2023 1:42:03 PM
Report Comment	---
Instrument Name	G3281A JP11481420

[He]

Sensitivity



Sampling Period [sec]	0.412
Integration Time [sec]	0.1

Mass	Range	Count	Resp [cps/ug/l]	Resp (Required) [cps/ug/l]	Resp (Flag)
59	10000	8415			
89	20000	9596			
205	20000	15339			
24	5000	2995			

Mass	Resp Ratio	Resp Ratio (Required)	Resp Ratio (Flag)
59		-	
89		-	
205		-	
24		-	

Mass	RSD%	RSD% (Required)	RSD% (Flag)
59	2.874		
89	3.132		
205	3.167		
24	4.084		

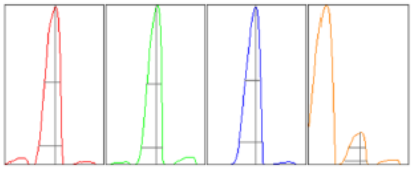
Mass	Background	Background (Required)	Background (Flag)
59	0.400		
89	1.300		
205	4.400		
24	0.000		

Oxide/Doubly Charged Ratio

Oxide	156 / 140 0.821 %
Doubly Charged	70 / 140 2.472 %

Resolution/Axis

Tune Check Report



Integration Time [sec]	0.1
Acquisition Time [sec]	29.92
Y Axis	Linear

Mass	Peak Height	Axis	Axis (Required)	Axis (Flag)
59	8658.87	59.05	58.90 - 59.10	
89	10230.53	89.05	88.90 - 89.10	
205	15233.50	205.00	204.90 - 205.10	
24	3038.83	24.05	-	

Mass	W-50%	W-10%	W-10% (Required)	W-10% (Flag)
59	0.49	0.708	0.900	
89	0.45	0.644	0.900	
205	0.46	0.695	0.900	
24	0.51	0.693		

Tune Parameters

Plasma Parameters

Plasma Mode	---	Nebulizer Gas	1.00 L/min	Makeup Gas	0.10 L/min
RF Power	1550 W	Option Gas	0.0 %	Auxiliary Gas	0.90 L/min
RF Matching	1.60 V	Nebulizer Pump	0.10 rps	Plasma Gas	15.0 L/min
Sample Depth	5.0 mm	S/C Temp	2 °C		

Lens Parameters

Extract 1	-5.0 V	Omega Lens	8.6 V	Deflect	-3.4 V
Extract 2	-200.0 V	Cell Entrance	-40 V	Plate Bias	-60 V
Omega Bias	-120 V	Cell Exit	-68 V		

Cell Parameters

Use Gas	Yes	3rd Gas Flow	---	Energy Discrimination	3.0 V
He Flow	4.0 mL/min	OctP Bias	-19.0 V		
H2 Flow	---	OctP RF	200 V		

QP Parameters

Mass Gain	127	Axis Gain	0.9997	QP Bias	-16.0 V
Mass Offset	124	Axis Offset	-0.02		

Hardware Settings

Torch

Torch H	-0.1 mm	Torch V	0.5 mm		

EM

Discriminator	4.7 mV	Analog HV	2182 V	Pulse HV	1845 V

A5.2: Summary of element concentrations in the tissues of school sharks and their young

Table A5.2.1: *Concentrations of elements (mg kg^{-1}, wet weight) in maternal tissues. The error associated with the reported values is the relative standard deviation. For concentrations reported as < LOQ, they were below the Limit of Quantification for that element.*

Mother	Tissue	Ag	As	Cu	Hg	Pb	Se	U	Zn
ES3	Liver	0.0120± 0.0004	34.7±1.6	1.08±0.05	1.87±0.08	<LOQ	5.73±0.28	0.00281± 0.00008	9.39±0.26
ES3	Muscle	0.00030± 0.00004	15.20±0.24	0.0995± 0.0033	2.67±0.06	0.000656± 0.000083	0.4240± 0.0067	<LOQ	2.580± 0.057
ES4	Liver	0.00742± 0.00023	43.8±1.7	1.38±0.05	4.51±0.16	0.00184± 0.00009	8.72±0.33	0.00615± 0.00019	17.50±0.58
ES4	Muscle	<LOQ	25.60±0.64	0.087± 0.002	2.38±0.03	0.00409± 0.00011	0.357± 0.011	0.000100± 0.000007	2.520± 0.067
ET1	Liver	0.01430± 0.00029	51.4±2.0	1.52±0.06	1.39±0.04	0.00113± 0.00006	7.80±0.31	0.00257± 0.00007	15.00±0.51
ET1	Muscle	0.00033± 0.00004	15.0±0.4	0.114± 0.003	1.82±0.02	<LOQ	0.433± 0.022	<LOQ	2.880± 0.066
MK1	Liver	0.0121± 0.0006	26.4±1.5	1.32±0.07	1.12±0.06	<LOQ	11.00±0.66	0.00106± 0.00005	6.05±0.31
MK1	Muscle	0.00050± 0.00015	10.10±0.19	0.1610± 0.0033	1.51±0.03	<LOQ	0.5310± 0.0089	0.0000473± 0.0000372	2.610± 0.054
RK1	Liver	0.01780± 0.00079	17.10±0.96	1.30±0.07	1.95±0.10	0.00114± 0.00013	8.46±0.52	0.00184± 0.00004	11.80±0.61
RK1	Muscle	0.000463± 0.000041	10.60±0.13	0.0893± 0.0012	1.86±0.02	0.001630± 0.000082	0.483± 0.015	0.0000411± 0.0000036	2.50±0.04
RK2	Liver	0.07590± 0.00083	42.8±1.4	4.20±0.13	5.13±0.13	0.00486± 0.00013	7.21±0.26	0.00886± 0.00032	25.30±0.68
RK2	Muscle	0.000407± 0.000036	19.5±0.3	0.0963± 0.0017	2.14±0.04	0.00542± 0.00012	0.2640± 0.0049	<LOQ	2.410± 0.038
ST1	Liver	0.05010± 0.00086	33.2±1.2	1.59±0.04	12.1±0.4	0.00248± 0.00012	14.80±0.58	0.01080± 0.00025	18.90±0.59
ST1	Muscle	0.000549± 0.000027	11.1±0.2	0.0942± 0.0012	2.97±0.05	0.001230± 0.000094	0.464± 0.015	<LOQ	2.810± 0.042

Table A5.2.2: *Concentration of elements (mg kg^{-1}, wet weight) in embryo tissues. The error associated with the average tissue concentrations is the standard deviation of the mean. For concentrations reported as < LOQ, they were below the Limit of Quantification for that element.*

Mother	Element	n	Liver Range	Liver Average	Muscle Range	Muscle Average	Yolk sac Range	Yolk sac Average
ES3	Ag	4	0.115 - 0.179	0.151±0.027	0.000903 – 0.007201	0.00370± 0.00278	0.00949 – 0.01172	0.01048± 0.00098
ES3	As	4	16.2 - 21.7	18.71±2.55	3.87 - 5.21	4.43±0.57	7.25 - 9.06	8.24±0.75
ES3	Cu	4	4.30 - 9.08	7.67±2.27	0.293 - 0.645	0.481±0.156	1.25 - 1.52	1.36±0.12
ES3	Hg	4	0.0396 – 0.0641	0.0537± 0.0116	0.136 - 0.165	0.155±0.013	0.0650 – 0.0951	0.0798± 0.0137
ES3	Pb	4	0.00543 – 0.01639	0.00961± 0.00473	0.0166 – 0.0469	0.0313± 0.0124	0.00169 – 0.01069	0.00583± 0.00458
ES3	Se	4	7.47 - 9.25	8.34±0.74	2.59 - 3.36	2.88±0.34	3.91 - 4.54	4.31±0.28
ES3	U	4	0.0000833 – 0.0004202	0.000230± 0.000145	0.000145 – 0.000244	0.000177± 0.000047	0.000513 – 0.000671	0.000618± 0.000074
ES3	Zn	4	4.43 - 5.32	4.91±0.41	3.44 - 4.63	4.08±0.49	8.41 - 9.50	9.15±0.51
ES4	Ag	8	0.0813 – 0.0932	0.0876± 0.0038	0.00128 – 0.00390	0.00272± 0.00105	0.00654 – 0.00773	0.00728± 0.00047
ES4	As	8	12.4 - 15.2	14.45±0.85	3.36 - 4.26	3.87±0.25	6.15 - 8.36	6.94±0.73
ES4	Cu	8	8.67 - 10.10	9.45±0.48	0.370 - 0.588	0.454±0.082	1.53 - 1.79	1.69±0.11
ES4	Hg	8	0.0202 – 0.0370	0.0248± 0.0055	0.0594 – 0.0939	0.0740± 0.0107	0.027 - 0.052	0.0408± 0.0100
ES4	Pb	8	0.000973 – 0.041025	0.0112± 0.0136	0.0101 – 0.0529	0.0373± 0.0144	0.00214 – 0.00361	0.00279± 0.00056
ES4	Se	8	7.83 - 11.50	8.91±1.19	2.02 - 3.71	2.58±0.68	3.55 - 6.14	4.80±0.98
ES4	U	8	0.000195 – 0.000379	0.000280± 0.000063	0.0000914 – 0.0003664	0.000161± 0.000089	0.000440 – 0.000733	0.000602± 0.000094
ES4	Zn	8	5.34 - 6.33	5.94±0.34	3.55 - 4.84	4.34±0.39	10.4 - 12.2	11.43±0.76
RK1	Ag	8	0.0381 – 0.0483	0.0439± 0.0035	<LOQ – 0.00892	0.00213± 0.00308		
RK1	As	8	13.8 - 25.2	21.48±3.72	1.36 - 1.84	1.53±0.14		
RK1	Cu	8	3.47 - 5.76	5.03±0.80	0.213 - 1.448	0.411±0.421		

Mother	Element	n	Liver Range	Liver Average	Muscle Range	Muscle Average	Yolk sac Range	Yolk sac Average
RK1	Hg	8	0.0473 – 0.1082	0.0766± 0.0202	0.157 - 0.239	0.196±0.029		
RK1	Pb	8	0.00311 – 0.00783	0.00559± 0.00202	0.00167 – 0.06807	0.0235± 0.0255		
RK1	Se	8	9.96 - 25.32	14.93±5.38	2.16 - 5.06	3.28±1.01		
RK1	U	8	0.0000327 – 0.0001599	0.0000768± 0.0000377	0.0000380 – 0.0003178	0.000140± 0.000101		
RK1	Zn	8	4.77 - 5.92	5.18±0.40	3.44 - 4.74	3.87±0.40		
RK2	Ag	8	0.0121 – 0.0478	0.0392± 0.0115	0.000390 – 0.000978	0.000615± 0.000228		
RK2	As	8	29.2 - 41.2	34.02±3.99	1.74 - 2.27	1.98±0.17		
RK2	Cu	8	1.51 - 7.31	4.29±1.60	0.201 - 0.555	0.270±0.117		
RK2	Hg	8	0.0252 – 0.1018	0.0470± 0.0257	0.114 - 0.182	0.155±0.023		
RK2	Pb	8	<LOQ – 0.0240	0.00853± 0.00934	<LOQ – 0.0822	0.0231± 0.0274		
RK2	Se	8	7.60 - 13.08	10.55±2.01	1.89 - 4.32	2.69±0.84		
RK2	U	8	0.0000708 – 0.0001407	0.000106± 0.000025	0.0000481 – 0.0003089	0.000117± 0.000084		
RK2	Zn	8	4.11 - 5.18	4.74±0.39	3.58 - 4.07	3.79±0.17		

Table A5.2.3: *Concentration of elements (mg kg^{-1}, wet weight) in egg yolk. The error associated with the average tissue concentrations is the standard deviation of the mean. For concentrations reported as < LOQ, they were below the Limit of Quantification for that element.*

Mother	Element	n	Egg yolk Range	Egg yolk Average
ES3	Ag	2	0.0159 - 0.0170	0.01647±0.00082
ES3	As	2	9.01 - 9.11	9.060±0.066
ES3	Cu	2	1.81 - 1.89	1.851±0.061
ES3	Hg	2	0.0681 - 0.0799	0.0740±0.0084
ES3	Pb	2	<LOQ	<LOQ
ES3	Se	2	4.96 - 5.30	5.13±0.24
ES3	U	2	0.000761 - 0.000820	0.000791±0.000041
ES3	Zn	2	11.1 - 11.3	11.21±0.20
ET1	Ag	4	0.0104 - 0.0113	0.01073±0.00039
ET1	As	4	11.6 - 12.8	12.31±0.54
ET1	Cu	4	1.53 - 1.65	1.579±0.053
ET1	Hg	4	0.0461 - 0.0618	0.0511±0.0073
ET1	Pb	4	0.000702 - 0.003888	0.0021±0.0014
ET1	Se	4	7.07 - 9.93	8.50±1.18
ET1	U	4	0.000719 - 0.000836	0.000773±0.000054
ET1	Zn	4	9.86 - 11.12	10.39±0.55
MK1	Ag	4	0.00983 - 0.01368	0.0110±0.0018
MK1	As	4	8.90 - 10.06	9.23±0.56
MK1	Cu	4	1.26 - 1.37	1.310±0.046
MK1	Hg	4	0.0444 - 0.0513	0.0469±0.0030
MK1	Pb	4	<LOQ - 0.000654	0.000654
MK1	Se	4	7.20 - 9.70	8.16±1.08
MK1	U	4	0.000792 - 0.000834	0.000810±0.000020
MK1	Zn	4	10.6 - 11.8	11.16±0.59
ST1	Ag	4	0.0124 - 0.0162	0.0140±0.0017
ST1	As	4	5.86 - 9.13	7.72±1.36
ST1	Cu	4	1.61 - 1.87	1.77±0.12
ST1	Hg	4	0.0634 - 0.1344	0.0839±0.0339
ST1	Pb	4	<LOQ - 0.0130	0.00582±0.00641
ST1	Se	4	4.31 - 5.71	5.03±0.57
ST1	U	4	0.000842 - 0.000952	0.000903±0.000051
ST1	Zn	4	12.1 - 13.6	12.99±0.65

