

Life-history characteristics of the eastern shovelnose ray, *Aptychotrema rostrata* (Shaw, 1794), from southern Queensland, Australia

Matthew J. Campbell^{ID} A,B,C, Mark F. McLennan^A, Anthony J. Courtney^A and Colin A. Simpfendorfer^B

^AQueensland Department of Agriculture and Fisheries, Agri-Science Queensland, Ecosciences Precinct, GPO Box 267, Brisbane, Qld 4001, Australia.

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

^CCorresponding author. Email: matthew.campbell@daf.qld.gov.au

Abstract. The eastern shovelnose ray (*Aptychotrema rostrata*) is a medium-sized coastal batoid endemic to the eastern coast of Australia. It is the most common elasmobranch incidentally caught in the Queensland east coast otter trawl fishery, Australia's largest penaeid-trawl fishery. Despite this, age and growth studies on this species are lacking. The present study estimated the growth parameters and age-at-maturity for *A. rostrata* on the basis of sampling conducted in southern Queensland, Australia. This study showed that *A. rostrata* exhibits slow growth and late maturity, which are common life-history strategies among elasmobranchs. Length-at-age data were analysed within a Bayesian framework and the von Bertalanffy growth function (VBGF) best described these data. The growth parameters were estimated as $L_0 = 193$ mm TL, $k = 0.08$ year⁻¹ and $L_\infty = 924$ mm TL. Age-at-maturity was found to be 13.3 years and 10.0 years for females and males respectively. The under-sampling of larger, older individuals was overcome by using informative priors, reducing bias in the growth and maturity estimates. As such, the results can be used to derive estimates of natural mortality for this species.

Keywords: life history, growth, age-at-maturity, elasmobranch, *Aptychotrema rostrata*.

Received 4 December 2020, accepted 26 March 2021, published online 7 May 2021

Introduction

The Queensland east coast otter trawl fishery (QECOTF) is the largest penaeid-trawl fishery in Australia. This fishery targets shrimps (Penaeidae: *Melicertus* spp., *Penaeus* spp., *Metapenaeus* spp.), sea scallops (Pectinidae: *Ylistrum balloti*), bugs (Scyllaridae: *Thenus* spp. and *Ibacus* spp.) and squid (Teuthoidea) with demersal otter trawl gear. In 2019, logbook data indicated that 299 vessels fished 35 950 days and landed ~5986 t of product for sale at both domestic and international markets. Further, two vessels target stout whiting (*Sillago robusta*), using Danish seine and fish trawl gear, in southern Queensland and are subject to an annual total allowable catch (TAC) of ~1100 t.

It has been estimated that 55% of the global catch from penaeid trawls is discarded (Gilman *et al.* 2020). The discard rate from the QECOTF is higher at 70%, resulting in >25 000 t being discarded annually (Wang *et al.* 2020), representing 28.5% of Australia's total annual discards (Kennelly 2020). Consequently, quantifying and mitigating discards have been the subjects of significant research efforts in Queensland since the mid-1990s (e.g. Robins-Troeger 1994; Robins and McGilvray 1999). Hundreds of species comprise the discarded portion of

the QECTOF catch (Courtney *et al.* 2006; Courtney *et al.* 2008), some of which are of conservation concern, such as sea turtles (McGilvray *et al.* 1999).

Elasmobranchs (i.e. sharks and rays) are one component of penaeid-trawl discards that have received increasing attention in the past two decades (Dulvy *et al.* 2017). Elasmobranch life-history strategies, including late maturity, few offspring, long life spans and slow growth (Dulvy *et al.* 2008), make this group vulnerable to over-exploitation (Stevens *et al.* 2000). Twenty-five per cent of elasmobranchs have an elevated risk of extinction as a result of capture in fisheries (Dulvy *et al.* 2017; Simpfendorfer and Dulvy 2017) and the species of Rhinopristiformes (wedgfishes and guitarfishes) are of a particular concern (Kyne *et al.* 2020). The introduction of turtle excluder devices (TEDs) has gone some way to reduce this risk in penaeid-trawl fisheries, particularly for larger species: however, TEDs remain ineffective for smaller elasmobranchs (Campbell *et al.* 2020).

The TEDs used in the QECOTF have no effect on the catch rate of the eastern shovelnose ray (Trygonorrhinidae: *Aptychotrema rostrata*, Shaw 1794; Courtney *et al.* 2008). This is the most common elasmobranch in the discarded portion of the

penaeid-trawl (Kyne *et al.* 2002) and *S. robusta* (Rowse and Davies 2012) catches in southern Queensland (>22°S). *Aptychotrema rostrata* is endemic to the eastern coast of Australia between Halifax Bay in northern Queensland (18°30'S) and Merimbula in southern New South Wales (36°53'S). The species rarely exceeds 1 m total length (TL), generally in depths of <100 m (Last and Stevens 2009), and feeds on crustaceans, teleost fish and squid (Kyne and Bennett 2002a). In southern Queensland, parturition occurs in November and December after a gestation period of 3–5 months, with litter sizes of 4–18 pups (Last *et al.* 2016).

In Queensland, the incidental capture of *A. rostrata* in the QECOTF is the main source of fishing mortality, although post-release survival is high (Campbell *et al.* 2018). In 2010, the two vessels targeting *S. robusta* caught 3075 *A. rostrata* individuals, of which ~22% were released alive (Rowse and Davies 2012). Recreational anglers land *A. rostrata* (Kyne and Stevens 2015); however, the catch is negligible in Queensland (J. Webley, Fisheries Queensland, pers. comm.).

Despite its frequent occurrence in trawl catches, age and growth studies on *A. rostrata* are lacking. Diet (Kyne and Bennett 2002a), dentition (Gutteridge and Bennett 2014), sensory characteristics (Hart *et al.* 2004; Wueringer *et al.* 2009) and post-trawl survival (Campbell *et al.* 2018) have been the subject of recent research. Although reproductive strategies were described in two studies (Kyne and Bennett 2002b; Kyne *et al.* 2016), no previous study has quantified growth and age-at-maturity.

The lack of these data and the absence of information regarding the number of *A. rostrata* individuals caught annually are the main impediments for the assessment of population status. Currently, the IUCN Red List of Threatened Species categorises *A. rostrata* as 'Least Concern' (Kyne and Stevens 2015). In Australia, all fisheries are subject to environmental assessment, whereby jurisdictions are required to demonstrate that the impacts on individual species, both target and non-target, are sustainable in the long-term. Failure to do so can result in the revocation of export privileges, prohibiting access to lucrative international markets.

Previous qualitative ecological risk assessments (ERAs) have indicated that trawling in Queensland (Pears *et al.* 2012; Jacobsen *et al.* 2018) and New South Wales (Astles *et al.* 2009) poses a high ecological risk to *A. rostrata* in the respective jurisdictions. These ERAs rely on qualitative assessments of a species' exposure and resilience to trawling, rather than empirical data, to assess risk. Generally, qualitative ERAs overestimate the ecological risk posed by fishing than the quantitative ERAs when compared with results from formal stock assessments (Zhou *et al.* 2016). As such, life-history data are fundamental to assessing stock status and form the basis of quantitative ERAs, an improved method for assessing data-poor species such as *A. rostrata*. The aim of the present study, therefore, was to estimate the growth parameters and age-at-maturity of *A. rostrata*.

Materials and methods

Specimens of *A. rostrata* were primarily obtained from the operator of a Danish seine vessel, the FV *San Antone II*, targeting *S. robusta* in southern Queensland on an *ad hoc* basis in

the period between April 2016 and November 2017. The *San Antone II* is a 17 m steel twin-hulled vessel powered by two 148 kW diesel engines. The Danish seine gear consisted of two 2500 m sweeps separated by a single net with a headline length of 34.75 m, with a mesh size of 85 mm in the wings and 55 mm in the codend. Samples were collected in southern Queensland waters between Sandy Cape (24°42.043'S, 153°16.027'E) and Coolangatta (28°09.844'S, 153°32.942'E) in depths between 35 and 50 m. During commercial operations, *A. rostrata* individuals were removed from the catch and stored whole in the vessel's freezer for processing in the laboratory.

