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ORIGINAL PAPER

Age, growth and maturity of Southern Ocean skates (*Bathyraja* spp.) from the Kerguelen Plateau

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Abstract

Three species of Southern Ocean skates, *Bathyraja eatonii, Bathyraja irrasa* and *Bathyraja murrayi,* are commonly caught as incidental by-catch in fisheries around Heard Island and McDonald Islands of the Kerguelen Plateau. We used length-at-age data to present the species' life history information (age, growth and maturity for the first-time). Length- and age-at-maturity analyses revealed that *B. irrasa* matured at > 6 years old and > 1000 mm total length (TL), which was older and larger than *B. murrayi* (> 5 years old and > 400 mm TL) but similar to *B. eatonii* (> 5 years old and > 900 mm). We fitted growth models using a multi-model Bayesian framework. Our findings support the assumption that *B. irrasa* is slow growing and late maturing compared to *B. eatonii* and *B. murrayi*, consequently putting it at greater risk to fishery-induced increases in mortality compared to other species (e.g., *B. murrayi*). This is the first-time age and growth has been estimated for these species, however sample sizes for *B. murrayi* and *B. eatonii* were small and hence growth models should be interpreted with caution. Our results represent vital information for population projection models and can therefore assist in the development and/or revision of current by-catch limits to inform ongoing management strategies and conservation efforts.

Keywords Antarctica · By-catch · Elasmobranch · Life history · *Rajidae* · Vertebral ageing

Introduction

Overfishing threatens over one-third of shark, skate and ray (class: Chondrichthyes, subclass Elasmobranchii) species with extinction and has profoundly altered their population dynamics (Dulvy et al. 2014, 2021). Global declines in elasmobranch populations have been attributed to targeted fishing and incidental capture as by-catch (Barausse et al. 2014), raising concerns about their conservation status (Baje et al. 2018). Several elasmobranch species are particularly vulnerable to overfishing due to a combination of biological characteristics including slow growth, late maturity, and low fecundity (Baje et al. 2018; Caltabellotta et al. 2019). In many cases, such as for skates (superorder: Batoidae, order: Rajiformes), a lack of available life history information presents a problem for determining the vulnerability of a species to overfishing. Without this information, fishing may remain unsustainable and increases the risk of a population decline for a given species.

Commercial longline and trawl fishing occurs on the Kerguelen Plateau in the Southern Ocean. In the Australian Exclusive Economic Zone (EEZ) surrounding Heard Island

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and McDonald Islands (HIMI), Patagonian toothfish, *Dissostichus eleginoides*, is targeted in both demersal longline and trawl fisheries and mackerel icefish, *Champsocephalus gunnari*, is targeted by trawl only (Nowara et al. 2017). Since the Australian fishery first started in 1997, there has been 100% scientific observer coverage on all fishing trips. The fisheries are managed by the Australian Fisheries Management Authority (AFMA), in accordance with decisions by the Commission for the Conservation of Antarctic Living Resources (CCAMLR; Nowara et al. 2017). Stock assessment and population models provide the basis for determining annual target catch quotas and by-catch limits (Nowara et al. 2017). Other marine animals are often caught as incidental by-catch in the HIMI fisheries, including macrourids, other icefish species and skates (Nowara et al. 2017). Life history traits can vary greatly between skate species (Barnett et al. 2013). As such, species-specific life history information is central to the development of evidence-based management strategies. This includes species-specific by-catch mitigation approaches and catch limits, which can reduce the risk of overexploitation of skate species like that witnessed with the common skate (*Dipturus batis*) in the Irish Sea (Brander 1981; Dulvy et al. 2000).

