A re-examination of the growth of the gummy shark (*Mustelus antarcticus*) from Queensland, Australia

Matthew J. Campbell and Cassandra L. Rigby

**ABSTRACT**

The gummy shark (*Mustelus antarcticus*) is endemic to Australia and is the target of commercial fisheries in southern Australia. However, the Queensland population is subjected to low levels of fishing mortality. The present study re-analysed a limited length-at-age dataset collected from central Queensland to estimate growth parameters in a Bayesian framework, with informative priors for size-at-birth and maximum size. Growth parameters were estimated using a multi-model approach. This study showed that *M. antarcticus* caught in Queensland exhibits slow growth compared with conspecifics in southern Australia, and females grow slower and larger than do males. The combined length-at-age data for males and females was best described by the von Bertalanffy growth function and the growth parameters were $L_\infty = 1852$ mm (total length, TL), $L_0 = 261$ mm TL and $k = 0.044$ year$^{-1}$ for males and females combined. The ‘BayesGrowth’ R package offers a simple method to minimise bias in the estimation of growth parameters from a limited length-at-age dataset in a Bayesian framework.

**Keywords**: BayesGrowth, elasmobranch, growth, gummy shark, length-at-age, life history, *Mustelus antarcticus*.

**Introduction**

The gummy shark (*Triakidae: Mustelus antarcticus*) is endemic to Australia and has been the target of a commercial fishery since the 1920s (Moulton et al. 1992). The species occurs to a depth of 400 m (Kyne et al. 2021) in southern and north-eastern Australia between Geraldton, Western Australia (28°S), and Hinchinbrook Island in Queensland (~18°20' S; Kyne et al. 2021). Prior to the study by White et al. (2021), the mustelid found in Queensland was classified as the eastern spotted gummy shark (*M. walkeri*). However, White et al. (2021) found no genetic or morphological difference between *M. walkeri* and *M. antarcticus*, which extended the distribution of *M. antarcticus* beyond the previous northern boundary located at Port Stephens, New South Wales (32°S) (Walker 2016). An extensive tagging program conducted in southern Australia provided evidence that the southern population extended northward to New South Wales, but not into Queensland waters (White and Last 2008).


*Mustelus antarcticus* is also caught as bycatch by vessels operating in Australia’s largest penaeid-trawl fishery, the Queensland eastern coast otter trawl fishery (QECOTF, Rigby et al. 2016). Fishers are required to return all individuals to the sea as soon as practicable. Like all of the chondrichthyans (sharks, rays and chimeras) interacting with
the QECOTF, catch and survival of discarded *M. antarcticus* are unquantified. The lack of these data impedes the robust quantitative assessment of the species’ population status in Queensland. As such, qualitative assessments of a species’ exposure and resilience to trawling are used to assess the ecological risk posed to chondrichthysans by the QECOTF (e.g. Pears et al. 2012). A previous quantitative ecological risk assessment demonstrated that the penaeid-trawl fishery posed a low risk to the long-term sustainability of *M. antarcticus* (Campbell et al. 2017). However, the authors stated that improvements to life-history information for this, and other, species are required to ensure the accurate assessment of risk. Moulton et al. (1992) described the growth of *M. antarcticus* from a broad geographical range in southern Australia. These authors fit variants of the von Bertalanffy growth function (VBGF) to length-at-age and tag-recapture data and found that growth varied spatially and temporally, and by sex. The VBGF growth completion parameter derived in Moulton et al. (1992) varied between 0.047 and 0.304 year−1. More recently, Rigby et al. (2016) reported the VBGF growth parameters for *M. antarcticus*, formerly *M. walkeri*, on the basis of length-at-age samples collected from the QECOTF in central Queensland, and found that the species was slow growing (k = 0.033 year−1) and late to mature (females: 10–14 years). However, the VBGF asymptotic length at which growth is zero (i.e. L∞) was found to be 2245 mm (total length, TL) despite a reported maximum size of 1852 mm TL. The low sample size (n = 44) prompted the authors to state that the estimates should be considered preliminary. The aim of the current study was to update the growth estimates of *M. antarcticus* in Queensland, reported by Rigby et al. (2016), in a Bayesian framework, using prior information to reduce bias in parameter estimates.