Sample collection on the *San Antone II* was supplemented by specimens obtained during the post-trawl survival (PTS) experiments conducted by Campbell *et al.* (2018).

Laboratory processing

All *A. rostrata* individuals were thawed, sexed, weighed (± 0.01 g) and measured (total length, TL, ± 0.1 cm). In accordance with Pierce and Bennett (2009), a segment of four or five vertebrae, located at the posterior of the abdominal cavity, was excised. Each segment was cleaned following Goldman *et al.* (2004) and air dried. The neural and haemal arches were removed, along with any remnant connective tissue. After drying, each segment was embedded in polyester resin and sectioned with a Buehler IsoMet Low Speed cutting saw (www.buehler.com/isoMet-low-speed-cutter.php), at a width of ~200 μ m, and mounted on a microscope slide. The vertebral sections were examined with a Leica M60 stereo microscope (www.leica-microsystems.com/products/stereo-microscopes-microscopes/p/leica-m80/) under reflected light on a matt black background, and photographed with a Leica IC90 E digital camera (www.leica-microsystems.com/products/microscope-cameras/p/leica-ic90-e/).

The maturity of each individual was assessed according to Kyne *et al.* (2016). Maturity in males depended on the calcification of the claspers, categorised as immature (possessing short, flexible, uncalcified claspers) or mature (rigid, calcified and elongated claspers). A mature female *A. rostrata* possessed one or more of the following: developed ovaries with yellow vitellogenic follicles of ≥ 5 mm diameter, fully developed oviducal glands and uteri, uterine eggs, and embryos *in situ*. Immature females were categorised by undifferentiated ovaries, undeveloped oviducal glands and thin uteri.

Ageing

Nominal age was estimated by two readers on the basis of the number of band pairs. A band pair was defined following Fig. 1c from Rolim *et al.* (2020) as one (narrow) translucent band and one wide (opaque) band, combined. Initially, the birth mark was defined as an angle change along the corpus calcareum (White *et al.* 2014), associated with the first distinct opaque band after the focus (called the 'birth mark', Campana 2014). However, preliminary investigation showed that the birth mark and the change of angle was absent or difficult to identify in a high proportion of individuals. As such, the first growth band (i.e. 1 year of age) was identified using a method described by Campana (2014). The mean distance between the waist and distal edge of the first growth band was calculated by measuring this distance for those 1-year-old animals (<~25 cm TL) where the birthmark was

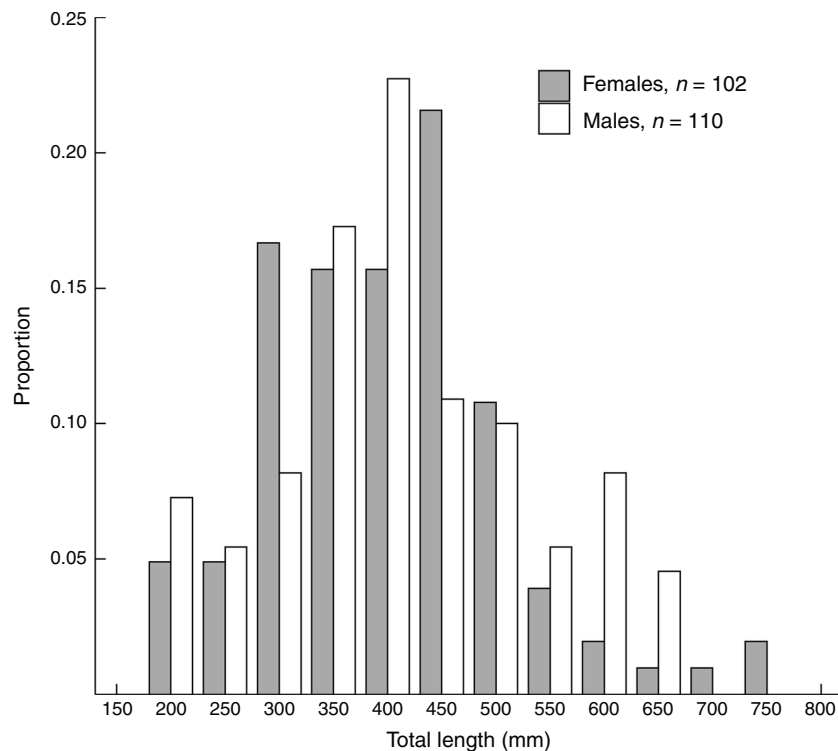


Fig. 1. Length–frequency (TL, cm) distribution for 212 *Aptychotrema rostrata* individuals caught in south-eastern Queensland, Australia, between April 2016 and November 2017, as a function of sex.

visible. This distance was measured with the Leica Application Suite software associated with the camera used to view centrum images. A line of this length was superimposed on the image of each sectioned centrum to determine the expected location of the first complete opaque band after the birth mark.

Counts were made without knowledge of the size or sex of the animal and the readability of each section was qualitatively assessed in accord with Officer *et al.* (1996). Where counts differed between readers, the count by the experienced reader was accepted. The following three measures of precision were calculated to assess consistency between readers: (1) percentage agreement (PA); (2) average percentage error (APE, Beamish and Fournier 1981); and (3) average coefficient of variation (ACV, Chang 1982). Further, Bowker's test of symmetry was used to assess bias among readers.

Marginal increment ratio (MIR)

To determine the periodicity of band formation, monthly MIR was calculated following Natanson *et al.* (1995), who defined MIR as $MIR = (CR - CR_n) / (CR_n - CR_{n-1})$, where CR is the centrum radius, CR_n is the radius of the final complete band pair and CR_{n-1} is the radius of the next to last complete band pair. Given this method, MIR was calculated only for animals aged ≥ 2 years. Following (Simpfendorfer *et al.* 2000), MIR was compared among months using the Kruskal–Wallis one-way analysis of variance on ranks.

Edge type was qualitatively assessed to provide further evidence of band formation periodicity (Cailliet *et al.* 2006) and was classified into three levels, namely, 'new', 'intermediate' and

'wide'. A 'new' edge was one where an opaque zone occurred at the distal edge of the centrum irrespective of the width of the opaque band. An edge of a centrum with any translucence visible beyond the last complete band pair was categorised as 'intermediate' and an edge was classified as 'wide' if the width of the translucent band beyond the last complete band pair was $\geq 2/3$ the width of the previous translucent band. A chi-square test was used to compare the observed frequency of each edge type, as a function of month, with the expected frequencies. In this case, the null hypothesis of the test was that the frequency of edge type was not dependent on month of capture.

Growth

Band pair counts (i.e. nominal age) were adjusted for growth beyond the last complete band pair on the basis of edge type (Pierce and Bennett 2009). Nominal age was increased by 0.33 year for intermediate edges and by 0.66 year for wide edges.

Initial analysis indicated that younger individuals were under-sampled. As such, back-calculation techniques were used to increase the sample size of smaller size classes. The linear-modified Dahl–Lea method (Francis 1990) was used to estimate the total length (L_a) of each individual at age a , as follows:

$$L_a = L_c \times \left(\frac{b + mCR_a}{b + mCR_c} \right)$$

where L_c is the length at capture; CR_a is the centrum radius at age a ; CR_c is the centrum radius at capture; and b and m are the coefficients of the linear regression between CR_c and L_c . This

method was preferred to the Dahl–Lea direct proportions method because the $CR_c - L_c$ relationship did not pass through the origin (Goldman 2005). Following Goldman (2005), the quadratic-modified Dahl–Lea method (Francis 1990) was used for comparison with the linear-modified Dahl–Lea method to determine the most appropriate approach for estimating L_a as a function of CR_a . Francis (1990) defined the quadratic-modified Dahl–Lea equation as

$$L_a = L_c \times \left(\frac{d + eCR_a + fCR_a^2}{d + eCR_c + fCR_c^2} \right)$$

where d , e and f are the quadratic regression estimates. The mean observed lengths and the mean back-calculated lengths, as a function of age, were compared using two-sample Student's t -tests where sample size permitted. In this case, the observed lengths were restricted to those animals where new or intermediate edges occurred at the distal edge of the centrum.