Three species of Southern Ocean skates are commonly caught in HIMI fisheries: Kerguelen sandpaper skate (*Bathyraja irrasa*), Eaton's skate (*Bathyraja eatonii*) and Murray's skate (*Bathyraja murrayi*; Nowara et al. 2017). Amongst them, *B. eatonii* is the most frequently caught species in the icefish trawl fishery (Nowara et al. 2017). This species grows to over 1200 mm total length (TL) and may be found in depths up to 1100 m (Nowara et al. 2017). *Bathyraja irrasa* reaches a maximum length of ~ 120 mm TL and is found at 300–1700 m depth, whereas the smaller *B. murrayi* reaches a maximum length of ~ 70 mm TL and is found in shallower depths of 30–650 m (Nowara et al. 2017). The International Union for Conservation of Nature (IUCN) has listed *B. eatonii* and *B. murrayi* as 'Least Concern' on the IUCN Red List of Threatened Species, while *B. irrasa* is listed as 'Near Threatened' (Dulvy et al. 2020). Two of the species appear to have a limited distribution (Smith et al. 2008; Nowara et al. 2017). *Bathyraja irrasa* and *B. murrayi* are only found on the Kerguelen Plateau, while *B. eatonii* occurs on the Kerguelen Plateau, in Antarctic shelf waters in the South Indian sector of the Southern Ocean, the South Atlantic Ocean, and the Ross Sea (Smith et al. 2008). The skates at HIMI have limited movement based on mark-recapture tagging experiments between 2001 and 2013, which revealed that they were, on average, recaptured up to 7.5 km from their initial release point (Nowara et al. 2013). This indicates limited movement for all three species (Nowara et al. 2017).

Species-specific biological parameters, including age-based characteristics, along with accompanying growth rates, are key for reliable population assessments and the development of sustainable fisheries management strategies (Caltabellotta et al. 2019; James 2019). Researchers most commonly use a frequentist approach to estimate length-at-age growth models (Smart and Grammer 2021). However, Bayesian inference approaches may yield increased benefits to fisheries studies by having the ability of incorporating a priori knowledge about data distributions along with the data to be modelled (Doll and Jacquemin 2019). Age estimates are typically determined by examining hard structures such as otoliths in teleosts, or vertebral centra in elasmobranchs (James 2019). Growth zones are examined for characteristic band pairs consisting of alternating opaque and translucent bands, each pair assuming to correspond to a year of age (Cailliet et al. 2006). A preliminary population assessment of *Bathyraja* spp. at HIMI used a Generalised Yield Model to estimate a sustainable catch limit of 50–210 t (Constable et al. 1998), and subsequently an annual catch limit of 120 t for the HIMI fishery was set by CCAMLR. However, this assessment relied on growth estimates for *Raja clavata* from the North Sea, and estimates of maturity of the three *Bathyraja* spp. were pooled together (Brander and Palmer 1985; Constable et al. 1998). Age-related information for Southern Ocean skates is largely lacking due, in part, to a lack of biological specimens available for scientific research (Smith et al. 2008). Therefore, the aim of this study was to generate new life history information and present the first species-specific age, growth, and maturity estimates for the three *Bathyraja* spp. from HIMI.

Methods

Sample collection

Fisheries observers on board commercial vessels operating within HIMI collected vertebrae samples from 249 *B. irrasa*, 22 *B. eatonii* and 21 *B. murrayi* between November 2013 and April 2018 (Fig. 1, S1 in Online Resource 1). Detailed sampling methodology followed the protocols described by Nowara et al. (2017). Biological measurements collected from each sample included the date of capture, total length (mm), sex, and maturity stage. Maturity was determined by examination of gonads and then categorisation according to the developmental stage of ovaries and uteri in females, and claspers in males (Table 1).

Age estimation

We collected, cleaned, and stored the vertebrae samples following standard protocols described by Cailliet and Goldman (2004). Vertebral sections were viewed using a charge-coupled device (CCD) digital camera mounted onto a Leica M80 dissecting microscope under transmitted light,