A5.3: Element concentration vs stage and mother capture location

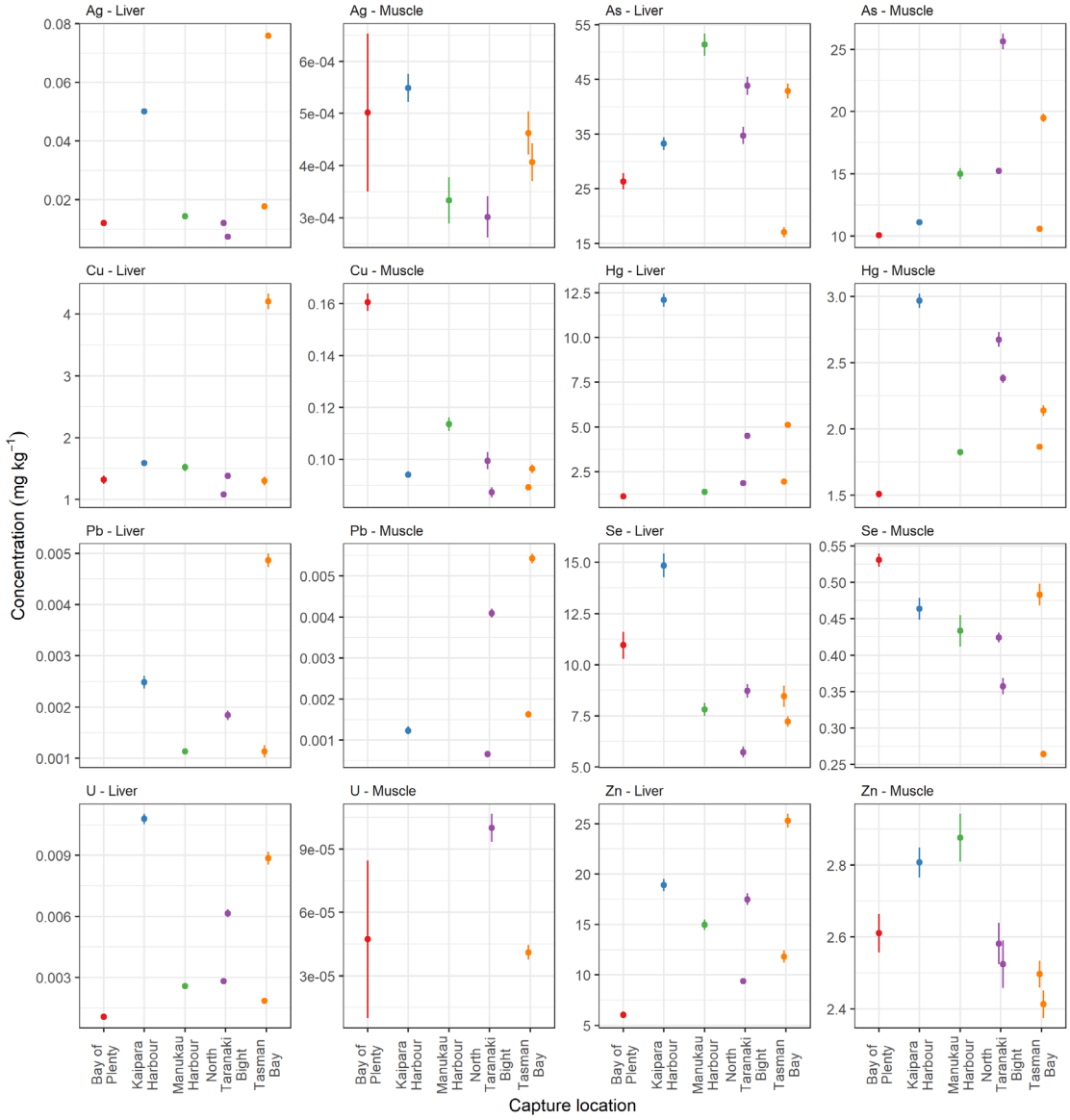


Figure A5.3.1: *Concentrations of elements in maternal liver and muscle tissue across capture locations. The vertical lines are the relative standard deviations of the measured concentrations. Points represent individual mothers.*

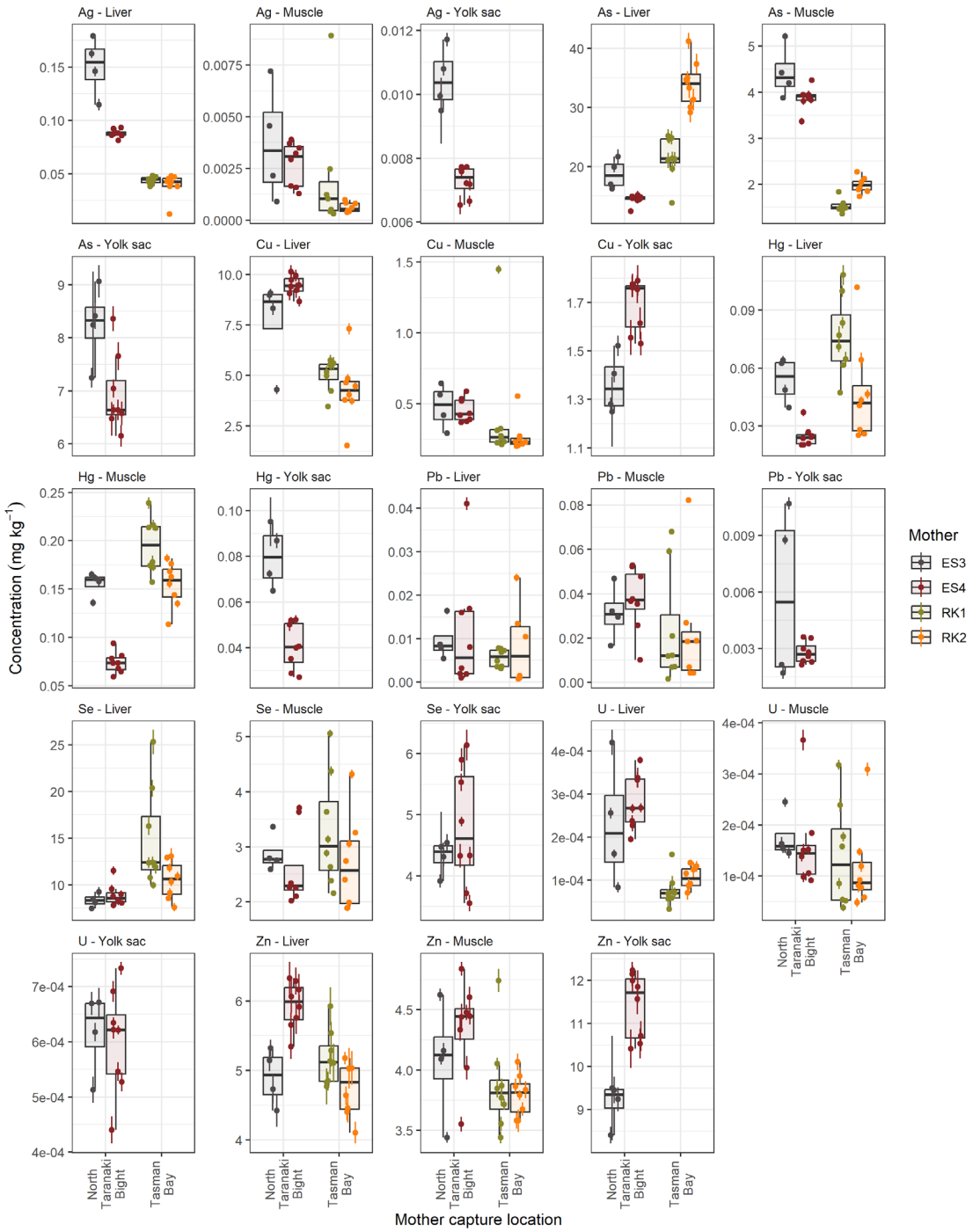


Figure A5.3.2: *Concentrations of elements in embryo liver and muscle tissue across capture locations. The vertical lines are the relative standard deviations of the measured concentrations. Mother represents the litter the embryos were a part of.*

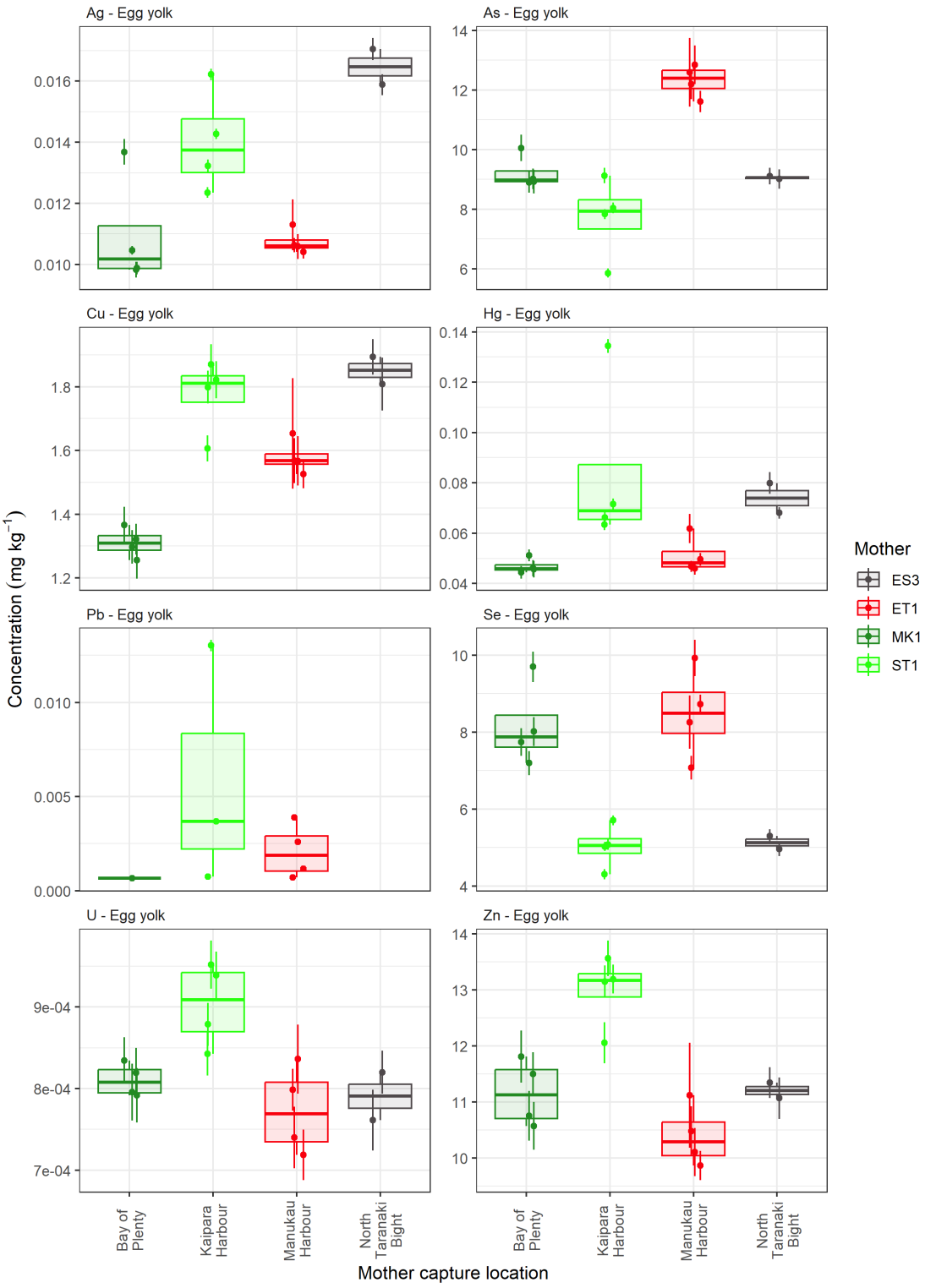


Figure A5.3.3: *Concentrations of elements in egg tissue across capture locations. The vertical lines are the relative standard deviations of the measured concentrations. Mother represents the litter the eggs were a part of.*

A5.4: Metal partitioning ratios between tissues

Table A5.4.1: *Tissue partitioning ratio between maternal liver and muscle for each metal.*

Mother	Element	Maternal liver and muscle partitioning ratio
ES3	Ag	39.8
ES3	As	2.28
ES3	Cu	10.8
ES3	Hg	0.701
ES3	Se	13.5
ES3	Zn	3.64
ES4	As	1.71
ES4	Cu	15.8
ES4	Hg	1.89
ES4	Pb	0.450
ES4	Se	24.4
ES4	U	61.5
ES4	Zn	6.93
ET1	Ag	43.0
ET1	As	3.42
ET1	Cu	13.4
ET1	Hg	0.760
ET1	Se	18.0
ET1	Zn	5.20
MK1	Ag	24.1
MK1	As	2.62
MK1	Cu	8.21
MK1	Hg	0.744
MK1	Se	20.6
MK1	U	22.4
MK1	Zn	2.32
RK1	Ag	38.5
RK1	As	1.61
RK1	Cu	14.5
RK1	Hg	1.05
RK1	Pb	0.696
RK1	Se	17.5
RK1	U	44.7
RK1	Zn	4.74
RK2	Ag	186
RK2	As	2.20
RK2	Cu	43.7

Mother	Element	Maternal liver and muscle partitioning ratio
RK2	Hg	2.40
RK2	Pb	0.896
RK2	Se	27.3
RK2	Zn	10.5
ST1	Ag	91.3
ST1	As	2.99
ST1	Cu	16.9
ST1	Hg	4.07
ST1	Pb	2.01
ST1	Se	32.0
ST1	Zn	6.73

Table A5.4.2: *Tissue partitioning ratio between embryonic liver and muscle for each metal.*

Mother	Element	Embryonic liver and muscle partitioning ratio
ES3	Ag	46.0
ES3	As	4.28
ES3	Cu	17.6
ES3	Hg	0.348
ES3	Pb	0.270
ES3	Se	3.00
ES3	U	1.32
ES3	Zn	1.20
ES4	Ag	28.3
ES4	As	3.75
ES4	Cu	22.1
ES4	Hg	0.326
ES4	Pb	0.151
ES4	Se	3.73
ES4	U	1.86
ES4	Zn	1.35
RK1	Ag	57.8
RK1	As	14.4
RK1	Cu	20.2
RK1	Hg	0.378
RK1	Pb	0.483
RK1	Se	4.12
RK1	U	0.576
RK1	Zn	1.34
RK2	Ag	79.5

Mother	Element	Embryonic liver and muscle partitioning ratio
RK2	As	17.2
RK2	Cu	18.5
RK2	Hg	0.264
RK2	Pb	0.319
RK2	Se	4.13
RK2	U	1.20
RK2	Zn	1.27

A5.5: Ratios of element concentrations between maternal liver and embryonic tissues

Table A5.5.1: *Overall median ratios of element concentrations between maternal liver and embryonic tissues.*

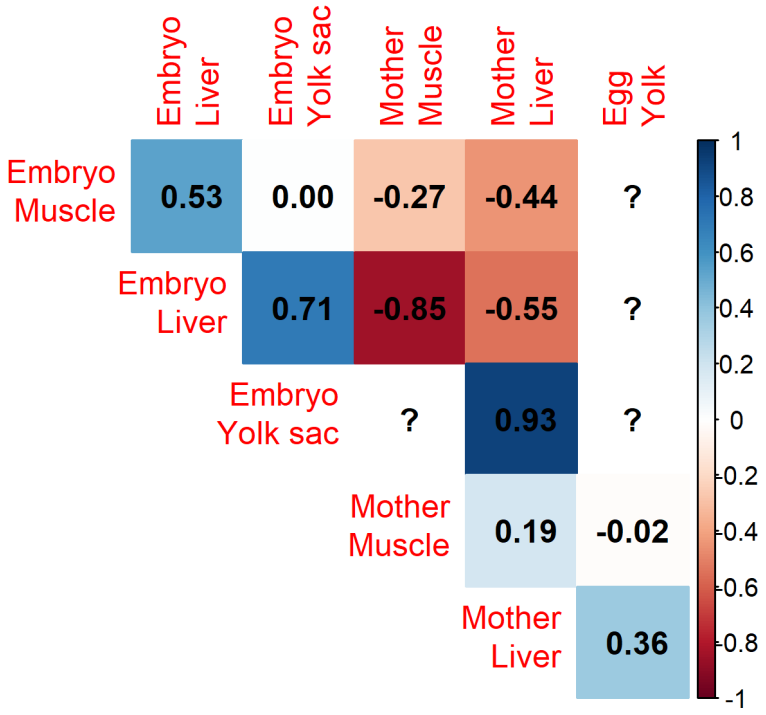
Element	Maternal liver vs embryo liver	Maternal liver vs embryo muscle	Maternal liver vs embryo yolk sac	Maternal liver vs egg yolk
Ag	0.339	14.1	2.09	1.26
As	1.83	18.6	5.43	4.28
Cu	0.248	4.33	0.872	0.848
Hg	72.0	20.5	63.3	51.6
Pb	0.262	0.0699	0.683	1.92
Se	0.867	3.15	1.92	1.32
U	34.9	31.7	7.21	5.47
Zn	3.16	4.15	1.53	1.44