### Materials and methods

The length-at-age data of *M. antarcticus* obtained by Rigby et al. (2016) were re-examined. Three growth functions were used to estimate mean length-at-age, namely, von Bertalanffy growth function (VBGF), logistic growth function and Gompertz growth function (Table 1; Smart et al. 2016). The biologically relevant length-at-birth (L0) was estimated (Cailliet et al. 2006). Growth was estimated in a Bayesian framework using Markov-chain Monte Carlo (MCMC) to overcome the low number of length-at-age observations. Bayesian models were fit using the ‘BayesGrowth’ package (ver. 0.3.0, J. J. Smart, see https://github.com/jonathansmart/BayesGrowth, accessed 11 May 2022) by using R statistical software (ver. 4.0.2, R Foundation for Statistical Computing, Vienna, Austria, see https://www.R-project.org/, accessed 11 May 2022), in accord with methods described by Smart and Grammer (2021) and Emmons et al. (2021). Four MCMC chains with 10 000 simulations, with a burn-in period of 5000 simulations, were used to determine parameter posterior distributions. Model convergence was assessed using the Gelman–Rubin test and diagnostic plots were generated using the ‘Bayesplot’ package (ver. 1.7.2, J. T. M. Gabry, see https://mc-stan.org/bayesplot, accessed 18 February 2021) in R.

Models were fit to length-at-age data for both sexes combined, females only and males only. Each model was fit with normal residual error structures (σ). Prior distributions for the L0 and L∞ estimates were informed by Walker (2016). Walker (2016) also reported that the maximum size of *M. antarcticus* differed as a function of sex with females and males attaining 1852 mm (total length, TL) and 1482 mm TL respectively. Rigby et al. (2016) reported five near-term pups with umbilical scars had a mean length of 257.8 mm (s.d. = 5.8). Given this information, normally distributed priors (μ, σ) were set at L∞ ~ N(1852, 25), and L0 ~ N(258, 5.8) for both sexes combined and for females only. Additionally, a prior of L∞ ~ N(1482, 25) was used for males. A non-informative prior was used for σ and a common non-informative prior was used for the growth coefficients of the three candidate models (k, g1, and g2, Table 1). An upper bound was nominated for the uniform distributions of σ and k of 100 and 0.3 year−1 respectively. The common non-informative prior for the growth coefficients allowed for comparison of the three candidate growth functions, each with identical priors, as outlined by Smart and Grammer (2021).

Differences in growth parameters between sexes were assessed by comparing the 10 000 posterior estimates of L∞, k and L0. A frequency histogram of the values in a vector (vdiff), representing the result of subtracting the vector of posterior estimates of each parameter for males from the vector of posterior estimates for females, was generated. A significant difference was detected if the 95% confidence interval of the distribution of vdiff did not include zero.

The original research was undertaken in accord with James Cook University Animal Ethics Approval A1566, Great Barrier Reef Marine Park Authority Permit G10/33603.1 and Department of Fisheries, Agriculture and Forestry Permits S5105 and 147714.

<table>
<thead>
<tr>
<th>Model</th>
<th>Growth function</th>
</tr>
</thead>
<tbody>
<tr>
<td>Von Bertalanffy</td>
<td>L_t = L_0 + (L_∞ − L_0)(1 − e^{-kt})</td>
</tr>
<tr>
<td>Gompertz function</td>
<td>L_t = L_0 × e^{(ln(L_∞/L_0))(1−e^{-kt})}</td>
</tr>
<tr>
<td>Logistic function</td>
<td>L_t = L_0 × e^{(ln(L_∞/L_0))(1−e^{-kt})}/(1+e^{−kt})</td>
</tr>
</tbody>
</table>