In accord with Smart *et al.* (2016), the following three growth functions were used to estimate mean length-at-age: von Bertalanffy growth function (VBGF), logistic function and Gompertz function (Table 1). In all instances, the biologically relevant length-at-birth (L_0) was estimated, rather than the age when length is zero (i.e. t_0), as recommended for elasmobranchs by Cailliet *et al.* (2006). Relevant parameters were estimated via non-linear least-squares regression: however, the under-sampling of larger individuals resulted in an under-estimate of L_∞ . As such, a Bayesian approach using Markov-chain Monte Carlo (MCMC) was used to estimate biologically appropriate growth parameters (Emmons *et al.* 2021).

Bayesian models were fit using the 'BayesGrowth' package (Smart 2020; accessed 18 February 2021), by using R statistical software (ver. 3.6.1, R Foundation for Statistical Computing, Vienna, Austria, see <https://www.R-project.org/>, accessed 18 February 2021), in accord with methods described by Smart and Grammer (2021) and Emmons *et al.* (2021). The 'BayesGrowth' package uses the 'Stan' computer program (Carpenter *et al.* 2017), via the 'Rstan' package (Stan Development Team 2020) to perform MCMC using no U-turn sampling (NUTS). 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 generated using

Table 1. Equations of the three candidate growth functions used to assess the growth of 212 *Aptychotrema rostrata* individuals caught in south-eastern Queensland, Australia, between April 2016 and November 2017

L_t , the length at Age t ; L_∞ , the asymptotic length; L_0 , the length at $t = 0$; and k , g_1 and g_2 , coefficients of the respective growth functions to be estimated

Model	Growth function
Von Bertalanffy	$L_t = L_0 + (L_\infty - L_0)(1 - e^{-kt})$
Gompertz function	$L_t = L_0 \times e^{\left(\ln \left(\frac{L_\infty}{L_0} \right) (1 - e^{-g_1 t}) \right)}$
Logistic function	$L_t = \frac{L_\infty \times L_0 (e^{(g_2 t)})}{L_\infty \times L_0 (e^{(g_2 t - 1)})}$

the 'Bayesplot' package (Gabry 2020; accessed 18 February 2021) in R.

The models were fit with a normal residual error structure (σ). Prior distributions for the L_0 and L_∞ estimates were informed by data published by Last *et al.* (2016). These authors reported the maximum size of *A. rostrata* as 1200 mm TL and with a length-at-birth (L_0) of 130–150 mm TL. Given this information, priors were set at $L_\infty \sim N(1200, 50)$ and $L_0 \sim N(140, 10)$. A non-informative prior was used for σ and a common non-informative prior was used for the growth coefficients of candidate models (k , g_1 and g_2 , 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. Leave-one-out-information-criterion weights (LOOICw), calculated within the 'BayesGrowth' package using the 'loo' R package (Vehtari *et al.* 2020), were used to determine the most appropriate candidate model. As with the Akaike weights in the frequentist approach, the candidate model with the highest LOOICw was considered the most appropriate.

Maturity

To overcome the under-sampling of larger, older animals, Beverton–Holt life-history invariants (BH–LHI) were used to estimate of age-at-maturity (t_{50}) and length-at-maturity (L_{50}). Life-history ratios described by Jensen (1996) and Frisk *et al.* (2001) were used to estimate t_{50} and L_{50} by using natural mortality (M) and the previously defined k and L_∞ ($L_{50}/L_\infty = 0.66$, $\ln(M) = 0.42 \times \ln(k) - 0.83$ and $M \times t_{50} = 1.65$).

Results

Overall, 214 *A. rostrata* individuals were collected to assess growth; 142 were collected by the crew of the *San Antone II* and 72 were collected as part of the PTS experiments conducted by Campbell *et al.* (2018). The animals caught during the PTS experiments had significantly smaller TL than those caught on the *San Antone II* ($t = -4.180$, d.f. = 166.7, $P < 0.001$). Two animals were excluded from the analysis, because age could not be determined from the respective vertebral centra. Of the 212 animals assessed for growth, 102 were female with a mean TL of 403 mm (s.e. = 11.00, range = 192–753) and 110 were male with a mean TL of 413 mm (s.e. = 11.16, range = 193–671). No significant difference in size was detected between sexes ($t = -0.670$, d.f. = 209.9, $P = 0.504$; Fig. 1).

Ageing

Generally, ageing between readers was consistent (PA = 82.67%, ACV = 4.21, APE = 2.97), with the age bias plot showing little variation from the 1:1 line of equivalence (Supplementary material Fig. S1, available at the journal's website). Further, Bowker's test of symmetry showed no between-reader bias ($\chi^2 = 13.93$, d.f. = 12, $P = 0.305$). The nominal age (i.e. the number of complete band pairs) range of males and females was 0–15 years and 0–17 years respectively. The oldest female was 750 mm TL and the two males assigned the nominal age of 15 years were 624 and 648 mm TL.

Marginal increment ratio

Marginal increment ratio was lowest during August and September (Fig. S2). New edges were also most likely to occur during these months. The Kruskal–Wallis test on ranks indicated that MIR varied significantly among months ($\chi^2 = 23.927$, d.f. = 4, $P < 0.001$). Mean MIR decreased from March through to August, before increasing in September. The highest mean MIR occurred in November, at the end of the austral spring.

Wide edges were also most likely to occur in November; however, the frequency of each edge type was not dependent on the month ($\chi^2 = 12.67$, d.f. = 8, $P = 0.124$).

Growth

The relationship between TL and CR was best described by the quadratic-modified Dahl–Lea method (TL = $-0.038CR^2 + 12.312CR - 17.01$, $R^2 = 0.964$). Back-calculated and observed lengths-at-age were not significantly different (Supplementary material Table S1). As such, the observed and back-calculated data were combined, resulting in a dataset containing 1112 measures of length-at-age.

The VBGF was found to best fit the length-at-age data (Table 2, LOOICw = 1). There was no support for either the Gompertz (LOOICw = 0) or the Logistic (LOOICw = 0) growth functions. With the sexes combined, the estimated VBGF parameters were $L_\infty = 923$ mm TL, $L_0 = 193$ mm TL and $k = 0.08$ year⁻¹ (Table 2, Fig. 2, Fig. S3). Estimates of L_∞ and L_0 were higher for females (1141 and 193 mm respectively) than males (813 and 187 mm respectively; Fig. 3). The growth coefficient for females ($k = 0.05$ year⁻¹) was half of that for males ($k = 0.10$ year⁻¹).

Maturity

Of the 212 *A. rostrata* individuals used to assess growth, only nine females and nine males were sexually mature. The oldest immature animals (female and male) were >10 years of age,

whereas the youngest mature animals were 6 years. Using the BH–LHI described by Jensen (1996) and Frisk *et al.* (2001), age-at-maturity for both sexes combined was 10.9 years, and 13.3 and 10.0 years for females and males respectively. Further, length-at-maturity was 609 mm TL for both sexes combined, and 753 and 555 mm TL for females and males respectively.