Table A5.5.2: *Mother-specific median ratios of element concentrations between maternal liver and embryonic tissues.*

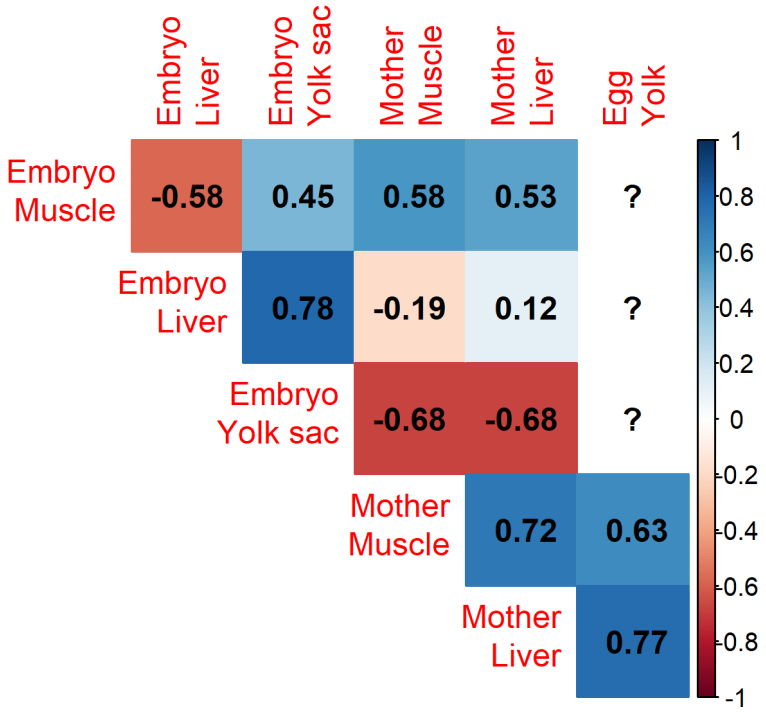
Mother	Element	Maternal liver vs embryo liver	Maternal liver vs embryo muscle	Maternal liver vs embryo yolk sac	Maternal liver vs egg yolk
ES3	Ag	0.0779	3.58	1.16	0.730
ES3	As	1.88	8.05	4.17	3.83
ES3	Cu	0.125	2.19	0.803	0.582
ES3	Hg	33.7	11.7	23.5	25.3
ES3	Pb				
ES3	Se	0.688	2.07	1.30	1.12
ES3	U	13.5	17.7	4.37	3.55
ES3	Zn	1.9	2.28	1.01	0.838
ES4	Ag	0.0851	2.41	1.00	
ES4	As	2.98	11.2	6.61	
ES4	Cu	0.147	3.24	0.786	
ES4	Hg	188	61.3	112	
ES4	Pb	0.329	0.0495	0.683	
ES4	Se	1.02	3.81	1.89	

Mother	Element	Maternal liver vs embryo liver	Maternal liver vs embryo muscle	Maternal liver vs embryo yolk sac	Maternal liver vs egg yolk
ES4	U	23.0	42.7	9.90	
ES4	Zn	2.92	3.94	1.49	
ET1	Ag				1.35
ET1	As				4.14
ET1	Cu				0.970
ET1	Hg				28.7
ET1	Pb				0.605
ET1	Se				0.919
ET1	U				3.34
ET1	Zn				1.45
MK1	Ag				1.19
MK1	As				2.94
MK1	Cu				1.01
MK1	Hg				24.4
MK1	Pb				
MK1	Se				1.39
MK1	U				1.31
MK1	Zn				0.544
RK1	Ag	0.399	23.0		
RK1	As	0.801	11.5		
RK1	Cu	0.244	4.92		
RK1	Hg	26.4	9.97		
RK1	Pb	0.194	0.0939		
RK1	Se	0.682	2.81		
RK1	U	26.3	15.1		
RK1	Zn	2.31	3.11		
RK2	Ag	1.79	143		
RK2	As	1.26	21.6		
RK2	Cu	0.988	18.3		
RK2	Hg	122	32.2		
RK2	Pb	0.818	0.261		
RK2	Se	0.679	2.81		
RK2	U	85.4	103		
RK2	Zn	5.23	6.63		
ST1	Ag				3.65
ST1	As				4.19
ST1	Cu				0.878
ST1	Hg				175
ST1	Pb				0.297
ST1	Se				2.94
ST1	U				11.9
ST1	Zn				1.44

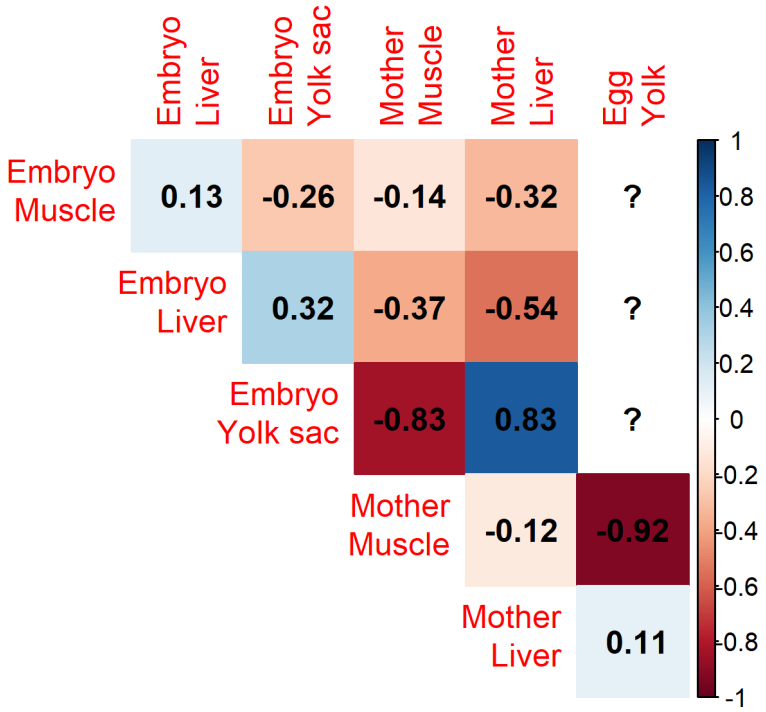
A5.6: Correlations between maternal and litter tissues by element



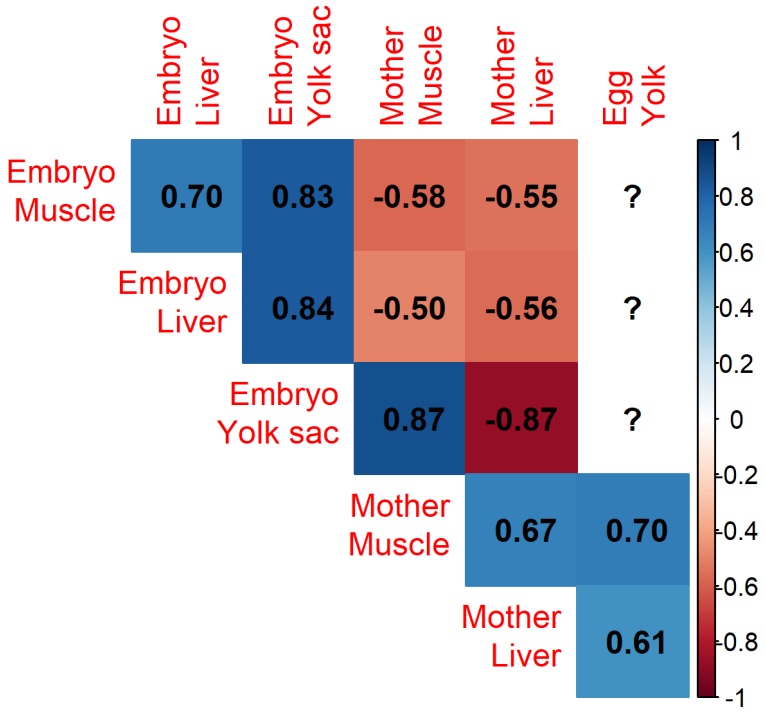
a) Ag


Embryo Liver
Embryo Yolk sac
Mother Muscle
Mother Liver
Egg Yolk
Embryo Muscle
-0.58
0.45
0.58
0.53
?
Embryo Liver
0.78
-0.19
0.12
?
Embryo Yolk sac
-0.68
-0.68
?
Mother Muscle
0.72
0.63
Mother Liver
0.77
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

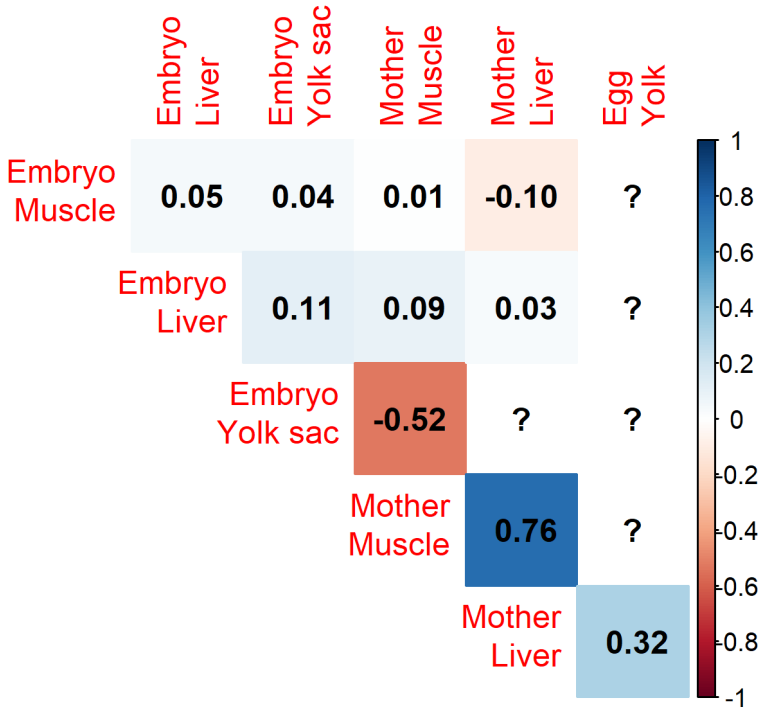
b) As


Embryo Liver
Embryo Yolk sac
Mother Muscle
Mother Liver
Egg Yolk
Embryo Muscle
0.13
-0.26
-0.14
-0.32
?
Embryo Liver
0.32
-0.37
-0.54
?
Embryo Yolk sac
-0.83
0.83
?
Mother Muscle
-0.12
-0.92
Mother Liver
0.11
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

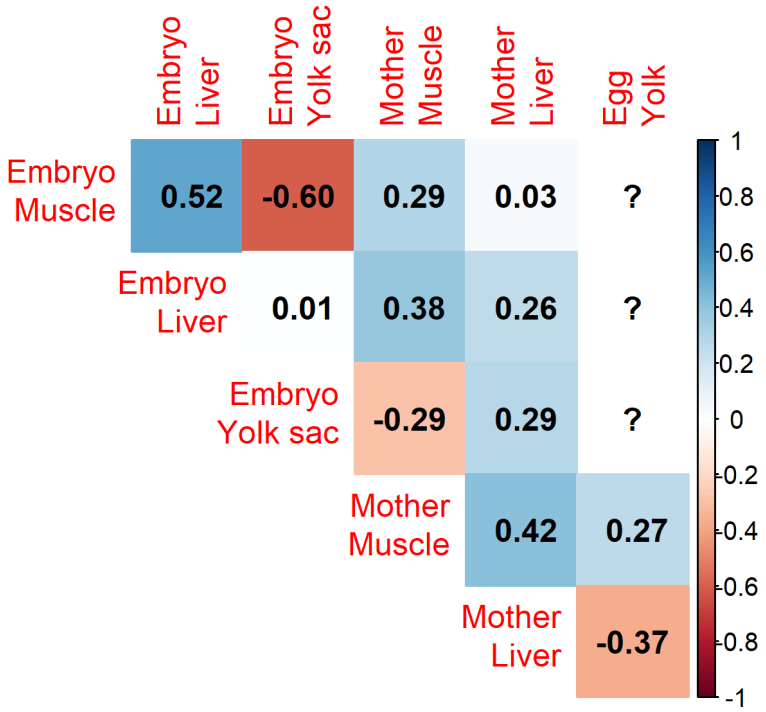
c) Cu


Embryo Liver
Embryo Yolk sac
Mother Muscle
Mother Liver
Egg Yolk
Embryo Muscle
0.70
0.83
-0.58
-0.55
?
Embryo Liver
0.84
-0.50
-0.56
?
Embryo Yolk sac
0.87
-0.87
?
Mother Muscle
0.67
0.70
Mother Liver
0.61
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

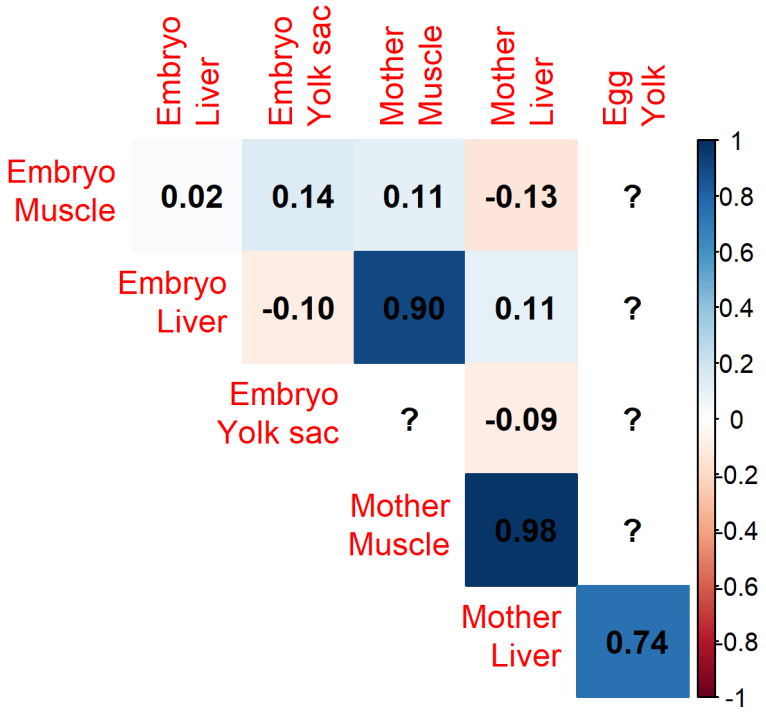
d) Hg


Embryo Liver
Embryo Yolk sac
Mother Muscle
Mother Liver
Egg Yolk
Embryo Muscle
0.05
0.04
0.01
-0.10
?
Embryo Liver
0.11
0.09
0.03
?
Embryo Yolk sac
-0.52
?
?
Mother Muscle
0.76
?
Mother Liver
0.32
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