L_t is the length (mm) at Age t (years); L_∞ is the asymptotic length (mm); L_0 is the length at t = 0 (mm); and k, g_1, and g_2 are coefficients of the respective growth functions to be estimated (year−1).
Results

The VBGF was found to best fit the length-at-age data for both sexes combined (Supplementary Table S1, LOOICw = 1). There was no support for either the logistic (LOOICw = 0) or the Gompertz (LOOICw = 0) growth functions. With the sexes combined, the estimated VBGF parameters were $L_\infty = 1852$ mm TL, $L_0 = 261$ mm TL and $k = 0.044$ year$^{-1}$ (Fig. 1, Table S1). The VBGF was also found to best fit the female length-at-age data (LOOICw = 1, Table S1), with the estimated parameters of $L_\infty = 1853$ mm TL, $L_0 = 260$ mm TL and $k = 0.044$ year$^{-1}$ (Fig. 2, Table S1). The VBGF also best fit the male length-at-age data (Fig. 2, Table S1) and the relevant parameters derived from this model were $L_\infty = 1483$ mm TL, $L_0 = 258$ mm TL and $k = 0.060$ year$^{-1}$ (Fig. 2, Table S1). Both $L_\infty$ and $k$ differed significantly as a function of sex (Supplementary Fig. S1).

Discussion

The results from the current study improve the growth parameter estimates originally reported by Rigby et al. (2016). Specifically, the $L_\infty$ estimates derived herein approximate the maximum reported size of the respective sexes. The under-sampling of larger, older animals by Rigby et al. (2016) resulted in a biased estimate of $L_\infty$ in their study. This was due to the larger animals escaping the penaeid trawls via turtle-excluder devices (TEDs: Brewer et al. 2006; Campbell et al. 2020) or decreased gear selectivity with an increasing shark length (Clarke et al. 2005). Consequently, the VBGF growth coefficient derived by Rigby et al. (2016) is also likely to be biased, given $k$ and $L_\infty$ covary negatively (Pardo et al. 2013). The use of informative priors improves growth parameter estimates, compared with estimates derived using frequentist priors.
methods, when the under-sampling of older animals occurs (Smart and Grammer 2021).

The higher $L_m$ and lower growth coefficients ($k$, Table 1) for female $M. antarcticus$, compared to males, derived herein are comparable to previous research (Lenanton et al. 1990; Moulton et al. 1992). Females growing slower, and to larger sizes, is a common life-history strategy among elasmobranchs (Cortés 2000). Similar life-history strategies have also been reported for the congeneric $M. canis$ (Conrath et al. 2002), $M. lenticulatus$ (Francis and Francis 1992), $M. californicus$ (Yudin and Cailliet 1990) and $M. henlei$ (Yudin and Cailliet 1990). The $M. antarcticus$ individuals caught in Queensland grow slower and to a smaller maximum size, than do those caught in southern Australia (Moulton et al. 1992), resulting in individuals of the same age being comparatively smaller in Queensland samples. These differences may be attributable to the depths at which the respective $M. antarcticus$ populations occur, given fish length and depth have been shown to covary negatively in mustelids (Smale and Compagno 1997) and other chondrichthyan species (Ribey and Simpfendorder 2015; Braccini et al. 2020). The Queensland population is generally restricted to relatively deep water (Ribey et al. 2016) compared with conspecifics in southern Australian, which mainly occur in shallow coastal waters (Moulton et al. 1992).