Discussion

The results from the current study represent the first estimates of growth and age-at-maturity published in the primary literature for *A. rostrata*. Slow growth and late maturity are common among elasmobranchs (Dulvy *et al.* 2008), making this group vulnerable to over-exploitation (Stevens *et al.* 2000). These characteristics, combined with intense fishing pressure, have resulted in an increasing concern for Rhinopristiformes, many of which are at an extremely high risk of extinction (Kyne *et al.* 2020). The landings and catch rates of Rhinopristiformes species have declined by up to 80% throughout most of their ranges (D'Alberto *et al.* 2019); however, a combination of reduced fishing pressure, prohibiting the retention of shark products and networks of marine protected areas have been shown to mitigate risk for this group (Kyne *et al.* 2020). This is especially the case for *A. rostrata*, which is considered abundant because of its diverse habitat use and the extent of refuges across its range (Kyne and Stevens 2015). Significant reduction in shrimp trawl effort since 2000 (Wang *et al.* 2020) is also likely to have had a positive effect on the species' abundance in Queensland.

These factors ensure the continued high levels of abundance in Queensland despite this species' low productivity. Delayed maturity and small maximum size imply a low maximum intrinsic population growth rate (r_{\max}) in Rhinopristiformes (D'Alberto *et al.* 2019). These authors evaluated population productivity in nine Rhinopristiformes and concluded that the trygonorhynchids exhibit low r_{\max} values compared with larger species such as the giant shovelnose ray (*Glaucoctegus typus*) and bottlenose wedgefish (*Rhynchobatus australiae*), both of

Table 2. Relative performance and mean parameter estimates for the three candidate growth functions used to assess the growth of 212 *Aptychotrema rostrata* individuals caught in south-eastern Queensland, Australia, between April 2016 and November 2017

After back-calculation, a total of 1112 length-at-age measures was assessed. The parameter estimates shown are the mean values of the posterior distributions of the respective parameters generated by the 'BayesGrowth' package via R statistical software. LOOIC, the leave-one-out-information-criterion; LOOICw, the LOOIC weights; L_∞ , the asymptotic length; L_0 , the length at $t = 0$; k and g , the growth coefficients of the von Bertalanffy, Gompertz and Logistic functions (see Table 1); and σ , the estimated residual error. Numbers in parentheses are the 95% credible intervals of the respective parameters from their posterior distributions

Function	LOOIC	LOOICw	L_∞ (mm)	L_0 (mm)	k/g (year ⁻¹)	σ
von Bertalanffy						
All	11 428.5	1	923 (843–953)	193 (185–200)	0.08 (0.06–0.09)	40.8 (39.2–42.6)
Female			1141 (1047–1175)	190 (183–197)	0.05 (0.05–0.06)	40.0 (37.7–42.6)
Male			813 (724–934)	187 (175–199)	0.10 (0.07–0.12)	40.6 (38.2–42.2)
Gompertz						
All	11 442.9	0	726 (691–766)	202 (195–208)	0.17 (0.16–0.19)	41.0 (39.3–42.7)
Female			985 (895–1083)	210 (203–217)	0.11 (0.10–0.13)	40.9 (38.5–43.5)
Male			652 (622–687)	192 (183–201)	0.22 (0.19–0.24)	40.2 (37.9–42.6)
Logistic						
All	11 452.3	0	666 (643–692)	210 (204–215)	0.27 (0.25–0.28)	41.4 (39.8–43.2)
Female			853 (786–931)	218 (211–226)	0.20 (0.18–0.22)	41.4 (39.0–44.1)
Male			631 (618–648)	207 (202–212)	0.29 (0.28–0.30)	40.6 (38.3–41.3)

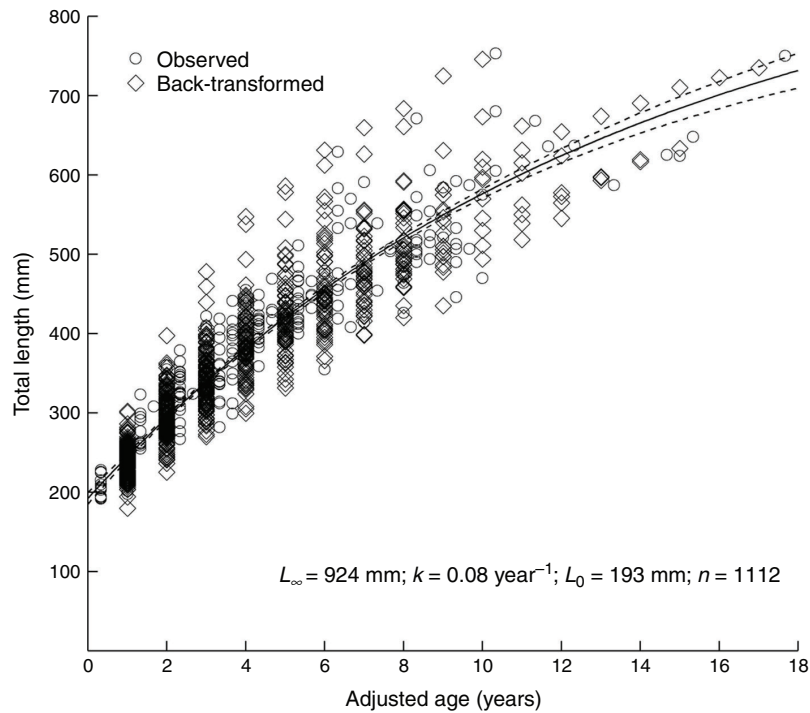


Fig. 2. Von Bertalanffy growth curve for 212 *Aptychotrema rostrata* individuals caught in south-eastern Queensland, Australia, between April 2016 and November 2017. Shown are both the observed and back-calculated lengths-at-age, which resulted in 1112 measures of length-at-age. Priors were set at $L_{\infty} \sim N(1200, 50)$ and $L_0 \sim N(140, 10)$. Dashed lines represent 95% credible intervals.

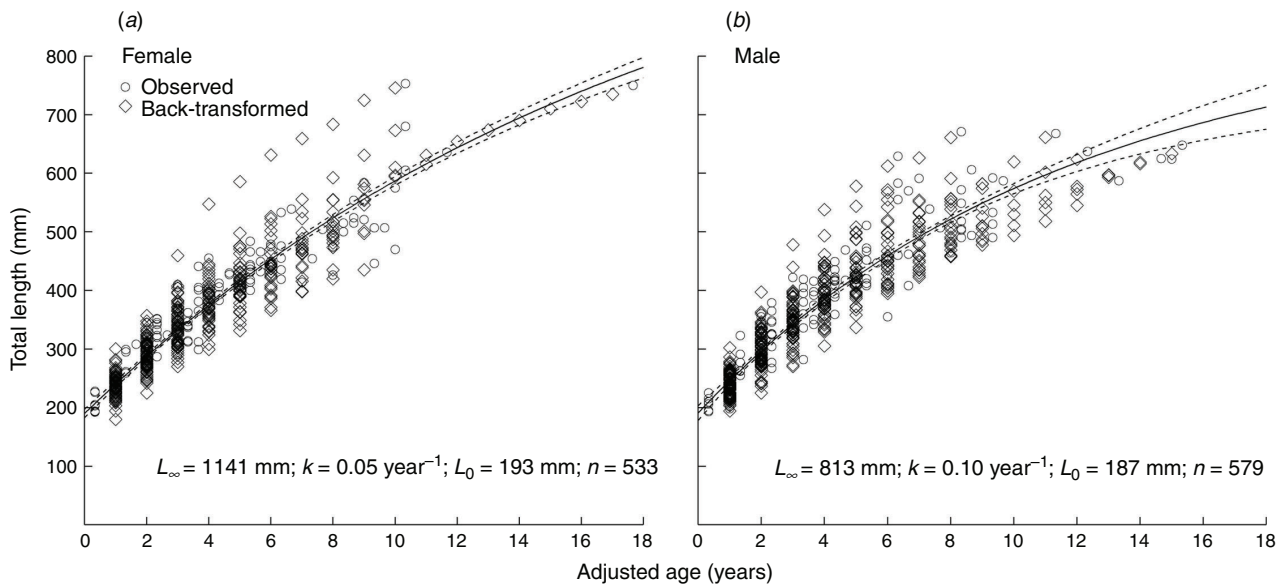


Fig. 3. Von Bertalanffy growth curve for (a) female and (b) male *Aptychotrema rostrata* individuals caught in south-eastern Queensland, Australia, between April 2016 and November 2017. Shown are both the observed and back-calculated lengths-at-age, which resulted in 533 and 579 measures of length-at-age for females and males respectively. Priors were set at $L_{\infty} \sim N(1200, 50)$ and $L_0 \sim N(140, 10)$ for both sexes. Dashed lines represent 95% credible intervals.

which co-occur with *A. rostrata*. This is due to the ability of these larger species to produce numerous and large offspring. Age-at-maturity was also found to be negatively correlated with

productivity and the t_{50} derived for *A. rostrata* using the BH-LHI is higher than the estimates for all nine species assessed by D’Alberto *et al.* (2019).