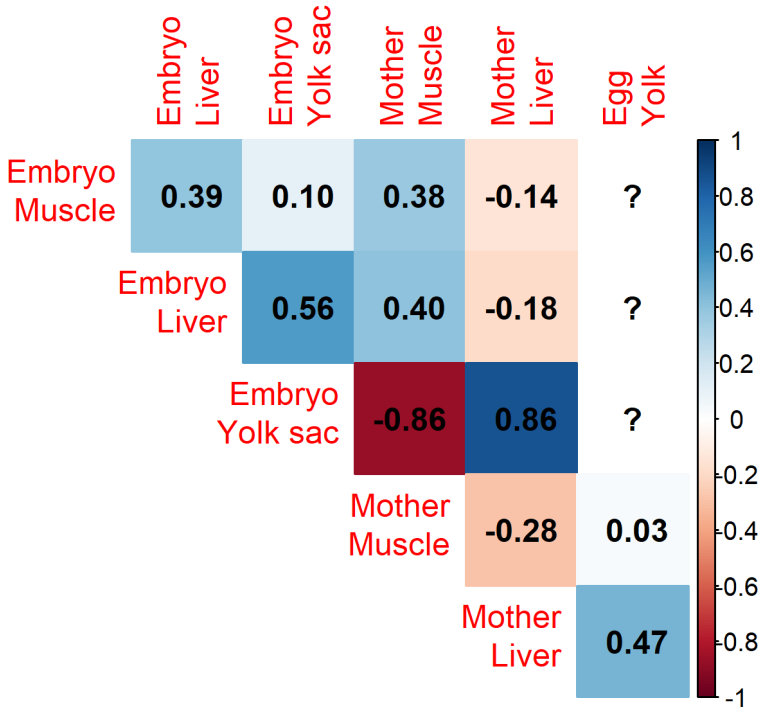
e) Pb


Embryo Liver
Embryo Yolk sac
Mother Muscle
Mother Liver
Egg Yolk
Embryo Muscle
0.52
-0.60
0.29
0.03
?
Embryo Liver
0.01
0.38
0.26
?
Embryo Yolk sac
-0.29
0.29
?
Mother Muscle
0.42
0.27
Mother Liver
-0.37
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

f) Se


Embryo Liver
Embryo Yolk sac
Mother Muscle
Mother Liver
Egg Yolk
Embryo Muscle
0.02
0.14
0.11
-0.13
?
Embryo Liver
-0.10
0.90
0.11
?
Embryo Yolk sac
?
-0.09
?
Mother Muscle
0.98
?
Mother Liver
0.74
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

g) U



h) Zn

Figure A5.6.1: *Correlations of element concentrations between tissue types.*

Appendix 6 – Massey University Animal Ethics Committee (MUAEC) Protocols

A6.1: MUAEC 19/98

AEC/20 (Amended 01/19)

Massey University
Animal Ethics Committee

To: The Secretary
Animal Ethics Committee
Research Ethics Office
Room 1.23
Courtyard Complex
Manawatu Campus PN221

Please provide one original single-sided application plus 15 copies
Due dates are provided on the MUAEC website

APPLICATION FOR APPROVAL OF PROPOSED RESEARCH, TESTING OR TEACHING PROCEDURES USING ANIMALS

1. **CHIEF APPLICANT:** *(Staff Member only)*
   - (a) **Name:** Adam Smith
     Qualifications: PhD (Statistics)
     Position: Senior Lecturer
     School/Institute: School of Computational and Natural Sciences

2. **OTHER APPLICANTS:** *(Refer Code of Ethical Conduct, Item 5.1.4, for those who should be listed)*
   - (a) **Name:** Alex Burton
     Qualifications: BSc (Major: Marine Ecology, Minors: Chemistry and Statistics), Rescue Diver
     Position: MSc research student
   - (b) **Name:** Clinton Duffy
     Qualifications: MSc (Zoology)
     Position: Technical Advisor - Department of Conservation
   - (c) **Name:** Dr Marie-Anne Thelen
     Qualifications: PhD (Chemistry)

OFFICE USE ONLY

RECEIVED 13 SEP 2019 Research Ethics

Date Received:

Copy for: Date sent: 3-7-20
Applicant
Head of School/Institute ✓
Office

Protocol No: 19/98

Decision: MASSEY UNIVERSITY ANIMAL ETHICS COMMITTEE APPROVED Date: 20-9-19

Position Senior Tutor – Massey University

3. **DETAILS OF PROJECT:**

(a) **Title** *(maximum 20 words)* Population Ecology of School Sharks in the Southern Kaipara Harbour

(b) **Type of project**

Research	X
Testing	
Teaching	
Course Number(s):	

(c) **Commercial sensitivity status**

No	X
Yes	

(d) **Does the project involve use of native species?**

No	
Yes	X

If yes:

Has DOC approval been:

Sought but not yet granted	
Granted	N A

Permit Number(s):
Not Applicable, Clinton from DOC has stated that we do not require DOC permission to carry out our proposed research on School sharks

Māori consultation:
(must be by applicant(s) directly with iwi)

(For guidance, click here)

Has been undertaken	
Is currently being undertaken	X

The project is approved by iwi*:
Yes ☐ No ☐

*(*Please refer to guidance opposite)*

4. **JUSTIFICATION OF PROJECT:**

(a) **What are the expected benefits of the proposed work?** *(Benefits may include improved basic knowledge, improved animal health, teaching)*

School shark (*Galeorhinus galeus*) provide the second largest inshore commercial shark fishery in New Zealand (NZ) [1,2]. Historically, school sharks have been important to the many indigenous Maori iwi, who travelled to the Kaipara Harbour to catch school sharks in high abundance during summer months [3–5]. Like many fisheries, with improvements in technology over time have seen the landings (tons caught) of this species increase during the mid-20th century, as commercial fisheries were able to harvest more and access more remote fishing grounds [2,6]. However, landings have declined in the years since 1986-1987 [2], possibly due to decline in the population under increased fishing pressure as 45-60% of their distribution range in New Zealand waters is vulnerable to fishing, including the Kaipara Harbour [7]. These vulnerable ranges also potentially include nursery grounds. With the high abundance of mature and pregnant female school sharks observed entering the Kaipara Harbour during spring and summer, it is presumed that they come into the Kaipara Harbour to pup

(give birth): indeed, juveniles and pups are often caught during this time [8,9]. However, the lack of information on school sharks in the Kaipara Harbour and the importance of the Harbour to school sharks may be allowing unseen harm to the population as pregnant females and/or pups are possibly being killed by a combination of human induced factors [8,10–14], preventing potential restocking of the population. This research will fill important gaps in our knowledge, to aid in the protection and conservation of the northern NZ school shark population and, in particular, the importance of the Kaipara Harbour to that population.

We aim to document the spatial distribution, diets, heavy metal concentration and habitat use of this species across its life history in the Kaipara Harbour, identifying important pupping and nursery grounds and key life history parameters (e.g. size range that mature females give birth, sex ratios in the harbour, size at maturity, size at birth) for school sharks. We hope to learn which areas and habitats of the harbour are key to the successful maintenance of the school shark population, and hence what areas should be protected and monitored to ensure sustainability. Protection of these areas would reduce inadvertently capture of juveniles and would allow for population growth of the New Zealand School shark population [15]. This not only means preventing the collapse of the school shark fishery which was witnessed in Australia [16,17], but it would mean Maori could still harvest school sharks for cultural purposes under the fishing rights of Tangata whenua [4] in the future. Moreover, protection of these areas may inadvertently protect other species nursery grounds within the same vicinity and help them restock their NZ populations. Due to the use of the Kaipara by larger predators to hunt smaller sharks [8,9], protecting school shark nursery grounds may also allow a bottom up cascading effect [18] of the food chain potentially allowing populations of vulnerable apex predators e.g. Great White Sharks (*Carcharodon carcharias*) to increase in size.

By analysing stomach contents across the different size and sex classes, we hope to learn what prey school sharks ingest whilst in the harbour, whether there is diet similarity or diet changes across the different size classes and habitats.

Quantification of heavy metal concentrations in school sharks will also help inform assessments of the health risks associated with ingesting school shark muscle and, school shark and ecosystem health. Moreover, by analysing late stage unborn pups it would suggest whether maternal offloading (the passing of heavy metals from mother to offspring)[19–21] of heavy metals occurs in New Zealand waters and potentially for this species.

Filling knowledge gaps around the school shark population in the Kaipara Harbour will also meet the research and information goal of the National Plan of Action for the Conservation and Management of Sharks 2013 which seeks to "Continuously improve information available to conserve sharks" [1]. Improving this knowledge will allow governmental organisations e.g. Department of Conservation and Fisheries New Zealand to better and further protect this species in New Zealand waters to ensure that New Zealand School shark population remains viable. Moreover, it will allow for better management of the ecosystem as there will be more understanding into the biology, chemistry and behaviour of one of the top predators in the ecosystem.

(b) How will the new knowledge be communicated to others?

The results from this study will be reported in a thesis and communicated to the wider scientific community via published journal articles and conference presentations. We will also report our findings to stakeholders, including the local community and iwi, via the Integrated Kaipara Harbour Management Group (IKHMG), with whom we have begun a dialogue.

(c) Why is it necessary to use animals for this activity? *(The term "animal" is defined in the Animal Welfare Act, Section 2(1))*

Direct observations are required to study how school sharks are distributed in the Kaipara Harbour. To fully understand how the harbour is used by this natural population of sharks, we need to

systematically sample and measure sharks of various size classes across the different habitats and in particular, where we find juvenile sharks to determine any potential nursery grounds and habitats. The vast majority of animals that we catch will be released alive at the places where they are caught. We will euthanise and retain a small number (30) of animals to conduct diet analyses and analyse their muscle and livers for bioaccumulated heavy metals. This is the only feasible way of confirming how the animals are using the habitats, whether they are being exposed to heavy metals, and if maternal offloading in school shark pups occur.

Commercial fishing of this species does occur in the harbour to an extent. Although school sharks will be kept on request, we cannot rely on commercial fishermen to also supply accurate information on exactly the time and location of capture and provide information on the other environmental variables that we will record at each longline deployment. Commercial fishermen also have different handling and retrieval procedures to what we will be using and could mean that the condition of the shark's internal organs that we will sample i.e. the liver and gastrointestinal tracts may not be suitable for analysis.

The use of video surveying techniques e.g. Baited Remote Underwater Video systems is not a suitable alternative to longline surveying due to the strong tidal and sedimentation conditions in the harbour that reduce visibility.

5. DESCRIPTION OF PROCEDURES AND MANIPULATIONS: *("Manipulation" is defined in the Animal Welfare Act, Section 3)*

(a) Give a brief description of your trial design/teaching demonstration. *(One or two paragraphs) (For complex protocols, it may be beneficial to provide information as a timeline or in tabulated form)*

Surveys of subtidal areas in the southern Kaipara Harbour will be completed using a stratified random sampling design with reference to habitat information presented by Morrison et al., 2014 [8], and other bathymetry (ocean floor) surveys. A stratified random sampling design consists of splitting up an area into designated strata or sections and then sampling at independent random GPS coordinates in each stratum. We aim to conduct surveys for 2-3 days each month during 2019-2020. By sampling each month, we will be able to determine which seasons the school sharks are present in the harbour and in what size and sex ratios. Moreover, monthly sampling will help outline whether there is monthly variation in shark population size and sex and size ratios. These surveys will consist of sharks being captured by longlines deployed from a research vessel. Longlines allow for a large number of individuals to be caught at a time making it more efficient than traditional fishing practices. Moreover, the bycatch rate of a (25 hook) longline is less than a gillnet as longlines are more selective, and mortality rates and stress levels in longlines are less than gillnets [22,23]. Reduction in mortality and bycatch can be accomplished by requiring less time out of the water; selecting species specific baits; hook shape and size, and by the use of wire appendages which prevents gut hooking [23–27]. Furthermore, in New Zealand school sharks are not known to avoid recapture with methods that include hooks [28]. These longlines are comprised of 25 hooks and will be deployed one at a time in each area, as assigned by the sampling design. Each line will sit in the water for a duration of 20 minutes. Location, depth and sea floor habitat at each deployment site will be recorded.

Figure 1: The proposed subtidal survey area of the southern Kaipara Harbour. The black lines indicate the boundaries of the proposed survey area. The two blue points indicate the proposed locations of launch of the research vessels.

Before surveys are undertaken, a **pilot study** will take place in late 2019 to evaluate, and if necessary, refine our capture procedures. The pilot will establish the time taken to deploy and retrieve one longline and the caught individuals from the water. Furthermore, it will help establish if a 20 minute soak time (time which the line will be left in the water) is adequate to catch the highest number of sharks whilst minimizing stress, and the likelihood of mortality. It will allow us to estimate how many lines can be deployed within the 6-hour period we have each day; duration is limited by tidal changes in the harbour. Moreover, the time taken to deploy and retrieve a longline will allow us to estimate how many days it will take to cover the sampling area. Once this information is known we will be able to more accurately estimate the number of sharks we anticipate to catch over the sampling period as opposed to the rough estimate in 5c. This pilot study will also help establish whether the design needs to be changed in order to further minimise stress or prevent casualties due to the duration of longline deployment. Photographs and videos will be taken and forwarded to the animal ethics committee to illustrate the capture, handling and tagging procedures.

Processing of captured shark.

After the individual sharks have been caught by a longline, they will be either brought aboard or moved into a shark cradle on the side of the research vessel. From there the individual will be examined, photographed, measured, weighed and tagged. After tag insertion a crew member will check to see if the tag is in place, record the tag ID number and will release the shark. Sharks less than 90cm Total Length (TL) will not be tagged. This procedure will be done with care and as quickly as possible in order minimise the stress and prevent the mortality of the individual.

Measurement data will help determine the sex and size ratios in the harbour. This will help determine whether school sharks in the harbour segregate by sex and size and whether there is a dominant sex and size classes that use different sections of the harbour. Moreover, the proportion of sex and size classes that are caught over the course of the survey and in the different areas will allow us to identify potential nursery areas in southern section of the Harbour, whether sharks vacate the harbour in winter, and what areas in the southern Kaipara Harbour are important to the school sharks present. Measuring the mature females in the harbour in conjunction with assessing pregnancy state during examination will also allow us to estimate a range of sizes and weights that females give birth in the

harbour. Locations of recaptures will also allow us to track the movements of the school sharks within the harbour and around New Zealand and may indicate if multiple school shark populations are using the harbour and where they go once they vacate the harbour. Recaptures will also allow us to model and estimate the population size of school sharks in the Kaipara Harbour once effort is accounted for by using catch per unit effort (CPUE).

Minimisation of by-catch will be achieved through using selective bait, use of an array of circle hook sizes, and the duration of soak time (time in the water). 20 minutes of soak time allows for a standardised time for sharks to catch on the line all year round whilst minimising mortality. If non-target species are caught due to eating the bait or preying on smaller sharks or prey already caught (depredation), this will be managed as follows. Smaller animals will be hoisted onto the boat where the hook can be taken out and the fish released. If the animal is too big for this, attempts will be made to remove the hook on the side of the boat, however, if it is a larger shark or stingray species then the line will be cut a safe distance from the animal to avoid harm to personnel and the animal. Further detail on dealing with larger shark and stingray bycatch is outlined in section 8a.

Heavy metal and stomach contents analyses

A total of 30 sharks (five from each size class) will be euthanised for heavy metal and stomach contents analyses. These individuals will be caught on the longline throughout the course of the research. Once brought aboard they will be euthanised. Euthanised sharks will then be placed into a chill bin with salt ice to ensure preservation of tissue until return to the Albany's Oteha Rohe campus. The stomach will be obtained, weighed, and the volume measured. Prey items will be identified to the lowest classification/taxonomic level. Any prey items that are not able to be identified will be sent to an expert to classify. Moreover, the size of the prey will also be recorded. Also, during this procedure samples of the trunk musculature and the liver will be taken for heavy metal analysis and will be stored in a -80° freezer until processing. These samples will be dried and then digested. Digested samples will then be analysed by Microwave Plasma Atomic Emission Spectrometry to quantify the concentrations of Lead (Pb), Zinc (Zn), Copper (Cu), and Mercury (Hg).

(b) Describe the statistical methods that you will use to analyse these data.