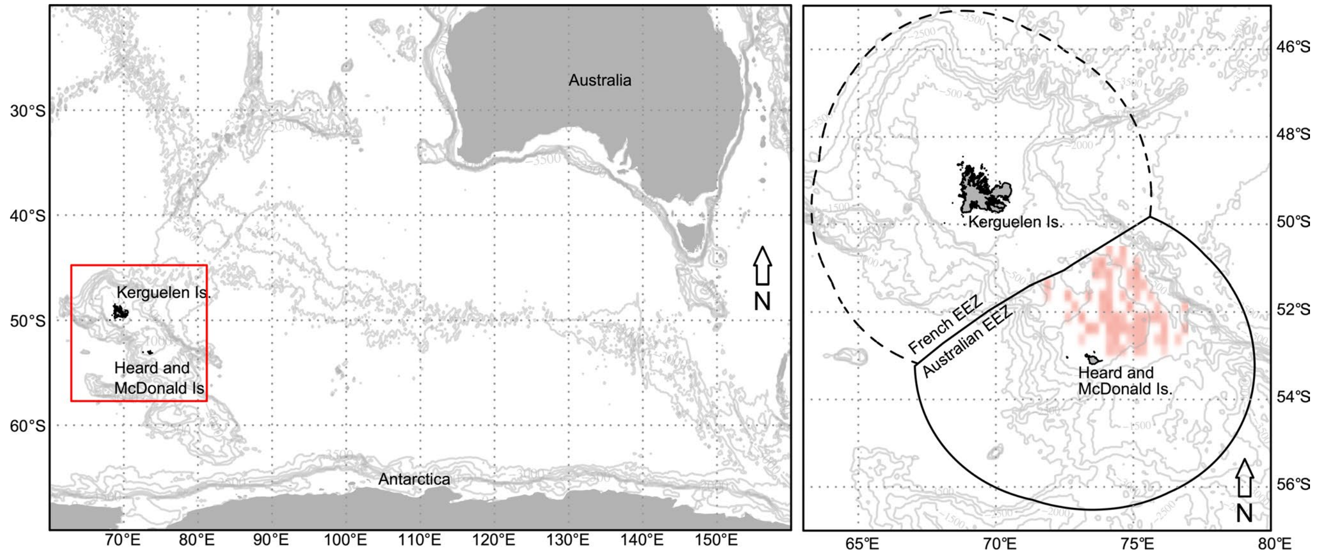

Fig. 1 Map of Heard and McDonald Islands. This region in the Kerguelen Plateau is where the Patagonian toothfish, *Dissostichus eleginoides,* and mackerel icefish, *Champsocephalus gunnari,* fisheries operations occur. The resolution of the raster on the right showing skate sampling locations is 0.25 degrees, and the contours shown are 500 m isobaths (3500 m to 0 m)

Table 1 Maturity stages of *Bathyraja* spp.

	Description	Binary category
Males		
1. Immature	Claspers short (not extending beyond pelvic fins) and uncalcified	0
2. Maturing	Claspers extend beyond pelvic fins but are soft and uncalcified	0
3. Mature	Claspers extend beyond pelvic fins and are hard, rigid and calcified	1
Females		
1. Immature	Ovary invisible or contains only small (pinhead-sized) ova that have no trace of yellow or orange yolk. Uteri thread like. No uterine egg cases	0
2. Maturing	Ovary contains small to medium (up to marble-sized) white to orange ova. Uteri may have visible swellings at anterior or posterior ends. No uterine egg cases	0
3. Mature	Ovary contains some large (greater than marble-sized) yellow or orange ova, in addition to small and medium ova. Uteri enlarged (> 1 cm) and may contain egg cases. The presence of uterine egg cases guarantees that the female is mature. However, females without uterine egg cases are still mature if they have some large ovarian eggs	1

Maturity of male and female skate samples were determined through examination of the claspers in males, and ovaries and uteri in females. A binary category was assigned to each maturity stage for the purpose of statistical analyses

at a magnification of ×10. Customised image analysis and ageing software were used to estimate age and derive annual growth measurements (Fig. 2). First, a birth band reflecting the time an individual hatched from their egg case was identified as the first distinct growth band after an angle change in the *corpus calcareum*. Next, the number of growth bands along a transect on the vertebrae section were counted, from the focus (time of birth) to the outer edge (time of death). Our samples did not span a wide enough range of months of capture to conduct a formal marginal increment analysis. We therefore assumed annual formation of growth bands, which is consistent with validated ageing protocols of several other closely related species (e.g., Cailliet and Goldman 2004; Okamura et al. 2013). Precision and bias were checked using average percent error (APE), Bowker's test of symmetry, Chang's coefficient of variation (CV) and age bias plots (Hoenig et al. 1995; Morison et al. 1998).