Maximum intrinsic population growth rate was calculated for only nine species of Rhinopristiformes because of the lack of reliable life-history information. Only three of the eight species that comprise Trygonorrhinidae have published growth information, namely, southern fiddler ray (*Trygonorrhina dumerilii*), shortnose guitarfish (*Zapteryx brevirostris*) and banded guitarfish (*Zapteryx exasperata*). The VBGF growth coefficient derived in the current study, $k = 0.08 \text{ year}^{-1}$, is lower than any of those published for Trygonorrhinidae. Values of k have been published for *T. dumerilii* and *Z. brevirostris* at 0.13 year^{-1} (Izzo and Gillanders 2008) and 0.12 year^{-1} (Carmo *et al.* 2018) respectively. Cervantes-Gutiérrez *et al.* (2018) reported a higher growth coefficient for male and female *Z. exasperata* of $k = 0.174 \text{ year}^{-1}$ and $k = 0.144 \text{ year}^{-1}$ respectively. Additionally, Caltabellotta *et al.* (2019) reported faster growth in the smaller *Z. brevirostris* of $k = 0.24 \text{ year}^{-1}$.

Only *T. dumerilii* has a higher published estimate of L_{∞} than that presented here. Izzo and Gillanders (2008) reported an L_{∞} for *T. dumerilii* of 1129 mm TL for females and males combined. The L_{∞} (1157 mm TL) for female *A. rostrata* is similar to that derived in the current study for female *A. rostrata* (1141 mm TL), despite *T. dumerilii* reaching a higher maximum size (1460 mm TL, Last *et al.* 2016). Cervantes-Gutiérrez *et al.* (2018) reported estimates of L_{∞} for female and male *Z. exasperata* of 1007 mm and 898 mm respectively. In contrast, Caltabellotta *et al.* (2019) reported an L_{∞} of 624 mm and 602 mm for female and male *Z. brevirostris*, whereas Carmo *et al.* (2018) derived smaller values of 56.0 cm and 50.4 cm respectively. In accord with other elasmobranchs, the published estimates of L_{∞} for the trygonorhinids were higher for females; Cortés (2000) found that the maximum size of males was, on average, ~10% smaller than that of females in 164 shark species.

Kyne *et al.* (2016) reported an L_{50} for male *A. rostrata* of 597.3 mm. This is comparable to the present study: however, their L_{50} for females (639.5 mm) is lower than the L_{50} reported here. This difference in L_{50} may be a result of using the BH-LHs calculated using the estimates of k and L_{∞} derived here. The under-sampling of large, mature females resulted in biased estimates of female L_{50} , necessitating the use of the BH-LHI. This under-sampling may have been due to the selectivity of the sampling gears used in the respective studies. Kyne *et al.* (2016) conducted sampling using shrimp (*Melicertus plebejus*) trawls in water depths to 100 m. In contrast, samples in the present study were predominantly (67%) collected on the *San Antone II*, which deploys Danish seine gear to target *S. robusta* in water of <50 m. The Danish seine used in this fishery is characterised by slow haul speeds and short haul times (Rowell and Davies 2012), which may allow larger *A. rostrata* to escape capture.

The difference in water depth is unlikely to be the cause of the under-sampling of large animals. Kyne and Bennett (2002b) collected *A. rostrata* individuals from Moreton Bay, adjacent to the grounds in the current study, and reported that 41 of 48 (~85%) females sampled were mature. These authors used rod-and-reel in water depths of 3–10 m and reported a female L_{50} similar to that in Kyne *et al.* (2016). The number of mature females was higher than from the current study; only 9 of the 102 females caught aboard the *San Antone II* were mature and no mature animals were collected during the PTS experiments conducted by Campbell *et al.* (2018).

Sexual bimaturism is a common life-history strategy among viviparous elasmobranchs (Colonello *et al.* 2020) because of less investment by females in growth to compensate for attaining a larger size to support pups (Cortés 2000). The higher L_{50} and t_{50} derived here for female *A. rostrata* are consistent with Kyne *et al.* (2016), who estimated a higher L_{50} for female *A. rostrata*. Similarly, Jones *et al.* (2010) reported a higher L_{50} for females for the congeneric *A. vincentiana* caught in southern Western Australia. Delayed female maturity has been reported for the confamilial banded guitarfish (*Zapteryx exasperata*) caught in Mexico (Cervantes-Gutiérrez *et al.* 2018).

The MIR analysis suggested that band pair formation occurs annually. Ideally, sampling should have occurred throughout the year to ensure a complete analysis of the periodicity of band pair formation; however, the seasonal nature of fisheries that catch *A. rostrata* as by-catch resulted in irregular access to samples during the study period. Similarly, Cervantes-Gutiérrez *et al.* (2018) reported that fishery closures hampered year-round sampling of *Z. exasperata* in Mexico and published incomplete measures of marginal increments; however, these authors assumed annual band pair formation when quantifying growth. Caltabellotta *et al.* (2019) suggested annual band formation for *Z. brevirostris* by using MIR and, like in the previous studies on the growth of trygonorhinids (Izzo and Gillanders 2008; Carmo *et al.* 2018), this assumption is also reasonable for *A. rostrata*. The minimum MIR occurred in August, indicating a period of slow somatic growth coinciding with minimum monthly mean sea-surface temperature (Meynecke and Lee 2011) and high reproductive activity (Kyne *et al.* 2016). The chi-square test conducted on the edge frequency data somewhat contradicted the results from the MIR analysis and, as such, further sampling should be undertaken throughout the year to confirm that band pair formation occurs annually.

The back-calculated lengths-at-age were not significantly different from the observed values. However, the mean back-calculated lengths were higher than the observed mean lengths for ages 0–6 years because of the inclusion of those vertebral centra where intermediate edges were observed. The low number of vertebral centra with new edges at each age necessitated the inclusion of the centra with intermediate edges for robust comparison between back-calculated and observed lengths-at-age.

The under-sampling of older animals resulted in biased growth parameter estimates. However, estimating the VBGF parameters in a Bayesian framework allowed for the use of informed priors to estimate L_{∞} , overcoming the lack of larger animals sampled. Similarly, back-calculation increases the number of measures of length-at-age for smaller size classes, resulting in improved growth parameter estimates for elasmobranchs where age data are sparse for smaller individuals (e.g. Smart *et al.* 2013; D'Alberto *et al.* 2017; Carmo *et al.* 2018). These two techniques allowed for the estimation of reasonable growth parameters for use in assessing the population status of *A. rostrata*.

Various methods correlate k and L_{∞} to natural mortality (M , e.g. Pauly 1980; Frisk *et al.* 2001; Then *et al.* 2015). As such, biased estimates of growth result in biased estimates of M (D'Alberto *et al.* 2019), leading to inaccurate assessments of stock status (Pardo *et al.* 2013). Estimating growth parameters in a Bayesian framework overcomes this bias (Smart and Grammer

2021). Campbell *et al.* (2017) quantified the ecological risk posed to *A. rostrata* by the ECOTF, by using the sustainability assessment for fishing effects (SAFE) quantitative ERA developed by (Zhou *et al.* 2009). In this instance, risk was quantified via comparison between the level of fishing mortality (F) and the maximum sustainable fishing mortality (F_{msm}), where $F_{msm} = 0.41M$ (Zhou *et al.* 2012). Hence, the growth parameter estimates derived here allow for the calculation of unbiased estimates M and F_{msm} , which enable the accurate assessment of the population status.