Data analysis will be done using R and PRIMER. To model the recapture data, we will use modern mark-recapture models to estimate the population size and patterns of connectivity of school sharks e.g., population dynamics models to account for numerous variables that affect the population and connectivity e.g. immigration, emigration, natural mortality, season etc. [29,30].

To model likely locations of nursery grounds within the Kaipara, kernel density estimations would be used to show areas of high densities of pups in the Kaipara Harbour [31]. Generalised Linear Mixed Models (GLMMs) [32] will be used to analyse counts of sharks (CPUE) whilst taking demographic parameters, habitat variables, and the structure of the sampling design into account [15,28,30,32,33].

Non-metric Multidimensional scaling (MDS) will be used to visualise differences in diet and location [34]. To model potential differences in diet and location we will employ ANOSIM, PERMANOVA, and/or Bayesian modelling [34–37].

Once concentrations of heavy metals have been estimated for each euthanised individual, the data will be modelled with a Bayesian ANOVA to assess if there were any differences between the size classes.

(c) Provide justification for the group sizes that you propose.

Anticipated catch over monitoring period:
During **spring and summer** mature and pregnant females as well as juveniles and pups occur in large frequencies [8,28,38]. Generally during these months school sharks come inshore to breed and feed [8,28,38]. Therefore, during the summer months of the main survey we are anticipating

that the majority of the hooks on the longlines will be catching all sizes of school sharks [8]
Therefore, estimated maximum number of sharks captures during that period, assuming no recaptures, only target species were caught and no loss of lines due to unforeseen circumstances will be:

One longline deployment at a time, 25 hooks assuming all hooks have caught school sharks
5-6 lines a day (limited due to tidal conditions)
3 days a month to cover sampling area
Sampling through spring and summer = 18 days(3*6)*150 Hooks a day(6*25) = 2700 sharks.

A 22% recapture rate of dart tagged school sharks was witnessed in New Zealand by Hurst et al., 1999 [28]. The anticipated number of sharks that could be caught once is 2106 with 594 being caught more than once.

During **autumn and winter** the observed abundance of school sharks in the Kaipara Harbour is low. It is assumed that the adults return to the deeper waters offshore, whereas, the pups can stay in the nursery for up to two years [28,38]. Therefore, during these months not all of the hooks will be catching school sharks due to multiple environmental conditions, and potentially only catching smaller individuals in potential nursery areas. Thus, estimated maximum number of sharks captures during that period is highly variable, however, assuming no recaptures, and no loss of lines due to unforeseen circumstances the range of sharks that could be caught will be:

One longline deployment at a time, 25 hooks with only 1-12 hooks catching school sharks.
5-6 lines a day (limited due to tidal conditions)
3 days a month to cover sampling area
Sampling through autumn and winter = 18 days(3*6)* 6 Hooks a day(6*1) = 108 sharks
Sampling through autumn and winter = 18 days(3*6)*72 Hooks a day(6*12) = 1296 sharks
Number of sharks during winter is estimated to vary between 108-1296 sharks. Given a 22% recapture rate of dart tagged school sharks witnessed in New Zealand by Hurst et al., 1999 [28]. The anticipated proportion of sharks that could be caught once varies between 84-1011 and the number caught more than once, 24-285.

Overall the **total estimated maximum number** of sharks that are anticipated to be caught over the duration of the survey period is 3117 captured and 879 recaptured (not accounting for bycatch and/or the loss of lines). This is an estimate only. Shark capture on longlines can be effected by the variable seasonal abundance in the harbour; environmental conditions including tides, weather, sedimentation and freshwater loads; depredation, and potentially nursery grounds where tagged individuals could stay for an extended period of time, thus can cause this estimate to vary significantly.

The pilot study that is going to be carried out will help give a better estimate of these numbers as mentioned in section 5a. This study will be conducted during spring and summer when there is an increased abundance of school sharks. The timeframe of this study is how many days it takes to cover the sample area, currently anticipated to be three days.
One longline deployment at a time, 25 hooks with all hooks catching school sharks.
5-6 lines a day (limited due to tidal conditions)
3*(6*25) = 450 sharks.
Given a 22% recapture rate of dart tagged school sharks witnessed in New Zealand by Hurst et al., 1999 [28], the **total estimated maximum number** of sharks that could be caught once during the pilot survey is 351, and the number of sharks that could be caught more than once is 99. As previously stated this is only an estimate and it can vary.

Number for tagging

Currently, we aim to tag 500 sharks throughout the duration of the study.

Number for euthanasia:

A total of 30 sharks will be euthanised, five sharks, irrespective of sex, from each of the six size classes (<30, 30-63, 64-97, 98-130, 131-163, 164-196 kg). Five individuals across the size ranges of these sharks is the minimum number required to see if there are statistically significant differences in metal concentration between size classes.

Considering the five unborn individuals will be examined for maternal offloading, the overall total estimated maximum number of individuals that are planned to be used during the course of the study will be 3473.

(d) Describe the manipulations to be performed on the animals.

In order to capture school sharks, 25 circular hook longlines will be used. Longline hooks will be modified to have wire appendages (Figure 2) to prevent gut hooking of sharks to prevent further loss of life, damage and/or stress to the animal [26,39].

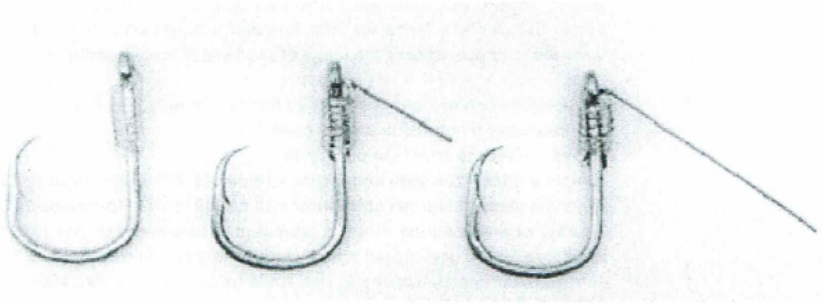


Figure 2: A picture of a wire appendage on a J-shaped hook, sourced from Chin et al., 2015 [26].

Caught sharks will be brought up next to the boat one at a time whilst the longline is being retrieved. Other caught individuals will be left in the water for up to hour (depending how long it takes to lift individual sharks onto the boat and process them). This allows for other sharks and fish that have been caught on other hook traces to stay in the water for a longer period of time to minimise air related stress [40]. Once next to the boat, if the individual is small enough, they will be hoisted onto the boat by pulling on the hook trace and handling the body trunk with wet gloves to prevent excessive removal of protective mucous. When on board they will be put into a tank of aerated seawater or restrained and process immediately. If the individual is too big to be hoisted onto the vessel, they will be guided into a shark cradle [41] by pulling on the hook trace and then the cradle will be lifted onto the boat or the shark will be held alongside the boat. Once aboard we intend to

- examine the external features of the shark e.g. condition of the body, and the maturity and pregnancy states
- photograph the individual and its tag
- measure the total length, proxies for total length i.e. head length or jaw width
- weigh them by placing individuals in a scale sling
- tag

We will then release school sharks as quickly as possible.

Tagging

The tags that are to be used are spaghetti/dart tags supplied by the TMRCT (Figure 3). These 3x90mm tags have a plastic barb on one end to keep the tag in place once deployed. The use of plastics barbs

is less invasive than stainless steel barbs due to the smaller size of the plastic barb [42,43]. Moreover, dart tags with plastic barbs have a higher retention rate compared to stainless steel barbs [42]. The tags have unique identification numbers that allow for the identification of individuals of one species. The reason for using dart tags for dorsal musculature insertion was based on the short time it takes to insert the tag into the shark's muscle, reducing the time out of the water and also to minimise stress from handling. Other tags that can be applied e.g. dorsal fin tags take longer to apply, with some creating larger wound sites than dart tags, and have been documented to split the fin in some individuals [43–45]. Moreover, sharks have limited capacity for nociception, particularly reception to do with agonising pain [46]. Rose et al., 2014 further stating that sharks have been noted to be behaviourally unaffected by severe wounds and unresponsive to injury [46]. Once the shark is hoisted out of the water it will be handled in a manner that will minimize stress, following the TMRCT tagging code of practice and tagging instructions. This would include placing a wet towel over the individual's eyes; restraining the individual with one to two crew (depending on size) to prevent the individuals self-harm from thrashing around (restraint method outlined in section 5f); inserting the tag in an dorsal musculature just below the dorsal fin (Figure 4); checking the tag is in place by pulling on the exposed region of the tag, and release the individual back into the water. Sharks under 90cm TL will not be tagged. Furthermore, to ensure correct tagging methodology is being used training of inexperienced participants, and supervision of tagging, will be provided by tagging experts.

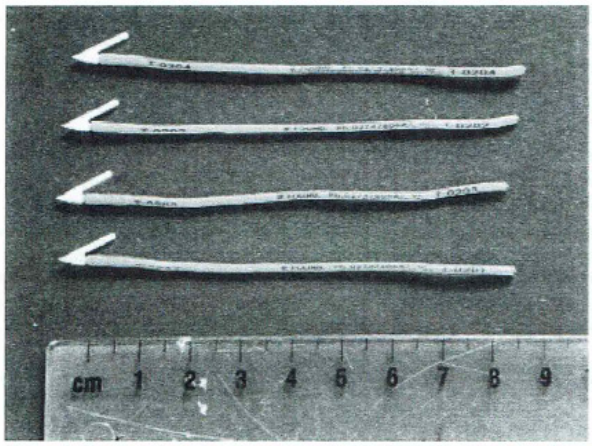


Figure 3: Picture of spaghetti tags supplied by TMRCT with a ruler for measurement reference. Sourced from: https://tindaleresearch.org.nz/tagging-program/

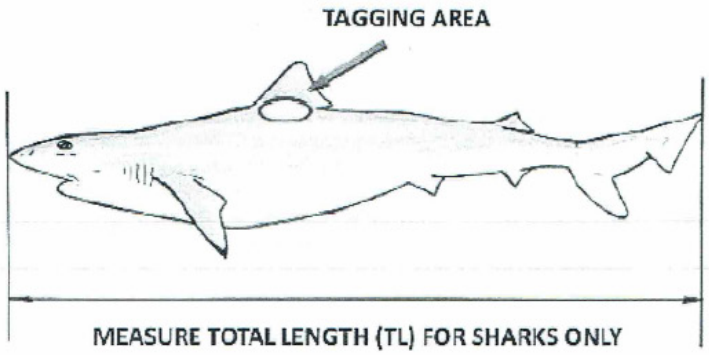


Figure 4: Illustration of the tagging area on a shark for spaghetti tag deployment. Sourced from: TMRCT tagging code of practice (https://www.tmrct.org.nz/wp-content/uploads/2016/11/Tagging-code-of-practice-version-3.1.pdf)

Over the course of the survey 30 individuals will be euthanised for stomach contents and heavy metal analyses. Five individuals from the six size classes will be euthanised when encountered on longline deployments. Size classes are defined in section 5c. Once hoisted aboard they will be euthanised as quickly as possible. Euthanasia of the sharks is described in Section 7b.

(e) How will the proposed manipulation affect the well-being of the animals?

Some studies have noted that the capture and handling procedure for the mark and recapture process is the more energy intensive and stressful stage [27,39], noting that the depth of capture; the time in the water (soak time); and the sharks ventilation and physiology had large effects on shark stress and mortality rates [27,47]. Moreover, air exposure is also a common stressor for shark [40]. Elevated stress levels in sharks can lead to death and alterations in behaviour, growth and immune system functions, and imbalance of blood components e.g. metabolites and electrolytes [40,48]. Other risks that are posed to school sharks due to soak time include drowning and depredation. Within the plasma elevated levels of potassium, lactate and chloride was detected in Carcharhinidae sharks [27]. However, studies into the effects of longlines on Gummy sharks, of which the school shark is a close relative, found levels of the metabolites (lactate) and electrolytes (Potassium and Chloride) were not elevated immediately after capture, however, increased with time once captured [23].

After the tag has been applied into the dorsal musculature of the trunk, there are three distinct phases of wound repair [49]. The first phase is the immediate or acute response were haemorrhaging, tissue disruption and breakdown occurs. This occurs from just after tag insertion until 10hrs post tagging. The second stage is the intermediary inflammatory response and the beginning of tissue repair, the transition to this phase was observed after 10hrs post tagging and lasts for many days observed up to 10 days after tag insertion. The third stage was the formation of fibrous tissue encapsulation of the tag, separating the tag from the adjacent undamaged body tissues. This occurred by 10 days post tagging and can last over different periods of time. Research conducted by Reif 1978 also showed that Triakidae sharks i.e. Leopard Shark (*Triakis semifasciata*) secreted a mucous layer over the wound site to act as an osmoregulatory and infection-prevention barrier whilst the underlying tissue was being repaired [50]. Reif further stating that the wounds of leopard sharks started to have dermal scale replacement after 2-3 months post injury [45,50]. Considering wound recovery, many shark species wound repair and tissue regeneration occur very quickly especially in younger sharks, eventually the tag becomes embedded in the epidermal and muscle tissue where it will either be encapsulated or shed [39,45,49–52]. In School sharks tags can be shed on average after 706 days at liberty [28,38]. Moreover, Chin et al., 2015, Heupel 1997, 1998, and Reif 1978, all state that even though the dart tags can create drag, the appropriate selection of tag and with following appropriate tagging procedures the tags and tagging procedures do not appear to be detrimental to the long term health and survival of the shark [39,45,49,50]. Chin et al., 2015 further suggesting that the benefits of tags are likely to outweigh the risks associated with the procedure [39]. Similar tags have been used in previous studies in New Zealand to tag school sharks [28,29,53]. It has also been stated that the use of spaghetti/dart tags was a preferred tagging method as it allowed the shark to re-enter the water quickly reducing the risk of desiccation [28]. According to the tagging code of practice set out by the TMRCT any shark or fish that is gut hooked, injured or impaired (foul hooking in the eye or respiratory surfaces) or have signs of excessive bleeding will not be tagged nor released, instead the individual will be euthanised, necropsied and the results of the necropsy will be forwarded to the Animal Ethics committee.

(f) Describe any restraint applied to the animals.

When on the longline hook traces the hooks prevent sharks from swimming off, only allowing them to swim within the vicinity of longline. When the longline is being retrieved from the water the caught sharks be restrained alongside the boat ready to hoist them onto the boat. For hoisting methods please see section 5d. Sharks too big to be hoisted aboard will either be held in the water alongside the boat or restrained in a cradle. Sharks brought aboard will either be held in a tank filled with aerated seawater if small enough or restrained by a crew member and processed immediately. Restraining on board and next to the boat will be done by holding the shark with one or two crew or put the shark into the shark cradle to prevent it from self-harm from thrashing around.

(g) If the animals are to be transported, how will this be performed?

Not Applicable. All animals will either be tagged and released or euthanized.

6. CARE OF ANIMALS:

(a) What access will the animals have to water?

Fishes (target or non-target) caught on the longline will be held in a tank filled with aerated seawater or kept in the water for as long as possible to ensure adequate respiration and to reduce the risk of desiccation.

(b) Describe the feeding regimen for the animals.

Not Applicable.

(c) If the animals are to be housed indoors, describe how housing might impact animal welfare and what initiatives will be taken to mitigate any negative effects.

Not Applicable

(d) From where will the animals be sourced? *(Refer Code of Ethical Conduct, Item 5.1.12)*
(Where animals are personally owned, consent forms must be obtained)

Wild caught, southern Kaipara Harbour.

(e) Where will the animals be kept throughout the study period?

Not applicable. All animals will either be tagged and released or euthanized.

(f) Who is responsible for the routine care and health surveillance of the animals?