Maturity

Maturity stage was expressed as a binary maturity category (immature/maturing = 0 or mature = 1) for use in statistical

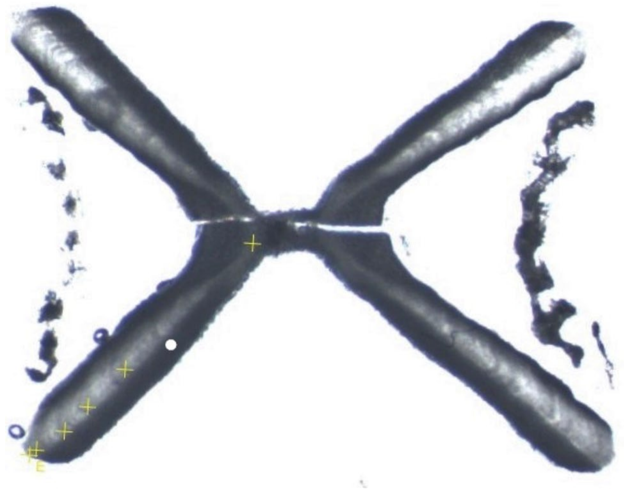

Fig. 2 Vertebrae cross section of a four-year old *Bathyraja irrassa* collected from Heard and McDonald Islands. The first (closest to the core) and last (demarcated with E) cross corresponds to the focus and outer bands, respectively, and were therefore excluded from the age counts. The white spot represents the birth band and the yellow crosses are the locations of the growth bands

analyses (Table 1). Length and maturity information was collected from 37,612 *B. irrasa*, 19,186 *B. eatonii* and 5922 *B. murrayi* between October 1998 and July 2020.

To estimate the length at 50% maturity (L_{50}) and 95% maturity (L_{95}), a three-parameter logistic model was fitted:

$$y = \frac{a}{1 + \left(\frac{L_t}{L_{50}}\right)^b}$$

where L_t is length as a function of time, y is the percentage of mature animals, a the asymptotic value, b the shape parameter. A single logistic regression model (FSA' R package version 0.8.30; Ogle 2016) was applied with the natural logarithm of the odds of an individual being mature (i.e., logit link) as a linear function of the explanatory variable, lengths, where maturity was assumed to follow a Bernoulli distribution. Age-at-maturity was estimated by converting length-at-maturity estimates with the formula:

$$A_{50} = \ln\left(\frac{1 - (L_{50} - L_0)}{L_\infty - L_0}\right) \Big/ -k$$

where A_{50} is the age at 50% maturity, L_0 the length at birth, L_∞ the asymptotic length, and k the growth-completion coefficient.

Growth model fitting and statistical analyses

Due to the small sample sizes for both *B. eatonii* and *B. murrayi,* we used two model-fitting approaches for each of the three species, (1) multi-model frequentist and (2) multi-model Bayesian. In both approaches, we fitted three candidate growth models to observed length-at-age data following the recommendations in Smart et al. (2016): (1) a von Bertalanffy growth model (VBGM); (2) a Gompertz growth function; and (3) a logistic growth model (Table 2).

Table 2 Equations of the three growth functions used in the multi-model approach

Model	Growth function
von Bertalanffy	$L(t) = L_0 + (L_8 - L_0)(1 - \exp(-kt))$
Logistic	$L(t) = \frac{L_8 L_0 (g_{\log^t})}{L_8 + L_0(\exp(g_{\log^t}) - 1)}$
Gompertz	$L(t) = L_8 \exp(-L_0 \exp(-g_{\mathrm{gom}^t}))$

L_t is length as a function of time, L_0 the length at birth, L_∞ the asymptotic length and *k/g* the growth-completion coefficient

Frequentist approach

We modelled the growth of each *Bathyraja* spp. using a frequentist multi-model approach, which used the Akaike Information Criterion (AIC) to select the best model fit based on the lowest AICc value (Akaike 1974). We fitted the growth models using the 'Estimate_Growth' function within the 'AquaticLifeHistory' R package (Smart 2019).