Campbell *et al.* (2017) assessed the risk posed to 47 elasmobranchs, only 18 of which had published growth estimates. Of these 18, growth was quantified for seven species on the basis of samples collected within the study area. This reinforces the need for basic life-history data to inform fishery impacts in batoids (Kyne 2016) and elasmobranchs in general. In the absence of life-history information, previous studies (Zhou *et al.* 2013; Zhou *et al.* 2015) have used the 'Life History Tool' on the Fishbase website (www.fishbase.se) to determine values for M . There is a need, therefore, to increase knowledge of life-history information to ensure the accurate assessment of fishery impacts on elasmobranchs with sparse catch data.

In conclusion, the current study has contributed to the scientific knowledge of *A. rostrata*, and Rhinopristiformes more broadly. Consistent with other elasmobranchs, *A. rostrata* exhibits slow growth, late maturity and a long lifespan. Despite this, the species is abundant in Queensland owing to its diverse habitat use and the extent of refuges throughout its range. This result contrasts with other Rhinopristiformes, many of which are at a high risk of extinction. The life-history characteristics derived from this research can be used in future studies to determine population status and inform management decisions.

Conflicts of interest

Colin Simpfendorfer is an Associate Editor for *Marine and Freshwater Research*. Despite this relationship, he did not at any stage have Associate Editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this journal. *Marine and Freshwater Research* encourages its editors to publish in the journal and they are kept totally separate from the decision-making process for their manuscripts. The authors declare that they have no further conflicts of interest.

Declaration of funding

The Fisheries Research and Development Corporation (FRDC Project Number 2015/014) and the Queensland Department of Agriculture and Fisheries provided the funding for this work. Our thanks go to these institutions for their continued support for fisheries research.

Acknowledgements

The authors extend sincerest thanks to Matt Wills, Master of the *C-Rainger*, for his patience and enthusiasm for this research. We are grateful to Michael Pinzone, Master of the *San Antone II*, and his crew for collecting samples. The authors thank Sean Maberly, Master of the FRV *Tom Marshall*, for his contribution during the PTS experiments. Jonathan Smart provided advice on the analysis of the length-at-age data in a Bayesian framework and his

assistance is gratefully acknowledged. Sophie Eammons provided an earlier version of her tiger shark growth study, which helped in the analysis of the length-at age data here. We sincerely thank Zalee Bates and Pat Abbott for their continued diligence in sourcing and supplying relevant literature. We thank two reviewers whose comments and suggestions improved this paper. This work was authorised under the Queensland Department of Agriculture and Fisheries General Fisheries Permit number 186281, The Queensland National Parks and Wildlife Marine Parks permit QS2015/MAN322, and the Queensland Animal Ethics Approval Number CA2015/06/867.

References

- Astles, K. L., Gibbs, P. J., Steffe, A. S., and Green, M. (2009). A qualitative risk-based assessment of impacts on marine habitats and harvested species for a data deficient wild capture fishery. *Biological Conservation* **142**(11), 2759–2773. doi:10.1016/J.BIOCON.2009.07.006
- Beamish, R., and Fournier, D. (1981). A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* **38**(8), 982–983. doi:10.1139/F81-132
- Cailliet, G. M., Smith, W. D., Mollet, H. F., and Goldman, K. J. (2006). Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. *Environmental Biology of Fishes* **77**(3–4), 211–228. doi:10.1007/S10641-006-9105-5
- Caltabellotta, F. P., Siders, Z. A., Murie, D. J., Motta, F. S., Cailliet, G. M., and Gadig, O. B. F. (2019). Age and growth of three endemic threatened guitarfishes *Pseudobatos horkelii*, *P. percellens* and *Zapteryx brevirostris* in the western South Atlantic Ocean. *Journal of Fish Biology* **95**(5), 1236–1248. doi:10.1111/JFB.14123
- Campana, S. E. (2014). 'Age determination of elasmobranchs, with special reference to Mediterranean species: a technical manual. Studies and Reviews.' (General Fisheries Commission for the Mediterranean: Rome, Italy.)
- Campbell, M., Courtney, T., Wang, N., McLennan, M., and Zhou, S. (2017). Estimating the impacts of management changes on bycatch reduction and sustainability of high-risk bycatch species in the Queensland East Coast Otter Trawl Fishery: final report for FRDC Project no. 2015/014. Queensland Department of Agriculture and Fisheries, Brisbane, Qld, Australia. Available at <http://frdc.com.au/Archived-Reports/FRDC%20Projects/2015-014-DLD.pdf>
- Campbell, M. J., McLennan, M. F., Courtney, A. J., and Simpfendorfer, C. A. (2018). Post-release survival of two elasmobranchs, the eastern shovelnose ray (*Aptychotrema rostrata*) and the common stingaree (*Trygonoptera testacea*), discarded from a prawn trawl fishery in southern Queensland, Australia. *Marine and Freshwater Research* **69**(4), 551–561. doi:10.1071/MF17161
- Campbell, M. J., Tonks, M. L., Miller, M., Brewer, D. T., Courtney, A. J., and Simpfendorfer, C. A. (2020). Factors affecting elasmobranch escape from turtle excluder devices (TEDs) in a tropical penaeid-trawl fishery. *Fisheries Research* **224**, 105456. doi:10.1016/J.FISHRES.2019.105456
- Carmo, W. P., Fávaro, L. F., and Coelho, R. (2018). Age and growth of *Zapteryx brevirostris* (Elasmobranchii: Rhinobatidae) in southern Brazil. *Neotropical Ichthyology* **16**(1), e170005. doi:10.1590/1982-0224-20170005
- Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., and Riddell, A. (2017). Stan: A Probabilistic Programming Language. 2017-01-11. Available at <https://www.jstatsoft.org/v076/i01>
- Cervantes-Gutiérrez, F., Tovar-Ávila, J., and Galván-Magaña, F. (2018). Age and growth of the banded guitarfish *Zapteryx exasperata* (Chondrichthyes: Trygonorrhinidae). *Marine and Freshwater Research* **69**(1), 66–73. doi:10.1071/MF16403
- Chang, W. Y. B. (1982). A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences* **39**(8), 1208–1210. doi:10.1139/F82-158