Crew aboard the vessel i.e. Adam Smith, Alex Burton, Clinton Duffy, and Massey Technical staff

(g) If the Chief Applicant is unavailable, who will make decisions if emergency care is required?

Clinton Duffy or Alex Burton

7. FATE OF ANIMALS:

Note: If any animal is either euthanased or dies due to the unexpected side effects of approved manipulations, the animal should be subjected to a post-mortem examination by an experienced person. The results of the post-mortem must be communicated to the Massey University Animal Ethics Committee along with any modifications put in place to minimise the occurrence of similar events to other animals.

(a) What will happen to the animals at the completion of the study?

No animals will be kept in captivity during the study. All fishes caught will either be tagged and released shortly after capture or euthanised immediately for chemical and stomach contents analyses.

(b) Will any animals be euthanased, either as part of the study or in the event of untoward outcomes? No ☐ Yes ☒

If yes:

Applicants must be familiar with the resource material on supporting staff involved with animal euthanasia at the following link:

Animal Euthanasia Support Guidelines.pdf

The Chief Applicant must also confirm that he/she understands his/her obligations in regard to discussing the availability of this material with all people listed on the application on a per-project basis. ☒ *Tick Box*

Describe the euthanasia method you will use.

Sharks will be pithed with an iki-spike or iki-gun (depending on what is available) and then the vertebral column immediately severed behind the chondrocranium. The size of the iki-spike will be dependent on the size of the shark captured to ensure that the euthanasia is as quick and humane as possible. Furthermore, euthanasia will only be conducted by trained personnel to ensure that the method is carried out properly to ensure a quick and humane death for the shark. Crew members who are not trained in this technique will be trained by experienced personnel

Iki-spike tool and iki-jime method outlined on http://www.ikijime.com/

(c) **What level of losses do you expect to occur during this work and how will you investigate any unexpected deaths?** *(Refer Code of Ethical Conduct, Items 5.6.3-5.6.5)*

Based on studies on a relative to the School shark, the Gummy Shark (*Mustelus antarcticus*), found that mortality on longlines did not occur until 5-8hrs and this was found with other species of shark caught on longlines [23,27]. Since sharks are anticipated to be on the longline in the water for only up to an hour, we are not anticipating any deaths related to soak time. However, due to the presence of larger predatory sharks in the harbour there is a greater risk of death associated with depredation. However, in some instances this cannot be prevented in our design as longlines need to stay in for a standardised period of time across the sampling effort and depending on the number of sharks on the line will dictate how long the retrieval time will be. Processing sharks as quickly as possible decreases the risk of death associated with depredation. Moreover, the possibility of depredation may also be dependent on time of year and deployment area, therefore, this risk can vary. Other losses that could be expected are sharks that are brought aboard that are not suitable for release and in this instance, they will be euthanised using the techniques outlined in section 7b. The pilot study will help determine whether the proposed methods will cause any unexpected deaths. Any unexpected losses will be investigated by necropsy to determine cause of death if unknown and methods that were used to catch this individual will be examined to see they need to be changed in order to prevent further deaths and will be communicated to the committee.

8. ALLEVIATION OF IMPACT OF MANIPULATIONS:

(a) **What features of the manipulations minimise their impact on the animals?**

We will make every effort to minimise incidental mortality of sharks by setting lines for a short time (20 minutes), using circular hooks with wire appendages to prevent gut hooking and to allow for easy retrieval of the hook [24–26], and by minimising the time that the shark will be out of the water. We will conduct a pilot study to establish the best methods to be used and to evaluate potential for

unexpected deaths of target and non-target species and will alter our approaches accordingly. We will record and report any unintentional deaths to the Animal Ethics Committee.

Once aboard the vessel processing will be done as quickly as possible to ensure a prompt return to the water. The use of gloves and wet towels to handle the animals, including cover their eyes, during on-board procedures will also reduce the risk of desiccation and the amount of protective mucus removed.

In the event that a larger predatory shark or stingray is caught on one of the longline hook traces, the trace that the large shark or stingray is on will be cut as close to the animal without jeopardising the safety of the crew member. Eventually the hook will be shed by these animals and will not affect the shark in the long term [39].

Tagging procedures will be as set out in the tagging code of conduct. The tagging procedure is quick and prevents injury to vital organs by inserting tags into dorsal musculature below the dorsal fin. The small size and streamlined profile of the tags means they will not create a lot of drag. The tags will eventually be overgrown and encapsulated or shed by the sharks.

(b) **If blood samples are to be collected, stipulate needle size, volume per sample and frequency of sampling.**

NA

(c) **Stipulate the use (and dose rate and route of administration) of any anaesthesia, analgesia, sedative, tranquilliser or other pharmacological agent applied to reduce the impact of manipulations on the animals.**

NA

(d) **What frequency of monitoring is to be maintained?**

NA, tagged sharks will be returned to the wild.

(e) **What advice regarding identification of any expected adverse effects will be given to staff responsible for the ongoing care of the animals?**

NA

9. **EXPERIENCE OF APPLICANTS:**

(a) **What is the experience of the applicants with the techniques being used in this project?**

Adam Smith is experienced sampling live fish species using angling methods and set-netting in a research environment

Alex Burton is experienced in recreational angling and handling of live fish species and setting hand-held nets in moderate currents. No prior experience in angling, longlining, or tagging in the research environment. Has previous experience in conducting heavy metal analyses on soft tissue using an array of digestion techniques and a Microwave Plasma – Atomic Emission Spectrometer in a research environment.

Clinton Duffy has more than 30 yrs experience catching, handling, sampling and tagging fishes, including sharks up to 4m total length. This includes the use of rod and line, longline and set net methods. His tagging experience includes the use of spaghetti, and pop-off and attached satellite tags. Clinton also has experience in many forms euthanasia of fish and sharks including iki-jime.

Marie-Anne Thelen is experienced in quantitatively determining metal concentrations in samples

(b) **If an applicant is using a technique with which he/she has no previous experience, what training will be provided?**

Training in catching, handling, tagging, and euthanising sharks will be provided by Clinton Duffy.

(c) **List the people providing professional services and the services provided.** *(Refer Code of Ethical Conduct, Item 5.1.4) (These personnel need not be applicants)*

Clinton Duffy. Services: training in fishing methods, safe handling of sharks and rays, tagging, guide to south Kaipara, and advice on shark biology

ANIMAL USE STATISTICS
APPLICATION/FINAL RETURN FORM
(Amended 01/19)

Protocol ID
19/98

If more than one animal type is required, then fill in one form for each type.

Application: When applying to MUAEC for approval of a manipulation, the applicant should complete Box 1, then enter in Boxes 2 to 7, in the *'Planned'* column (P), the appropriate figures for the number of animals required.

Final Return: When the manipulation is concluded, Boxes 2 to 10 should then be completed in the *'Used'* column (U) by entering appropriate figures for the number of animals that were actually used.

NOTE: Boxes 2, 3, 4, 5, 6, 8-9 and 10 must add up to the same number.

Chief Applicant: Dr Adam Smith

Inst/Sch/Dept: School of Natural and Computational Sciences

Title of Project: Population Ecology of School Sharks in the Southern Kaipara Harbour

1. Animal type: Shark, Selachimorpha (Fish) Code: 1x
(see bottom of this form)

2. Source of animals (number)

		P	U
Breeding unit	a		
Commercial	b		
Farm	c		
Born during project	d		
Captured	e	3668	
Imported	f		
Public sources	g		
TOTAL = A		3668	

3. Status of animals (number)

		P	U
Normal/conventional	a	3468	
*SPF/germ free	b		
Diseased	c		
Transgenic/chimaera	d		
Protected species	e		
Unborn/pre-hatched	f	200	
Other	g		

* *Specific pathogen free*

4. Purpose of manipulation/use (enter the total from 2 above in one box only)

		P	U			P	U			P	U
Teaching	a			Basic biological research	e			Production of biological agents	j		
Species conservation	b	3668		Medical research	f			Development of alternatives	k		
Environmental management	c			Veterinary research	g			Production of offspring with potential for compromised welfare	m		
Animal husbandry	d			Testing	h			Other	n		

5. Any re-use of animals (number to be inserted)

		P	U			P	U	
No prior use	a	3668		Previously used	b			Total a + b =

6. Grading of manipulations (number in each grade to be inserted)

(Download guidelines for selecting appropriate categories)

	Grade	P	U
A manipulation or use that causes no stress or pain or virtually no stress or pain. **No impact or virtually no impact.**	A		
A manipulation or use that causes stress or pain of a minor intensity for a short duration. **Little impact.**	B		
A manipulation or use that causes stress or pain of a minor intensity for a long duration or of a moderate intensity for a short duration. **Moderate impact.**	C	3299	
A manipulation or use that causes stress or pain of a moderate intensity for a long duration or of a severe intensity for a short duration. **High impact.**	D	369	
A manipulation or use that causes stress or pain of a severe intensity for a long duration or of a very severe intensity for any duration. **Very high impact.**	E		

7. Expected Date of Completion (maximum three years): 31/03/2021

ANIMAL DISPOSITION/FATE AT CONCLUSION OF RESEARCH, TESTING OR TEACHING OUTLINED IN THIS PROTOCOL

The data in Boxes 8 to 10 refer only to the animals noted in this protocol that actually entered the project and were manipulated - they do not refer to those it was proposed to manipulate but which were never used. This information is to be provided only when the research, testing or teaching has been completed and the animals have been disposed of as below.

8. Alive		Used
Retained by your institution's farms/colonies	a	
Returned to owner	b	
Released to the wild	c	
Disposed of to others	d	
Rehomed	e	
TOTAL ALIVE	=B=	

9. Dead		Used
Killed to use body or tissues	a	
Died/destroyed in the course of the manipulation/use	b	
Euthanased after manipulation or use	c	
Died/destroyed for reason not associated with manipulation/use	d	
TOTAL DEAD	=C=	

10. GRAND TOTAL MANIPULATIONS/USED = B + C =

Check on the final return that B + C = A in the "Used" column of Box 2.

BOX 1: ANIMAL TYPE CODES

Animal Type	Code	Animal Type	Code
Rodents	1 a = Mice	Birds	1 p = Fowls, Chickens
	1 b = Rats		1 q = Pigeons
	1 c = Guinea Pigs		1 r = Other Birds
	1 d = Hamsters	Miscellaneous	1 s = Marine Mammals
Rabbits	1 e = Rabbits		1 t = Possums
Farm Animals	1 f = Sheep		1 u = Reptiles
	1 g = Cattle		1 w = Amphibia
	1 h = Goats		1 x = Fish
	1 j = Deer		1 z = Octopus, Squid, Crab, Lobster, Crayfish
	1 k = Pigs	Other	1 y = Other Species (*name)
Other Domestic Mammals	1 m = Horses		
	1 n = Dogs		
	1 o = Cats		

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A6.2: MUAEC 19/98 Satellite tag amendment

A6.2.1: Satellite tag amendement May 2020

"To improve our examination of school shark movements and habitat use of school sharks in the southern Kaipara Harbour, we wish to attach mini-PAT satellite tags to least four and not more than eight school sharks. Ideally, the tags would be fitted to late-term pregnant female sharks in the first instance, as these are the most important individuals for recruitment to the population. We would seek to tag the sharks as they entered the harbour from October 2020 (see mini-PAT application methodology).

The mini-PAT tags will be programmed to release from the shark after 18 months, to allow us to potentially identify the precise locations of nursery grounds, understand whether individuals return the Kaipara Harbour after they have given birth, and give insight into what other national and potentially international habitats are important to this population. Early stage pregnant females and non-pregnant females over 1 m total length (TL) have also been observed in the harbour during summer (S. Tindale, C. Duffy, personal communication, December 16, 2019), and males may do so as well but they are not seen as often. In New Zealand, it is currently unknown whether sexual segregation occurs in school sharks. Considering that males and females and different sized individuals have been observed to have distinct movement patterns and habitat choice (Hurst et al., 1999; Morrison, Lowe, et al., 2014), it would be extremely informative to deploy tags onto eight individuals (> 1 m TL) to help assess the variability in movements and habitat use between individuals, sex, and size class (Sequeira et al., 2019). The deployment of eight tags would ensure that we have we still have a sufficient sample size in the event that we encounter tag failure during tag deployment (Sequeira et al., 2019). In most cases, the causes for tag failure during a deployment are relatively unknown, however, the likely causes can be, battery failure, corrosional link failure or transmission failure (Musyl et al., 2011). Therefore, **we seek permission to attach up to eight mini-PAT tags to school sharks that are greater than 1 m total length.** If any of the eight tags pop off after they are deployed, they will not be redeployed onto other individuals as part of this project.

Effects of mini-PAT tags and tether shedding rates

Mini-PAT tags are attached to a shark through insertion of an anchor into the dorsal musculature adjacent to the first dorsal fin. Small titanium anchors are preferred as they are small (45mm L x 14mm W) and made of an inert metal, so they do not create a large wound and do not corrode in the shark's muscle, and have better retention times compared to other anchors (Jepsen et al., 2015; Musyl et al., 2011). After implantation, the anchor and tether have a shedding rate similar to that of spaghetti tags (Kohler & Turner, 2001; Xiao et al., 1999). In great white sharks (*Carcharodon carcharias*), tether and anchors were observed to shed within one to four years (C. Duffy, personal communication, May 7, 2020).

From the literature, sharks have been observed to have limited capacity for pain perception, particularly to do with agonising pain (Rose et al., 2014). Rose et al. (2014) further state that sharks show no behavioural response to severe wounds and injury. Therefore, during the application of mini-PAT anchors, sharks may not feel any pain or should be affected by the application process.

Studies focusing on the effects of satellite tags have found that attachment of satellite tags via intramuscular anchorage has not been observed to affect shark behaviour, swimming, or metabolism (Jepsen et al., 2015; Lynch et al., 2017; Sundström & Gruber, 2002). Jepsen et al. (2015) also state that intramuscular anchorage requires less training, no anaesthetic (as sharks may have limited capacity for nociception), prevents interference with vital and reproductive organs or pups, and allows for the shark to be returned to the water immediately without a withdrawal period, when compared to other tagging methods.

Mini-PAT application methodology

The installation of mini-PAT tags will be done under the supervision and training of Department of Conservation shark scientist Clinton Duffy, who has over 30 years experience with handling and tagging sharks. The process of mini-PAT tag application is very similar to that of a spaghetti tag, but has some differences including being slightly more time intensive. After the shark is lifted out of the water, the hook will be removed, and it will be checked for suitability for satellite tagging following the Tindale Marine Research Charitable Trust tagging code of practice. Suitable sharks include individuals that are energetic and are not gut hooked, injured or impaired. Once a suitable shark has been selected, it will be placed on a wet foam mattress on the boat's deck and have a wet towel placed over its eyes to help prevent drying and to calm the shark. A pre-cleaned titanium anchor will then be inserted into the dorsal musculature at a shallow angle, to the side of the vertebral column via a pre-cleaned anchor applicator. This will avoid damaging any vital or reproductive organs or pups, and decrease the likelihood of infection (Jepsen et al., 2015; McMillan et al., 2019; Thorstad et al., 2013). Once the tag is in, it will be checked to see if it is in place by lightly tugging on it. The shark will be placed in the water and checked to see if it is responsive before release. This process will be done as quickly as possible to prevent any undue stress to the shark. To ensure correct tagging methodology is being used, training of inexperienced participants, and supervision of tagging, will be provided by tagging experts."