Bayesian approach

The informative priors specified for Bayesian models included L_∞ and L_0 as normal distributions with means and standard errors. Growth coefficients and sigma values were uniform priors with an upper and lower bound, and the growth curve had a normal error structure (Smart and Grammer 2021). Priors were set based on the observed species-specific length and maturity data and a review of growth parameters for deep water skates from the scientific literature (S2 in Online Resource 1). The priors for L_∞ was determined as the largest TL measured amongst all samples caught (1452 mm ± 132 SE for *B. irrasa*, L_∞ = 1322 mm ± 132 SE for *B. eatonii* and 477 mm ± 132 SE for *B. murrayi*) while that of L_0 was set using a presumed length-at-birth based on the smallest TL measured from age zero individuals (117 mm ± 29.25 SE for *B. irrasa* and 209 mm ± 30 SE for *B. murrayi*). However, as no age zero samples were obtained for *B. eatonii*, L_0 for this species was based on a hypothetical value (209 mm ± 30 SE) derived from averaging L_0 values of similarly sized Antarctic skate species (i.e., *B. irrasa* and *Amblyraja georgiana*; Francis and Maolagáin 2005). Standard error for L_∞ was consistent across all species at 132 mm, while the standard error for L_0 was set at 25% of the corresponding L_0 value. The L_0 standard error for *B. eatonii* was set at 50% of the L_0 value (55 mm) to account for uncertainties due to using a hypothetical TL value. Additionally, sensible upper bounds for non-informative priors *k* and σ were set at 3 and 300, respectively, while the lower bounds were set at zero (Smart and Grammer 2021). We also performed age adjustments of 0.5 years to the observed age classes for the Bayesian models to account for assumed asynchronous reproduction patterns for growth model fitting (Harry et al. 2010).

All Bayesian models were evaluated with the 'Estimate_MCMC_Growth' function within the 'BayesGrowth' R package version 0.3.1 (Smart 2020). We used 1000 iterations to determine parameter posterior distributions, after which convergence and auto-correlation of the models were checked using the Gelman-Rubin test ($\widehat{R} = 1$ for all models) and diagnostic plots, respectively (S3, S4 and S5 in Online Resource 1; Emmons et al. 2020.). The best fitting Bayesian model was identified using the leave-one-out cross validation information criterion (*LOOIC*) and selected as the model resulting in the lowest *LOOIC* value.

Results

Age estimation

For *B. irrasa*, corresponding values of APE and CV for the inter- and intra- reader variability were 4.21 and 5.96 and 2.83 and 4.01 (S6 in Online Resource 1), respectively, indicating a high degree of precision observed between reader 1 and reader 2. No systematic bias was detected between both readers by Bowker's test of symmetry (Bowker; $df = 16$, $x^2 = 25.30$, $P = 0.065$) and between the first read and second read (Bowker; $df = 11$, $x^2 = 18.00$, $P = 0.082$). Corresponding values of APE and CV for the intra-reader variability was 11.91 and 16.85 respectively for *B. eatonii* (S7a in Online Resource 1). These values are comparable to other elasmobranch age and growth studies despite being high relative to teleost ageing studies (Campana 2001; Cailliet et al. 2006; D'Alberto et al. 2016). For *B. murrayi*, corresponding values of APE and CV for the intra- reader variability were 6.32 and 8.94, respectively (S7b in Online Resource 1). Estimating the ages of *B. eatonii* and *B. murrayi* in this study proved to be difficult due to the small sizes of the collected samples, posing challenges in both preparation and interpretation of the vertebrae which resulted in inconsistencies in the age estimates.

Maturity

Length-at-maturity

We conducted length-at-maturity analysis based on a dataset of 62,720 individuals (37,612 *B. irrasa*; 19,186 *B. eatonii*; 5922 *B. murrayi*; S8 in Online Resource 1). Females were found to mature at greater lengths compared to males across all three species (Table 3; Fig. 3). There were 13,626 (36.22%) mature *B. irrasa* in the length samples (Table 4). Mean estimates of L_{50} and L_{95} for males were 1096 (1093–1098; 95% CI) mm TL and 1254 (1249–1259; 95% CI) mm TL, respectively (Table 3; Fig. 3a), while the mean

Table 3 Summary of length-at-maturity analysis for *Bathyraja irrasa*, *Bathyraja eatonii* and *Bathyraja murrayi* from the Heard and McDonald Islands

Species	Sex	L_{10}	L_{50}	L_{90}	L_{95}	L_{50} CI	
						2.5%	97.5%
B. irrasa	Combined ($n = 37{,}612$)	969.96	1118.99	1268.02	1318.70	1116.95	1120.93
	Male ($n = 24{,}206$)	977.33	1095.54	1213.75	1253.95	1093.64	1097.77
	Female ($n = 13{,}406$)	1003.93	1165.39	1326.85	1381.75	1161.98	1168.73
B. eatonii	Combined ($n = 19{,}186$)	899.42	1020.37	1141.31	1182.44	1017.46	1023.45
	Male ($n = 13{,}295$)	894.60	997.32	1100.05	1134.98	994.09	1000.81
	Female ($n = 5891$)	942.25	1084.48	1226.72	1275.09	1076.51	1092.59
B. murrayi	Combined ($n = 5922$)	394.12	461.38	528.64	551.51	459.35	463.51
	Male ($n = 3768$)	391.42	455.29	519.17	540.89	453.02	457.73
	Female ($n = 2154$)	388.78	485.83	582.87	615.87	478.37	494.06