Ribey et al. (2016) used a multi-model approach in the original study and, in accord with the results herein, found that the length-at-age dataset was best described by the VBGF. The use of growth functions other than the VBGF was suggested by Cailliet et al. (1990), who found that the growth of the star-spotted smooth-hound ($Mustelus manazo$) appeared linear. Similarly, the length-at-age data collected by Ribey et al. (2016) appeared linear and the applicability of the respective growth functions found to best fit the length-at-age data herein should be re-assessed in future studies, should subsequent length-at-age data be collected to better reflect the Queensland population of $M. antarcticus$. There is a clear need to undertake further sampling from the other fisheries accessing the Queensland population of $M. antarcticus$, such as net and line fisheries, given the likely selectivity issues associated with the inclusion of TEDs in penaeid trawls. This will further improve model fitting and increase the accuracy of the resultant growth parameter estimates.

Unlike the southern Australian states, the lack of a large-scale commercial fishery for $M. antarcticus$, and the resultant lack of reliable catch data, precludes the use of formal stock assessments for the Queensland portion of the $M. antarcticus$ stock. However, the post-trawl mortality associated with capture by penaeid trawls is a source of fishing mortality that is unquantified and this requires attention to ensure that current levels of trawl effort are sustainable in the long term. Subsequent studies should validate shark catch by commercial trawl, net and line fishers to ensure catches of $M. antarcticus$ are not misreported as other species or species groups (e.g. shark, unspecified).

The availability of the ‘BayesGrowth’ R package allows researchers with limited experience of Bayesian methods to assess growth from limited length-at-age datasets. Obtaining sufficient samples to quantify unbiased parameter estimates is often difficult due to infrequency of catch (Smart et al. 2013) or the selectivity of the sampling gear for individuals at the upper and lower portions of the length-frequency distribution (Campbell et al. 2021). Further, the cost of obtaining fish can limit sample sizes, particularly in remote areas or where samples are purchased from commercial fishers. Estimating growth parameters using prior information goes some way to overcoming biases resulting from a low sample size.

In conclusion, life-history information is necessary to determine sustainable levels of fishing mortality. The current study provides improved estimates of the growth parameters for $M. antarcticus$, which enables more accurate assessment of population status in Queensland. There is currently no targeted fishery for $M. antarcticus$ in Queensland and fishing mortality is likely to be low, although post-trawl mortality is unknown. Additional sampling will further improve future growth parameter estimates.

Supplementary material is available online.

References


Emmons SM, D’Alberto BM, Smart JJ, Simpfendorfer CA (2021) Age and growth of tiger shark (Galeocerdo cuvier) from Western Australia. Marine and Freshwater Research 72(7), 950–963. doi:10.1071/MF20291


Smart JJ, Grammer GL (2021) Modernising fish and shark growth curves with Bayesian length-age models. PLoS ONE 16(2), e0246734. doi:10.1371/journal.pone.0246734


---

Data availability. Data sharing is not applicable as no new data were generated or analysed during this study.

Conflicts of interest. The authors declare that they have no conflicts of interest.

Declaration of funding. C. L. Rigby was supported by an Australian Post-graduate Award during the original research work. The Oceania Chondrichthyan Society and Passions of Paradise provided funding to C. L. Rigby by a Student Research Award. The current study was funded by the Queensland Department of Agriculture and Fisheries.

Acknowledgements. The authors extend their sincerest thanks to the crews of the vessels boarded by C. L. Rigby during the at-sea sampling, and to the owner of the vessels, Steve Murphy, for his support of the original research. We also thank Jonathan Smart for his assistance in the use of his excellent R package, which will undoubtedly be the basis of many future elasmobranch growth studies.

Author contributions. Matthew Campbell was responsible for the conceptualisation, methodology, formal analysis, writing – original draft preparation, writing – reviewing and editing, visualisation; and Cassandra Rigby was responsible for the funding Rigby obtained, investigation, writing – original draft preparation, writing – reviewing and editing, resources.

Author affiliations

1Queensland Department of Agriculture and Fisheries, Agri-Science Queensland, Ecosystems Precinct, GPO Box 267, Brisbane, Qld 4001, Australia.

2Centre for Sustainable Tropical Fisheries and Aquaculture and College of Science and Engineering, James Cook University, 1 James Cook Drive, Townsville, Qld 4811, Australia.