A6.2.2: Satellite tag amendement August 2021

"To improve our assessment of the large-scale movements and connectivity between various aggregations of adult school sharks in New Zealand, we will need to deploy mini-PAT tags on up to 22 more school sharks (greater than one meter, TL) than what is currently approved (i.e., eight sharks). These tags would be primarily fitted to female school sharks (>1m, TL) as they start to enter the Kaipara Harbour during spring and summer (see appendix 2 for tag application methods). They will be programmed to record an individual's depth and temperature use as well as estimate their movements over a 12-month period, after which the tag will pop-off. During the deployment period, it is likely that some of these tags will release prematurely and be recovered. Once recovered these tags can have their data archive downloaded and be re-programmed and deployed, which allows for the use of a tag and subsequently the information on school shark movement and behaviour to be maximised. Therefore, **we seek permission to increase the number of mini-PAT tags that we can attach to school sharks (greater than one meter, TL) from eight to 50**. **This figure would**

include the deployment of up to 30 mini-PAT tags and the redeployment of up to 20 tags that prematurely release. It is unlikely that we would have to redeploy such a large quantity of tags over the course of this research due to the anchors (i.e., small titanium darts) and application methods that we are using."

Note: the anchors and application methods being referred to in Appendix 6.2.2 are mentioned in Appendix 6.2.1. Additionally, the references to the literature cited in this Appendix are available in 'References' section of the thesis.

A6.3: MUAEC 22/44

MASSEY UNIVERSITY
TE KUNENGA KI PŪREHUROA
UNIVERSITY OF NEW ZEALAND

Ethics Application

Application ID :	AEC 22/44
Application Title :	The life history, movement, and accumulation of heavy metals of school sharks
Date of Submission :	10/08/2022
Primary Investigator :	Dr Adam Smith (Chief Applicant)
Other Personnel :	Alex Burton (Co-Applicant)

Section 1

Important Information/Instructions

Animal Ethics

Application for Approval of Proposed Research, Testing or Teaching Procedures Using Animals

If you are unsure whether ethical approval is required, please view the flow chart.

Please click on this link to view our Helpful Hints page for instructions on how to fill in this form

Please select Animal Ethics Category from the list*

Animal

Applicants

1 Internal Project Team
Refer Code of Ethical Conduct, Item 5.1.4 for those who should be listed

1.a Chief Applicant (*must be a permanent Massey University staff member*)*

1	Preferred First Name	Adam
	Preferred Last Name	Smith
	Preferred Full Name	Dr Adam Smith
	Primary Investigator?	Yes
	Position	Chief Applicant
	Qualifications :	PhD
	AOU system code	School of Mathematical and Computational Sciences

1.b Internal Applicants

1	Preferred First Name	Alex
	Preferred Last Name	Burton
	Preferred Full Name	Alex Burton
	Position	Co-Applicant
	Qualifications :	MSc
	AOU system code	050 - Not Specified CoS

2 External Applicants

1	Preferred Full Name	Clinton Duffy
	Position	Co-Applicant
	Qualification :	MSc
	Organisation :	Department of Conservation
	Position within organisation :	Scientific Officer

Details of Project

1 Project Title:*

The life history, movement, and accumulation of heavy metals of school sharks

2 Type of Project:*

- [x] Research
- [ ] Testing
- [ ] Teaching

3 Commercial sensitivity status:*

- (•) No
- ( ) Yes

4 Does the project involve use of native species?*

- ( ) No
- (•) Yes

4.a DOC Approval:*

- ( ) Sought but not yet granted
- (•) Granted

4.b DOC Permit Number(s):*

NA -- Clinton Duffy (DOC) informed us that no permit is required

4.c Please upload a copy of the permit(s):

This question is not answered.

4.d Māori Consultation (must be by applicants directly with iwi):

- (•) Has been undertaken
- ( ) Is currently being undertaken

4.e Please upload a copy of the consultation document(s):

1	Name	E-Form_ IKHMG_Consultation_2019.pdf
	Document type	Document upload
	Document	E-Form_ IKHMG_Consultation_2019.pdf
2	Name	E-Form_ Iwi approval for mini-PAT tags.pdf
	Document type	Document upload
	Document	E-Form_ Iwi approval for mini-PAT tags.pdf

4.f The project is approved by iwi:

- (•) Yes
- ( ) No

Justification of Project

1 What are the expected benefits of the proposed work?
*(Benefits may include improved basic knowledge, improved animal health, teaching)**

Globally, many elasmobranch (sharks and rays) populations are declining, with many species facing extinction, as a result of anthropogenic impacts such as overfishing and habitat degradation (Dulvy et al., 2021; García et al., 2008). School sharks (Galeorhinus galeus) once supported many fisheries worldwide, but declines and multiple collapses of school shark populations have prompted this species to be classified as "Critically Endangered" by International Union for the Conservation of Nature, and added to appendix two of the Convention on the Conservation of Migratory Species of Wild Animals (Convention on the Conservation of Migratory Species of Wild Animals, 2020; Stevens et al., 2000; Walker, 1998; Walker et al., 2020). Efforts to manage this species back to recovery require fundamental knowledge of its biology and ecology, yet such knowledge is severely lacking and increasingly difficult to come by, given the scarceness of this species throughout most of its range (Walker, 1998). Fortunately, school sharks are still relatively abundant in New Zealand, though it is starting to show signs of decline (Tremblay-Boyer, 2021). The New Zealand population presents a unique opportunity to study the biology and ecology of school sharks, and thereby uncover knowledge critical to the future of the species worldwide.

The overall aim of this research is to document key aspects of the life history and biology of school sharks, relating to reproduction, movement, habitat use, growth, and the effects of pollution. More specifically, we aim to (1) quantify the size/age of transition between life-history stages in New Zealand and worldwide; (2) locate and characterise habitats important to juvenile school sharks in New Zealand; (3) examine the causes of geographic variation in the growth of juvenile school sharks; (4) describe the movements of school sharks among locations in Australasia; and (5) estimate the accumulation of heavy metals over their life history. Ultimately, this research will clarify potential threats to school sharks and the ecosystems they use, and establish tools and knowledge to deepen our understanding of elasmobranch ecology worldwide.

2 How will the new knowledge be communicated to others?*

The results from this research will be communicated to scientific audiences by thesis, publications, and conference presentations. We will also report our findings to our stakeholders through hui, public presentations, working group meetings, and various media streams such as magazine articles and social media.

3 Why is it necessary to use animals for this activity?
*(The term "animal" is defined in the Animal Welfare Act, Section 2(1))**

We aim to study the movement, growth, reproduction, toxicity, and diet of a population of wild aquatic animals. There is no way of studying movement without catching, tagging, and releasing some individuals. There is no way of collecting all the other information required for our research without catching, euthanising, and conducting post-mortem examinations of some individuals. We are taking all possible measures to minimise the number of animals killed for the purpose of our research, including opportunistically receiving donations of individuals caught and killed incidentally by commercial and recreational fishers, and during research trawls by the National Institute of Water and Atmospheric Research (NIWA). We have also acquired existing comparable data on school sharks from collaborators overseas, where available, to bolster the utility of the data we collect from the NZ population. However, we need to sample ourselves in our focal locations (Kaipara and Manukau Harbours and Kapiti Coast; up to 65 per location) due to limited commercial fishing or research activity there.

Description of Procedures and Manipulations

"Manipulation" is defined in the Animal Welfare Act, Section 3

If you require more than 4,000 characters to explain any of the answers in this page, or for complex protocols, it may be beneficial to provide information as a timeline or in tabulated form, please upload these as a document in the box below. You may also upload images/photographs in any of the following formats (png, jpg, jpeg, bmp, tif, tiff).

1	Name	Additional Information
	Document type	Document upload
	Document	ADDITIONAL INFORMATION.pdf
2	Name	Email to Fiona Kemp
	Document type	Document upload
	Document	Email to Fiona Kemp_Te Uri-o-Hau_2022-08-11.pdf
3	Name	Meeting minutes Micah Butt
	Document type	Document upload
	Document	Meeting minutes_Micah Butt_2021-10-14.pdf
4	Name	Meeting minutes Willie Wright
	Document type	Document upload
	Document	Meeting minutes_Willie Wright_2022-06-10.pdf

1 Give a brief description of your trial design/teaching demonstration:*

Overview. To undertake this research, we aim to conduct up to 32 days of fieldwork between August 2022 and March 2023 on small vessels primarily in the Kaipara Harbour, the Manukau Harbour, and possibly the Kapiti Coast. During this fieldwork, we will catch school sharks by setting short (25-hook) longlines and angling (rod and reel). We anticipate catching up to 480 school sharks, and up to 1920 incidental captures of other (bycatch) species. We plan to capture and release most school sharks. In total, we plan to deploy up to 400 elastomer 'dart' tags to school sharks and other species, and 30 satellite tags to mature female school sharks. In addition, we plan to collect up to 195 specimens for necropsy. These totals include our previous activities done previously under MUAEC Protocol 19/98: deployment of 17 dart tags and 18 Mini-PAT tags, and collection of 9 specimens. Thus, under the new protocol, we plan to deploy up to 383 dart tags and 16 mini-PAT tags, and collect up to 186 specimens. Please see "Additional Information" document for more details.

2 Describe the statistical methods that you will use to analyse these data:*

Using catch data from our own fieldwork and other sources, we will use GIS, kernel densities, and Bayesian analyses to identify the locations that are of significance to the early life history of school sharks in New Zealand. Additionally, we will also analyse and characterise the habitats and environmental conditions of these areas.
Data obtained from our own dart tags will be combined with tag-recapture records from our collaborators at the Tindale Marine Research Charitable Trust (https://tindaleresearch.org.nz/tagging-program/) and other Australasian tagging studies. These data will be analysed for movement, growth, density mapping, and network modelling among key habitats. Data from mini-PAT satellite tags will be analysed using Bayesian state-space models to analyse population connectivity and identify areas of intensive activity.
Growth models such as von Bertallanfy, Gompertz, and others will be fit to determine the growth rate of juvenile school sharks from vertebral ring counts observed on collected specimen vertebrae. A Bayesian multilevel approach will be used to model how growth rates of juvenile school sharks relate to individual factors, such as diet, condition, and heavy metal accumulation, and also location-level characteristics, such as habitat, temperature, and qualitative characteristics.
To determine the metal accumulation potential of school sharks over their lifespan, we will model the relationship between the muscle and liver concentrations of copper, lead, silver, and zinc and aspects of the biology of school sharks, such as growth and diet, using a Bayesian biodynamic model.

3 Provide justification for the group sizes that you propose:*

Tagging

Studies of movement require large numbers of fish to be tagged. Tagging and releasing fish with elastomer tags is routinely done in fisheries science. When tagged fish are recaptured, this can provide information on population size, growth, and movement. Recapture rates in similar studies average around 10-30%. Our recapture rate so far has been lower, at around 6%, though it is early in the project. Thus, in our focal study of the Kaipara Harbour, we estimate if we tag 400 sharks, we will obtain a recaptured sample of 80. This sample size is in line with similar studies (e.g., Hurst et al. 1999), and will provide good information on movement patterns within and among harbours and coasts.

For satellite tags, fewer fish are required because they do not need to be recaptured. Satellite tags attach to the animal and collect data for a set amount of time (e.g., one year) after which they are programmed to detach and transmit the data via satellite. Of course, multiple individuals are required to get a representative sample of the population. Sample sizes of satellite tagging studies are usually limited by the cost of tags (over US$4k per Mini-PAT). With funding from MPI, we have purchased 25 tags which will hopefully allow for 30 deployments. Previous studies of similar species have been informative with 20-30 tagged animals, but greater numbers can reveal more about the variation in annual migrations. For our study, we will focus on mature females (> 1 m total length) as they are key to the sustainability of the population. If we are able to obtain more tags, we may fit some (up to 10) tags to mature males to examine whether their movement patterns differ from females.

Euthanasia and specimen collection

Analyses of diet and growth require large sample sizes to determine the diet and growth rates across a species length range, and assess differences in these factors between sexes, life stages, and locations. Based on current data and previous studies, we estimate 65 individuals to be the minimum sample size required to provide accurate information on growth, diet, and heavy metal concentrations in juvenile school sharks, and assess for differences in these biological attributes among different demographic groups and locations. In particular, we wish to determine the extent to which school sharks maternal offload heavy metals to their pups, which requires collection of pregnant females. For this, we aim to collect up to 12 pregnant females, each of which will each likely contain 15-45 pups (see Additional Information). Much of this research concerns physical and physiological changes over the course of the sharks' life history (e.g., growth, heavy metal accumulation). Thus, we aim to ensure maximal utility of the data by dividing the length range into regular size intervals ('bins') and dividing our total sample size evenly among the bins, where practicable.

Anticipated total catch

Because this is a study of a wild and unpredictable population, there is some uncertainty around the sampling effort required to meet our objectives. Further, the total numbers of sharks and other fishes that we might catch when seeking individuals to tag and collect as specimens is difficult to predict. In total, we anticipate catching up to 480 school sharks and 1920 individuals of other species as bycatch. Please see Additional Information section "FURTHER INFORMATION ON GROUP SIZES" for more details on these estimates.

4 Describe the manipulations to be performed on the animals:*

Please see Additional Information section "Details of Manipulations".

5 How will the proposed manipulation affect the well-being of the animals?*

Please see Additional Information section "Well-being of the animals".

6 Describe any restraint applied to the animals:*

When on the longline or rod and reel traces, the hook(s) prevent sharks from swimming off, only allowing them to swim within the vicinity of the longline or the boat if angling. When the longline or rod and reel traces are being retrieved from the water, the caught sharks will be restrained alongside the boat ready for lifting onto the boat. For hoisting methods please see Q4. Sharks too big to be hoisted aboard will either be held in the water alongside the boat or restrained in a cradle. Sharks brought aboard will be restrained and processed as quickly as possible or placed in a tank filled with aerated seawater, if small enough. Sharks that are too big to be placed into the seawater tank, take priority for processing to reduce the time out of the water. Restraining on board and next to the boat will be done by holding the shark with one or two crew or putting the shark into the shark cradle to prevent it from self-harm from thrashing around.

7 If the animals are to be transported, how will this be performed?*

No live animals will be transported.

Care of Animals

1 What access will the animals have to water?*

School sharks and other by-caught animals will be kept in water as long as possible to ensure adequate respiration and to reduce the risk of desiccation. This includes removing one or two animals from the water at a time, handling and processing animals as quickly as possible, or temporarily placing animals that are small enough into a tank of aerated salt water until they can be processed

2 Describe the feeding regimen for the animals:*

NA

3 Are the animals to be housed indoors?*

○ Yes
◉ No

4 From where will the animals be sourced? *Refer Code of Ethical Conduct, Item 5.1.12 (Where animals are personally owned, consent forms must be obtained)**

Caught in the wild in the Kaipara Harbour, Manukau Harbour, and Kapiti Coast

5 Where will the animals be kept throughout the study period?*

NA

6 Who is responsible for the routine care and health surveillance of the animals?*

Crew aboard the vessel: Adam Smith, Alex Burton, Clinton Duffy, and Massey Technical staff

If the Chief Applicant is unavailable, who will make decisions if emergency care is required?
Full name (if known) and/or position within organisation*

Alex Burton, Clinton Duffy

Fate of Animals

Note:

- If any animal is either euthanised or dies due to the unexpected side effects of approved manipulations, the animal should be subjected to a post-mortem examination by an experienced person.
- The results of the post-mortem must be communicated to the Massey University Animal Ethics Committee along with any modifications put in place to minimise the occurrence of similar events to other animals.

1 What will happen to the animals at the completion of the study?*

All animals that are captured will be tagged and/or released as soon as possible after they are brought alongside the boat or euthanised immediately.