L_{10} total length (TL) at 10% maturity, L_{50} TL at 50% maturity, L_{90} TL at 90% maturity, L_{95} TL at 95% maturity, *CI* confidence interval

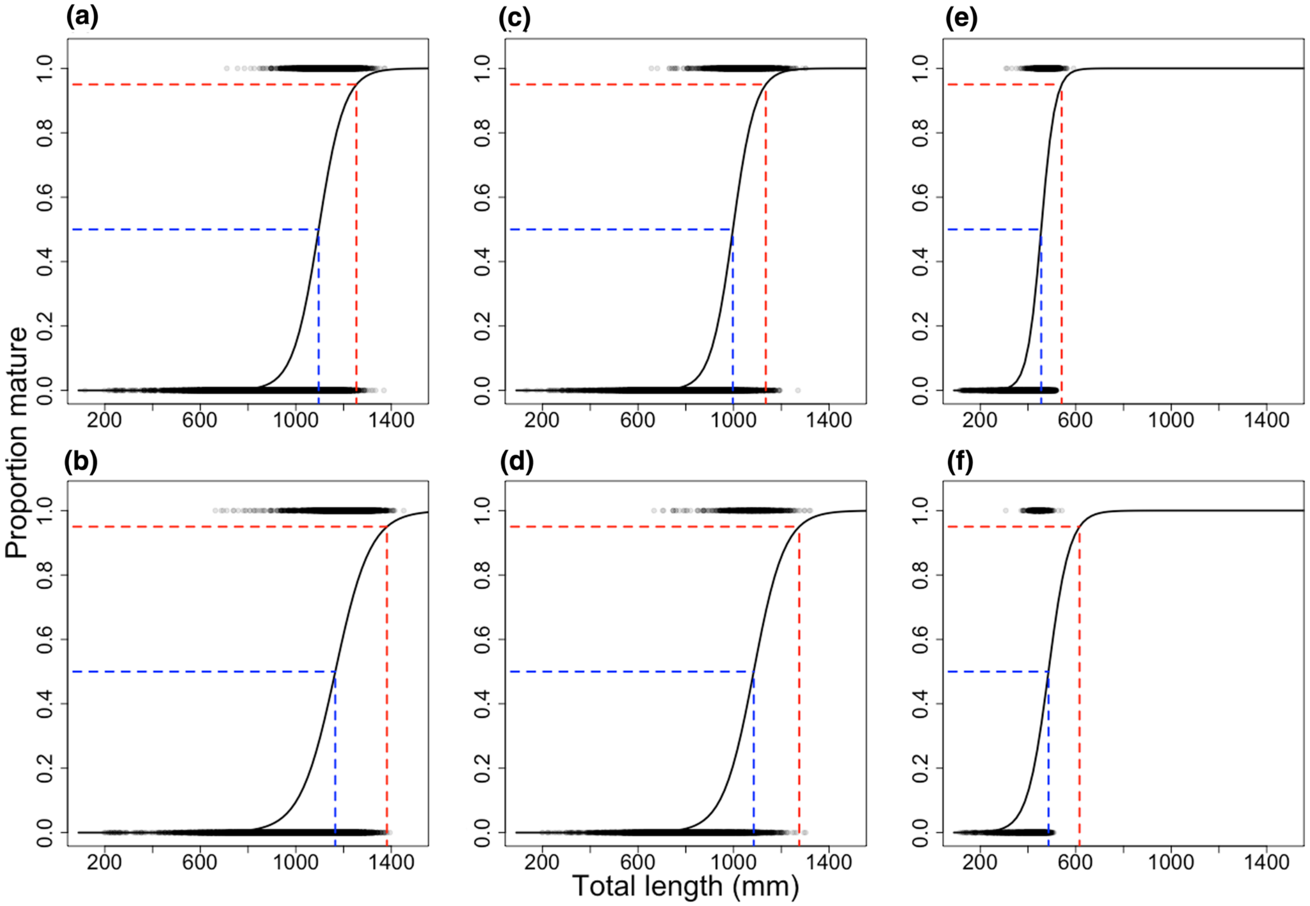

Fig. 3 Length-at-maturity of *Bathyraja* spp. Length-at-maturity ogives for **a** male ($n = 24{,}206$) and **b** female ($n = 13{,}406$) *Bathyraja irrasa*; **c** male ($n = 13{,}295$) and **d** female ($n = 5891$) *Bathyraja eatonii*; and **e** male ($n = 3768$) and **f** female ($n = 2154$) *Bathyraja murrayi*. Blue lines correspond to L_{50}, the length at which 50% of the population was mature while red lines correspond to L_{95}, the length at which 95% of the population was mature. Black points represent raw data points, where 1.0 represents a mature individual while 0.0 represents an immature individual

Table 4 Summary of length-at-maturity for *Bathyraja irrasa*, *Bathyraja eatonii* and *Bathyraja murrayi* from Heard and McDonald Islands

Species	Number mature		Smallest mature	Largest immature
B. irrasa	Male	8925	711	1369
	Female	4701	663	1394
B. eatonii	Male	2932	656	1270
	Female	738	667	1302
B. murrayi	Male	1494	308	520
	Female	445	307	509

Lengths are total length in mm

estimates of L_{50} and L_{95} for females were 1165 (1162–1169; 95% CI) mm TL and 1382 (1372–1391; 95% CI) mm TL, respectively (Table 3; Fig. 3b). There were 3670 (19.13%) mature *B. eatonii* in the length samples (Table 4). Mean estimates of L_{50} and L_{95} for males were 997 (994–1000; 95% CI) mm TL and 1135 (1127–1143; 95% CI) mm TL, respectively (Table 3; Fig. 3c), while the mean estimates of L_{50} and L_{95} for females were 1084 (1076–1093; 95% CI) mm TL and 1275 (1256–1295; 95% CI) mm TL, respectively (Table 3; Fig. 3d). There were 1939 (32.74%) mature *B. murrayi* in the length samples (Table 4). Mean estimates of L_{50} and L_{95} for males were 455 (453–458; 95% CI) mm TL and 541 (534–548; 95% CI) mm TL, respectively (Table 3; Fig. 3e), while the mean estimates of L_{50} and L_{95} for females were 486 (479–494; 95% CI) mm TL and 616 (595–640; 95% CI) mm TL, respectively (Table 3; Fig. 3f).