- Colonello, J. H., Cortés, F., and Belleggia, M. (2020). Male-biased sexual size dimorphism in sharks: the narrowmouth catshark *Schroederichthys bivius* as case study. *Hydrobiologia* **847**(8), 1873–1886. doi:10.1007/S10750-020-04219-9
- Cortés, E. (2000). Life history patterns and correlations in sharks. *Reviews in Fisheries Science* **8**(4), 299–344. doi:10.1080/10408340308951115
- Courtney, A. J., Tonks, M. L., Campbell, M. J., Roy, D. P., Gaddes, S. W., Kyne, P. M., and O'Neill, M. F. (2006). Quantifying the effects of bycatch reduction devices in Queensland's (Australia) shallow water eastern king prawn (*Penaeus plebejus*) trawl fishery. *Fisheries Research* **80**(2–3), 136–147. doi:10.1016/J.FISHRES.2006.05.005
- Courtney, A. J., Campbell, M. J., Roy, D. P., Tonks, M. L., Chilcott, K. E., and Kyne, P. J. (2008). Round scallops and square-meshes: a comparison of four codend types on the catch rates of target species and bycatch in the Queensland (Australia) saucer scallop (*Amusium balloti*) trawl fishery. *Marine and Freshwater Research* **59**, 849–864. doi:10.1071/MF08073
- D'Alberto, B. M., Chin, A., Smart, J. J., Baje, L., White, W. T., and Simpfendorfer, C. A. (2017). Age, growth and maturity of oceanic whitetip shark (*Carcharhinus longimanus*) from Papua New Guinea. *Marine and Freshwater Research* **68**(6), 1118–1129. doi:10.1071/MF16165
- D'Alberto, B. M., Carlson, J. K., Pardo, S. A., and Simpfendorfer, C. A. (2019). Population productivity of shovelnose rays: inferring the potential for recovery. *PLoS One* **14**(11), e0225183. doi:10.1371/JOURNAL.PONE.0225183
- Dulvy, N. K., Baum, J. K., Clarke, S., Compagno, L. J. V., Cortés, E., Domingo, A., Fordham, S., Fowler, S., Francis, M. P., Gibson, C., Martínez, J., Musick, J. A., Soldo, A., Stevens, J. D., and Valenti, S. (2008). You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation* **18**(5), 459–482. doi:10.1002/AQC.975
- Dulvy, N. K., Simpfendorfer, C. A., Davidson, L. N. K., Fordham, S. V., Bräutigam, A., Sant, G., and Welch, D. J. (2017). Challenges and priorities in shark and ray conservation. *Current Biology* **27**(11), R565–R572. doi:10.1016/J.CUB.2017.04.038
- Emmons, S. M., D'Alberto, B. M., Smart, J. J., and Simpfendorfer, C. A. (2021). Age and growth of tiger shark (*Galeocerdo cuvier*) from Western Australia. *Marine and Freshwater Research*. doi:10.1071/MF20291
- Francis, R. I. C. C. (1990). Back-calculation of fish length: a critical review. *Journal of Fish Biology* **36**(6), 883–902. doi:10.1111/J.1095-8649.1990.TB05636.X
- Frisk, M. G., Miller, T. J., and Fogarty, M. J. (2001). Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. *Canadian Journal of Fisheries and Aquatic Sciences* **58**(5), 969–981. doi:10.1139/F01-051
- Gabry, J. T. M. (2020). bayesplot: Plotting for Bayesian Models. R package version 1.7.2. Available at <https://mc-stan.org/bayesplot>.
- Gilman, E., Perez Roda, A., Huntington, T., Kennelly, S. J., Suuronen, P., Chaloupka, M., and Medley, P. A. H. (2020). Benchmarking global fisheries discards. *Scientific Reports* **10**(1), 14017. doi:10.1038/S41598-020-71021-X
- Goldman, K. J. (2005). Age and growth of elasmobranch fishes. *FAO Fisheries Technical Paper* **474**, 76–102.
- Goldman, K. J., Cailliet, G. M., Andrews, A. H., and Natanson, L. J. (2004). Age determination and validation in chondrichthyan fishes. In 'Biology of Sharks and their Relatives'. 2nd edn. (Eds J. C. Carrier, J. A. Musick, and M. R. Heithaus.) pp. 423–450. (CRC Press: Boca Raton, FL, USA.)
- Gutteridge, A. N., and Bennett, M. B. (2014). Functional implications of ontogenetically and sexually dimorphic dentition in the eastern shovelnose ray, *Aptychotrema rostrata*. *The Journal of Experimental Biology* **217**(2), 192–200. doi:10.1242/JEB.089326
- Hart, N. S., Lisney, T. J., Marshall, N. J., and Collin, S. P. (2004). Multiple cone visual pigments and the potential for trichromatic colour vision in two species of elasmobranch. *The Journal of Experimental Biology* **207**(26), 4587–4594. doi:10.1242/JEB.01314
- Izzo, C., and Gillanders, B. M. (2008). Initial assessment of age, growth and reproductive parameters of the southern fiddler ray *Trygonorrhina fasciata* (Müller & Henle, 1841) from South Australia. *Pan-American Journal of Aquatic Sciences* **3**(3), 321–327.
- Jacobsen, I., Zeller, B., Dunning, M., Garland, A., Courtney, T., and Jebreen, E. J. (2018). An ecological risk Assessment of the southern Queensland east coast otter trawl fishery and river and inshore beam trawl fishery. Department of Agriculture and Fisheries, Brisbane, Qld. Available at https://www.daf.qld.gov.au/__data/assets/pdf_file/0004/1402672/Sth-QLD-Trawl-ERA-Final.pdf
- Jensen, A. L. (1996). Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Canadian Journal of Fisheries and Aquatic Sciences* **53**(4), 820–822. doi:10.1139/F95-233
- Jones, A. A., Hall, N. G., and Potter, I. C. (2010). Species compositions of elasmobranchs caught by three different commercial fishing methods off southwestern Australia, and biological data for four abundant bycatch species. *Fishery Bulletin* **108**(4), 365–381.
- Kennelly, S. J. (2020). Bycatch Beknown: Methodology for jurisdictional reporting of fisheries discards—Using Australia as a case study. *Fish and Fisheries* **21**(5), 1046–1066. doi:10.1111/FAF.12494
- Kyne, P. M. (2016). Ray conservation. In 'Rays of the World'. Vol. 1. (Eds P. R. Last, W. T. White, M. R. de Carvalho, B. Séret, M. F. W. Stehmann, and G. J. P. Naylor.) pp. 21–24. (CSIRO Publishing: Melbourne, Vic., Australia.)
- Kyne, P. M., and Bennett, M. B. (2002a). Diet of the eastern shovelnose ray, *Aptychotrema rostrata* (Shaw & Nodder, 1794), from Moreton Bay, Queensland, Australia. *Marine and Freshwater Research* **53**(3), 679–686. doi:10.1071/MF01040
- Kyne, P. M., and Bennett, M. B. (2002b). Reproductive biology of the eastern shovelnose ray, *Aptychotrema rostrata* (Shaw Nodder, 1794), from Moreton Bay, Queensland, Australia. *Marine and Freshwater Research* **53**(2), 583–589. doi:10.1071/MF01063
- Kyne, P. M., and Stevens, J. D. (2015). *Aptychotrema rostrata*. The IUCN Red List of Threatened Species 2015: e.T161596A68609037. Available at <https://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T161596A68609037.en>
- Kyne, P., Courtney, A., Campbell, M., Chilcott, K., Gaddes, S., Turnbull, C., Van Der Geest, C., and Bennett, M. (2002). An overview of the elasmobranch bycatch of the Queensland East coast trawl fishery (Australia). *Northwest Atlantic Fisheries Organisation NAFO SCR Document* **2**, 1–11.
- Kyne, P. M., Courtney, A. J., Jacobsen, I. P., and Bennett, M. B. (2016). Reproductive parameters of rhinobatid and urolophid batoids taken as by-catch in the Queensland (Australia) east coast otter-trawl fishery. *Journal of Fish Biology* **89**(2), 1208–1226. doi:10.1111/JFB.13020
- Kyne, P. M., Jabado, R. W., Rigby, C. L., Gore, M. A., Pollock, C. M., Herman, K. B., Cheok, J., Ebert, D. A., Simpfendorfer, C. A., and Dulvy, N. K. (2020). The thin edge of the wedge: extremely high extinction risk in wedgefishes and giant guitarfishes. *Aquatic Conservation* **30**, 1337–1361. doi:10.1002/AQC.3331
- Last, P. R., and Stevens, J. D. (2009). 'Sharks and Rays of Australia.' (CSIRO Publishing: Melbourne, Vic., Australia)
- Last, P., Naylor, G., Séret, B., White, W., de Carvalho, M., and Stehmann, M. (2016). 'Rays of the World.' (CSIRO Publishing: Melbourne, Vic., Australia)
- McGilvray, J. G., Mounsey, R. P., and MacCartie, J. (1999). The AustED II, an improved trawl efficiency device 1. Design theories. *Fisheries Research* **40**(1), 17–27. doi:10.1016/S0165-7836(98)00221-5
- Meynecke, J.-O., and Lee, S. Y. (2011). Climate-coastal fisheries relationships and their spatial variation in Queensland, Australia. *Fisheries Research* **110**(2), 365–376. doi:10.1016/J.FISHRES.2011.05.004
- Natanson, L. J., Casey, J. G., and Kohler, N. E. (1995). Age and growth estimates for the dusky shark, *Carcharhinus obscurus*, in the western North Atlantic Ocean. *Fishery Bulletin* **93**(1), 116–126.