2 Will any animals be euthanised, either as part of the study or in the event of untoward outcomes?*

○ No
◉ Yes

2.a Applicants must be familiar with the resource material on supporting staff involved with animal euthanasia at the following link: Animal Euthanasia Support Guidelines.pdf*

☑ The Chief Applicant must also confirm that he/she understands his/her obligations in regard to discussing the availability of this material with all people listed on the application on a per-project basis.

2.b Describe the euthanasia method you will use.*

Sharks will be pithed in the hind-brain with an iki spike or knife (depending on what is immediately available). Once the spike or knife enters the chondrocranium (skull) it will be rotated to ensure that the hind-brain has been destroyed. A knife will then be used to sever the vertebral column directly behind the chondrocranium. Furthermore, euthanasia will only be conducted by trained personnel to ensure that the method is carried out properly to ensure a quick and humane death for the shark. The iki-spike tool and iki-jime method are outlined on http://www.ikijime.com/.

3 What level of losses do you expect to occur during this work and how will you investigate any unexpected deaths?
Refer Code of Ethical Conduct, Items 5.6.3-5.6.5*

We anticipate unintentional mortality to be less than 1%. During our work since 2020, under MUAEC Protocol 19/98, we caught a total of 211 animals and only 1, a snapper, was unintentionally killed after being foul-hooked through the heart. To our knowledge, no school sharks were unintentionally killed and all individuals not collected as specimens were released in good condition. See additional material for more details.
Unintentional mortality longlining is strongly related to the time the longline is left in the water ('soak time'). Studies of the gummy shark (Mustelus antarcticus), a close relative of school sharks, found that mortality on longlines did not occur until 5-8 hours, and similar results have been found with other species (Butcher et al., 2015; Frick et al., 2010). In previous studies in Australia and New Zealand, longlines targeting juvenile and adult school sharks have been left to soak for up to two hours before being retrieved. When captured individuals were observed, researchers noted that individuals were in good condition and they were released (Guida et al., 2017; Hernández Muñoz, 2013; McAllister et al., 2018; Stevens & West, 1997). In contrast, Rogers et al., (2017) soaked longlines for 8-9 hours and had a 25% mortality rate. We propose a maximum soak time of 60 minutes, meaning that sharks will be attached to the longlines for no longer than 75 minutes (60 minutes of soak time and between 5 and 15 minutes retrieval time). Thus, we are not anticipating any deaths related to long soak times. There is a risk of predation of hooked sharks by larger predators; this risk is unavoidable and is also mitigated by short soak times.
Any animals in very poor condition and unlikely to survive will be euthanised. Any unexpected losses will be investigated by necropsy to determine cause of death and we will then consider ways to avoid further losses. The losses will be reported to the committee.

Alleviation of Impact of Manipulations

1 What features of the manipulations minimise their impact on the animals?*

We will make every effort to minimise mortality of sharks by limiting the soak time of the longlines to a maximum of 60 minutes; keeping a constant eye on rod and reel traces to see when an animal hooks on and retrieve the line when they do, and use circle hooks to minimise gut hooking and allow for easy retrieval of the hook (Cooke et al., 2012; Danylchuk et al., 2014; Willis & Millar, 2001).
While angling, if in the event two animals hook onto the same or two different rods at the same time, both will be brought to the side of the boat. While one animal is being processed, the other animal, if small enough, will be brought aboard and put in a saltwater tank. If the animal is too big to fit in the saltwater tank, it will be held in the water, alongside the boat, until the other animal has been processed. If the shark begins to roll in the water, it will be held in a shark cradle to prevent any damage that may be inflicted from the mono-filament trace. If the animal cannot be held alongside the boat while the other shark is being processed, it will be released. The released animal will be observed to make sure it does not get tangled in any of the other gear or attempt to predate the other captured animal.
Once aboard the vessel, processing will be done as quickly as possible to ensure a prompt return to the water. If small enough and there is a backlog of individuals or a large individual comes aboard, animals will be placed in an aerated saltwater tank until they can be processed. During processing the use of gloves and wet towels to handle the animals, including covering their eyes, during on-board procedures will also reduce the risk of desiccation and the amount of protective mucus removed.
Tagging procedures will be based on the tagging code of conduct and the tagging instructions set out by the TMRCT. The tagging procedure is quick and prevents injury to vital organs by inserting tags into the radial cartilage and dorsal musculature at the base of the first dorsal fin. The dart tags will eventually be overgrown and encapsulated or shed by the sharks. This will be similar to the tethers for mini-PAT tags. However, the tag will detach after the pre-programmed release date (12 months after deployment).

2 Are blood samples to be collected?*

- (●) No
- ( ) Yes

3 Stipulate the use (and dose rate and route of administration) of any anaesthesia, analgesia, sedative, tranquilliser or other pharmacological agent applied to reduce the impact of manipulations on the animals.*

NA

4 What frequency of monitoring is to be maintained?*

NA

5 What advice regarding identification of any expected adverse effects will be given to staff responsible for the ongoing care of the animals?*

NA

Experience of Applicants

1 What is the experience of the applicants with the techniques being used in this project?*

Adam Smith is experienced with using angling and longlining methods in a research environment to sample, measure, and tag live fish and shark species. Adam has also worked on NIWA fisheries research voyages.

Alex Burton is experienced in angling and longlining for sharks and handling, tagging, and euthanising live sharks up to 1.7m long in a research environment. Tagging experience includes tagging school sharks with dart tags. Euthanasia experience includes use of iki-jime via iki-spike or knife. Alex is also experienced in performing necropsies of several shark species.

Clinton Duffy has more than 30 yrs experience catching, handling, sampling and tagging fishes, including sharks up to 4m total length. This includes the use of rod and line and longline methods. His tagging experience includes the use of spaghetti, and pop-off and fin-mounted satellite tags. Clinton also has experience in many forms euthanasia of fish and sharks including iki-jime.

2 If an applicant is using a technique with which he/she has no previous experience, what training will be provided?*

Anyone not experienced with dart tags will be trained by the applicants in accordance with guidelines of the TMRCT (https://tindaleresearch.org.nz/). Application of satellite tags will be done under the guidance of Clinton Duffy.

3. List the people providing professional services and the services provided.
(Refer Code of Ethical Conduct, Item 5.1.4) (These personnel need not be applicants).

This question is not answered.

Use of Restricted Medicines

1. Will personnel who are not registered veterinarians be required to administer restricted veterinary or human medicines?*

- (●) No
- ( ) Yes

Animal Use Statistics

Expected Date of Completion (maximum three years):

31/03/2024

Please ensure that this "Animal Use Statistics" section is completed.

Notes:

- Please refer to the Guidance Document for information about selecting the appropriate categories.

'Planned' fields : When applying to MUAEC for approval of a manipulation, the applicant should complete the *'Planned'* fields with the appropriate figures for the number of animals required.

'Used' fields : When the manipulation is concluded, the applicant should then complete the *'Used'* fields by entering appropriate figures for the number of animals that were actually used.

NOTE : There is no calculation function within this form so all figures and totals must be entered manually. Please ensure that all sections add up to the same number.

Please enter name of animal species, eg, dove, then choose variety as/where applicable

1	Species/Variety	Shark
	Category	Fish
	2. Source of Animals	
	a. Breeding Unit Planned number	
	Used number	
	b. Commercial Planned number	
	Used number	
	c. Farm Planned number	
	Used number	
	d. Born during project Planned number	
	Used number	
	e. Captured Planned number	840
	Used number	
	f. Imported Planned number	
	Used number	
	g. Public sources Planned number	
	Used number	
	TOTAL = A (Planned)	840
	TOTAL = A (Used)	
	3. Status of Animals	
	a. Normal/Conventional Planned number	480
	Used number	
	b. SPF/germ free* Planned number	
	Used number	
	c. Diseased Planned number	
	Used number	
	d. Transgenic/chimaera Planned number	

Used number	
e. Protected species Planned number	
Used number	
f. Unborn/pre-hatched Planned number	360
Used number	
g. Other Planned number	
Used number	
4. Purpose of manipulation/use (enter the total from 2 above in one box only)	
a. Teaching Planned number	
Used number	
b. Species conservation Planned number	840
Used number	
c. Environmental management Planned number	
Used number	
d. Animal husbandry Planned number	
Used number	
e. Basic biological research Planned number	
Used number	
f. Medical research Planned number	
Used number	
g. Veterinary research Planned number	
Used number	
h. Testing Planned number	
Used number	
i. Production of biological agents Planned number	
Used number	
j. Development of alternatives Planned number	
Used number	
k. Production of offspring with potential for compromised welfare	
Planned number	
Used number	
l. Other Planned number	
Used number	

5. Any re-use of animals (number to be inserted)	
a. No prior use Planned number	840
Used number	
b. Previously used Planned number	
Used number	
Total a + b =	840
6. Grading of manipulations (number in each grade to be inserted)	
a. A manipulation or use that causes no stress or pain or virtually no stress or pain. No impact or virtually no impact.	
Planned number	
Used number	
b. A manipulation or use that causes stress or pain of a minor intensity for a short duration. Little impact.	
Planned number	
Used number	
c. A manipulation or use that causes stress or pain of a minor intensity for a long duration or of a moderate intensity for a short duration. Moderate impact.	
Planned number	798
Used number	
d. A manipulation or use that causes stress or pain of a moderate intensity for a long duration or of a severe intensity for a short duration. High impact.	
Planned number	42
Used number	
e. A manipulation or use that causes stress or pain of a severe intensity for a long duration or of a very severe intensity for any duration. Very high impact.	
Planned number	
Used number	
Are you entering final animal usage for a protocol which is now completed?	No

Does total animal usage exceed original planned and approved numbers?

○ Yes
◉ No

Note: the references to the literature cited in this Appendix are available in 'References' section of the thesis.

Appendix 7 – Statements of Contribution for data chapters (Ch.2-6)

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GRADUATE RESEARCH SCHOOL

STATEMENT OF CONTRIBUTION DOCTORATE WITH PUBLICATIONS/MANUSCRIPTS

We, the student and the student's main supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the student's contribution as indicated below in the Statement of Originality.

Student name:	Alex Burton
Name and title of main supervisor:	Assoc. Prof. Winston Sweatman
In which chapter is the manuscript/published work?	Chapter 2

Describe the contribution that the student and members of the supervisory team have made to the manuscript/published work:[1]

Fieldwork and laboratory work, as well as data collation, conducted by Alex Burton. Original draft written by Alex Burton. Study conception, design, and methodology, statistical analysis, and funding acquisition carried out by Alex Burton and Adam Smith. Final manuscript reviewed by Alex Burton, Adam Smith, and Winston Sweatman.

Please select one of the following three options:

- ○ The manuscript/published work is published or in press
  Please provide the full reference of the research output:
- ○ The manuscript is currently under review for publication
  Please provide the name of the journal:
- ◉ It is intended that the manuscript will be published, but it has not yet been submitted to a journal

Student's signature:	Alex Burton — Digitally signed by Alex Burton Date: 2025.04.29 15:57:53 +12'00'	Main supervisor's signature:	Winston Sweatman — Digitally signed by Winston Sweatman Date: 2025.04.29 15:42:54 +12'00'

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We, the student and the student's main supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the student's contribution as indicated below in the Statement of Originality.

Student name:	Alex Burton
Name and title of main supervisor:	Assoc. Prof. Winston Sweatman
In which chapter is the manuscript/published work?	Chapter 3

Describe the contribution that the student and members of the supervisory team have made to the manuscript/published work:[1]

Field and laboratory work, as well as data collation, conducted by Alex Burton. Generative model developed by Adam Smith. Study conception, statistical analysis, and funding acquisition conducted by Alex Burton and Adam Smith. Study designed by Alex Burton, Adam Smith, and Clinton Duffy. Original draft written by Alex Burton. Final manuscript reviewed by Alex Burton, Adam Smith, and Winston Sweatman.

Please select one of the following three options:

○	The manuscript/published work is published or in press Please provide the full reference of the research output:
○	The manuscript is currently under review for publication Please provide the name of the journal:
◉	It is intended that the manuscript will be published, but it has not yet been submitted to a journal

Student's signature:	Alex Burton Digitally signed by Alex Burton Date: 2025.04.29 15:58:29 +12'00'	Main supervisor's signature:	Winston Sweatman Digitally signed by Winston Sweatman Date: 2025.04.29 15:44:23 +12'00'

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We, the student and the student's main supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the student's contribution as indicated below in the Statement of Originality.

Student name:	Alex Burton
Name and title of main supervisor:	Assoc. Prof. Winston Sweatman
In which chapter is the manuscript/published work?	Chapter 4

Describe the contribution that the student and members of the supervisory team have made to the manuscript/published work:[1]

Field work conducted by Alex Burton. Methodology developed by Alex Burton, John Harrison, Marie-Anne Thelen, and Clinton Duffy. Laboratory work conducted by Alex Burton, John Harrison, and Marie-Anne Thelen. Statistical analysis carried out by Alex Burton with assistance from Adam Smith. Study conception and design, as well as funding acquisition, conducted by Alex Burton, Adam Smith, John Harrison, Marie-Anne Thelen, and Clinton Duffy. Original draft written by Alex Burton. Final manuscript reviewed by Alex Burton, John Harrison, Adam Smith, and Winston Sweatman.

Please select one of the following three options:

○	The manuscript/published work is published or in press Please provide the full reference of the research output:
○	The manuscript is currently under review for publication Please provide the name of the journal:
◉	It is intended that the manuscript will be published, but it has not yet been submitted to a journal

Student's signature:	Alex Burton Digitally signed by Alex Burton Date: 2025.04.29 15:58:56 +12'00'	Main supervisor's signature:	Winston Sweatman Digitally signed by Winston Sweatman Date: 2025.04.29 15:44:13 +12'00'

This form should be placed at the beginning of each relevant thesis chapter.

[1] Refer to the Massey University Publishing and Authorship guidelines (OneMassey for staff, Stream for students) and/ or Contributor Roles Taxonomy (CRediT) guidelines for guidance.

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We, the student and the student's main supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the student's contribution as indicated below in the Statement of Originality.

Student name:	Alex Burton
Name and title of main supervisor:	Assoc. Prof. Winston Sweatman
In which chapter is the manuscript/published work?	Chapter 5

Describe the contribution that the student and members of the supervisory team have made to the manuscript/published work:[1]

Field work conducted by Alex Burton and Clinton Duffy. Methodology developed by Alex Burton, Adam Smith, and Clinton Duffy. Laboratory work conducted by Alex Burton. Statistical analysis carried out by Alex Burton with assistance from Adam Smith. Study conception and design, as well as funding acquisition, conducted by Alex Burton, Adam Smith, and Clinton Duffy. Original draft written by Alex Burton. Final manuscript reviewed by Alex Burton, Adam Smith, and Winston Sweatman.

Please select one of the following three options:

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STATEMENT OF CONTRIBUTION DOCTORATE WITH PUBLICATIONS/MANUSCRIPTS

We, the student and the student's main supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the student's contribution as indicated below in the Statement of Originality.

Student name:	Alex Burton
Name and title of main supervisor:	Assoc. Prof. Winston Sweatman
In which chapter is the manuscript/published work?	Chapter 6

Describe the contribution that the student and members of the supervisory team have made to the manuscript/published work:[1]

Method development and laboratory work carried out by Alex Burton, Marie-Anne Thelen, and John Harrison. Statistical analysis conducted by Alex Burton with assistance from Adam Smith and John Harrison. Study conception and design, as well as funding acquisition, carried out by Alex Burton, Adam Smith, John Harrison, and Marie-Anne Thelen. Original draft written by Alex Burton. Final manuscript reviewed by Alex Burton, Adam Smith, John Harrison, Marie-Anne Thelen, and Winston Sweatman.

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