Age-at-maturity

Mean estimates of A_{50} and A_{95} for male *B. irrasa* were 6.29 (6.05–6.54; 95% CI) and 11.80 (10.16–14.33; 95% CI) years, respectively (Table 5), while the mean estimates of A_{50} for females were 7.83 (7.48–8.20; 95% CI). A_{95} for female *B. irrasa* could not be determined due to

Table 5 Summary of age-at-maturity analysis for *Bathyraja irrasa*, *Bathyraja eatonii* and *Bathyraja murrayi* from Heard and McDonald Islands

Species	Sex	A_{50}	A_{95}	A_{50} CI	
				2.5%	97.5%
B. irrasa	Combined ($n=37{,}612$)	6.76	19.17	6.40	7.16
	Male ($n=24{,}206$)	6.29	11.80	6.05	6.54
	Female ($n=13{,}406$)	7.83	–	7.48	8.20
B. eatonii	Combined ($n=19{,}186$)	5.32	8.70	5.09	5.56
	Male ($n=13{,}295$)	5.02	7.50	4.87	5.17
	Female ($n=5891$)	6.30	13.61	6.02	6.61
B. murrayi	Combined ($n=5922$)	5.28	10.55	4.94	5.64
	Male ($n=3768$)	4.79	8.54	4.40	5.21
	Female ($n=2154$)	5.63	10.20	5.31	5.98

A_{50} age (years) at 50% maturity, A_{95} age (years) at 95% maturity, *CI* confidence interval

insufficient information of mature individuals (Table 5). Mean estimates of A_{50} and A_{95} for male *B. eatonii* were 5.02 (4.87–5.17; 95% CI) and 7.50 (6.92–8.16; 95% CI) years, respectively (Table 5), while the mean estimates of A_{50} and A_{95} for females were 6.30 (6.02–6.61; 95% CI) and 13.61 (10.75–31.17; 95% CI) years (Table 5), respectively. Mean estimates of A_{50} and A_{95} for male *B. murrayi* were 4.79 (4.40–5.21; 95% CI) and 8.54 (6.33–12.24; 95% CI) years, respectively (Table 5), while the mean estimates of A_{50} and A_{95} for females were 5.63 (5.31–5.98; 95% CI) and 10.20 (8.06–13.71) years (Table 5) respectively.