- Officer, R. A., Gason, A. S., Walker, T. I., and Clement, J. G. (1996). Sources of variation in counts of growth increments in vertebrae from gummy shark (*Mustelus antarcticus*, and school shark, *Galeorhinus galeus*): implications for age determination. *Canadian Journal of Fisheries and Aquatic Sciences* **53**(8), 1765–1777. doi:10.1139/F96-103
- Pardo, S. A., Cooper, A. B., and Dulvy, N. K. (2013). Avoiding fishy growth curves. *Methods in Ecology and Evolution* **4**(4), 353–360. doi:10.1111/2041-210X.12020
- Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES Journal of Marine Science* **39**(2), 175–192. doi:10.1093/ICESJMS/39.2.175
- Pears, R. J., Morison, A. K., Jebreen, E. J., Dunning, M. C., Pitcher, C. R., Courtney, A. J., Houlden, B., and Jacobsen, I. P. (2012). Ecological risk assessment of the East Coast Otter Trawl Fishery in the Great Barrier Reef Marine Park: technical report. Great Barrier Reef Marine Park Authority, Townsville, Qld, Australia. Available at http://elibrary.gbrmpa.gov.au/jspui/bitstream/11017/1148/1/ECOTF_ERA_Technical_web.pdf
- Pierce, S. J., and Bennett, M. B. (2009). Validated annual band-pair periodicity and growth parameters of blue-spotted maskray *Neotrygon kuhlii* from south-east Queensland, Australia. *Journal of Fish Biology* **75**(10), 2490–2508. doi:10.1111/J.1095-8649.2009.02435.X
- Robins, J. B., and McGilvray, J. G. (1999). The AusTED II, an improved trawl efficiency device 2. Commercial performance. *Fisheries Research* **40**, 29–41. doi:10.1016/S0165-7836(98)00222-7
- Robins-Troeger, J. B. (1994). Evaluation of the Morrison soft turtle excluder device: prawn and bycatch variation in Moreton Bay, Queensland. *Fisheries Research* **19**(3-4), 205–217. doi:10.1016/0165-7836(94)90039-6
- Rolim, F. A., Siders, Z. A., Caltabellotta, F. P., Rotundo, M. M., and Vaske-Júnior, T. (2020). Growth and derived life-history characteristics of the Brazilian electric ray *Narcine brasiliensis*. *Journal of Fish Biology* **97**(2), 396–408. doi:10.1111/JFB.14378
- Rowell, N., and Davies, J. (2012). At-sea observation of the stout whiting fishery 2009–10. Technical report. Department of Agriculture, Fisheries and Forestry, Brisbane, Qld, Australia. Available at <http://era.daf.qld.gov.au/id/eprint/6552/1/FOP%20Stout%20Whiting%20Report%202012%20final.pdf>
- Simpfendorfer, C. A., and Dulvy, N. K. (2017). Bright spots of sustainable shark fishing. *Current Biology* **27**(3), R97–R98. doi:10.1016/J.CUB.2016.12.017
- Simpfendorfer, C. A., Chidlow, J., McAuley, R., and Unsworth, P. (2000). Age and growth of the whiskery shark, *Furgaleus macki*, from south-western Australia. *Environmental Biology of Fishes* **58**(3), 335–343. doi:10.1023/A:1007624828001
- Smart, J. J. (2020). BayesGrowth: Estimate fish growth using MCMC analysis. R package version 0.3.0. Available at <https://github.com/jonathansmart/BayesGrowth>.
- Smart, J. J., and Grammer, G. L. (2021). Modernising fish and shark growth curves with Bayesian length-at-age models. *PLoS One* **16**(2), e0246734. doi:10.1371/JOURNAL.PONE.0246734
- Smart, J. J., Harry, A. V., Tobin, A. J., and Simpfendorfer, C. A. (2013). Overcoming the constraints of low sample sizes to produce age and growth data for rare or threatened sharks. *Aquatic Conservation* **23**(1), 124–134. doi:10.1002/AQC.2274
- Smart, J. J., Chin, A., Tobin, A. J., and Simpfendorfer, C. A. (2016). Multimodel approaches in shark and ray growth studies: strengths, weaknesses and the future. *Fish and Fisheries* **17**, 955–971. doi:10.1111/FAF.12154
- Stan Development Team (2020). RStan: the R interface to Stan. R package version 2.21.2. <http://mc-stan.org/>
- Stevens, J. D., Bonfil, R., Dulvy, N. K., and Walker, P. A. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* **57**(3), 476–494. doi:10.1006/JMSC.2000.0724
- Then, A. Y., Hoenig, J. M., Hall, N. G., and Hewitt, D. A. (2015). Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. *ICES Journal of Marine Science* **72**(1), 82–92. doi:10.1093/ICESJMS/FSU136
- Vehtari, A., Gabry, J., Magnusson, M., Yao, Y., Bürkner, P.-C., Paananen, T., and Gelman, A. (2020) loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models. R package version 2.4.1. <https://mc-stan.org/loo/>
- Wang, N., Courtney, A. J., Campbell, M. J., and Yang, W.-H. (2020). Quantifying long-term discards from Queensland's (Australia) east coast otter trawl fishery. *ICES Journal of Marine Science* **77**(2), 680–691. doi:10.1093/ICESJMS/FSZ205
- White, J., Simpfendorfer, C. A., Tobin, A. J., and Heupel, M. R. (2014). Age and growth parameters of shark-like batoids. *Journal of Fish Biology* **84**(5), 1340–1353. doi:10.1111/JFB.12359
- Wueringer, B. E., Tibbetts, I. R., and Whitehead, D. L. (2009). Ultrastructure of the ampullae of Lorenzini of *Aptychotrema rostrata* (Rhinobatidae). *Zoomorphology* **128**(1), 45–52. doi:10.1007/S00435-008-0073-5
- Zhou, S., Griffiths, S. P., and Miller, M. (2009). Sustainability assessment for fishing effects (SAFE) on highly diverse and data-limited fish bycatch in a tropical prawn trawl fishery. *Marine and Freshwater Research* **60**(6), 563–570. doi:10.1071/MF08207
- Zhou, S., Yin, S., Thorson, J. T., Smith, A. D. M., and Fuller, M. (2012). Linking fishing mortality reference points to life history traits: an empirical study. *Canadian Journal of Fisheries and Aquatic Sciences* **69**(8), 1292–1301. doi:10.1139/F2012-060
- Zhou, S., Daley, J., Fuller, M., Bulman, C., Hobday, A., Courtney, T., Ryan, P., and Ferrel, D. (2013). ERA extension to assess cumulative effects of fishing on species. Final report on FRDC Project 2011/029, Canberra, ACT, Australia. Available at http://frdc.com.au/research/Final_Reports/2011-029-DLD.pdf
- Zhou, S., Buckworth, R. C., Miller, M., and Jarrett, A. (2015). A SAFE analysis of bycatch in the Joseph Bonaparte Gulf fishery for red-legged banana prawns. CSIRO Oceans and Atmosphere Flagship, Brisbane, Qld, Australia. Available at http://www.afma.gov.au/wp-content/uploads/2014/02/JBG-SAFE-Report-2015_05_21-final.pdf
- Zhou, S., Hobday, A. J., Dichmont, C. M., and Smith, A. D. M. (2016). Ecological risk assessments for the effects of fishing: a comparison and validation of PSA and SAFE. *Fisheries Research* **183**, 518–529. doi:10.1016/J.FISHRES.2016.07.015

Handling Editor: Bradley Wetherbee