Growth model fitting

We applied three Bayesian and Frequentist growth models (Gompertz; von Bertalanffy; Logistic) to the observed length-at-age data for each species (Table 6). Comparison between male and female growth models showed minimal differences and therefore no sex-specific growth modelling was conducted.

While the Gompertz growth model was the best fitting Bayesian model for all three species, the *LOOIC* results show that all three models provide a very similar quality of fit to the data (*LOOIC* > 2 for all models; Table 6). Therefore, we decided to use the von Bertalanffy growth models for inferences due to its prominence in the fisheries literature (Kenchington 2013).

The Bayesian models for *B. irrasa*, displayed similar trends with one another (Fig. 4a), but differed in both L_0 and L_∞ estimates, ranging from 367.25 mm TL to 397.99 mm TL; and 1201.19 mm TL to 1241.03 mm TL, respectively (Table 6). The frequentist von Bertalanffy growth model applied for *B. irrasa* was found to be the best fitting frequentist model (Table 7). The frequentist growth curve was overly influenced by younger and older individuals, whereas the Bayesian growth curve displayed an improved fit between three to nine years of age, where most of the data were concentrated (Fig. 4b).

The Bayesian growth models for *B. eatonii* mostly displayed similar trends to each other, with differences only noticeable for older ages (Fig. 4c). The models differed in both length-at-birth and asymptotic length, ranging from 126.43 mm TL to 142.30 mm TL; and 846.32 mm TL to 907.49 mm TL, respectively (Table 6). The frequentist Gompertz growth model applied for *B. eatonii* was found to

Table 6 Total length (mm) estimates for *Bathyraja irrasa*, *Bathyraja eatonii* and *Bathyraja murrayi* from Heard and McDonald Islands

Species	Model	L_0 (±SE)	L_∞ (±SE)	*k/g* (±SE)	*LOOIC* (±SE)
B. irrasa	Gompertz	367.25 ± 21.09	1201.19 ± 27.39	0.34 ± 0.03	2608.71 ± 25.86
	VBF	317.39 ± 24.53	1241.03 ± 33.75	0.24 ± 0.02	2610.60 ± 25.30
	Logistic	397.99 ± 19.29	1177.05 ± 23.52	0.45 ± 0.04	2608.89 ± 25.30
B. eatonii	Gompertz	134.25 ± 53.29	861.42 ± 43.26	1.30 ± 0.35	273.42 ± 8.81
	VBF	126.43 ± 53.92	907.49 ± 75.97	0.74 ± 0.26	273.93 ± 11.23
	Logistic	142.30 ± 50.20	846.32 ± 36.40	1.95 ± 0.45	273.51 ± 7.32
B. murrayi	Gompertz	162.33 ± 22.04	586.99 ± 63.49	0.26 ± 0.06	195.96 ± 7.71
	VBF	155.40 ± 23.54	642.33 ± 74.66	0.15 ± 0.04	196.18 ± 7.94
	Logistic	168.84 ± 21.49	546.68 ± 55.66	0.38 ± 0.08	196.57 ± 7.79

Total length estimates were for combined sexes and generated by three Bayesian growth models: Gompertz, von Bertalanffy (VBF) and Logistic. Priors were set at $L_0 = 117$ mm ± 29.25 SE and $L_\infty = 1452$ mm ± 132 SE for *B. irrasa*, $L_0 = 110$ mm ± 55 SE and $L_\infty = 1322$ mm ± 132 SE for *B. eatonii* and $L_0 = 209$ mm ± 30 SE and $L_\infty = 477$ mm ± 132 SE for *B. murrayi*. L_0 length-at-birth, L_∞ asymptotic length, *k/g* growth coefficient, *LOOIC* leave-one-out cross-validation information criterion

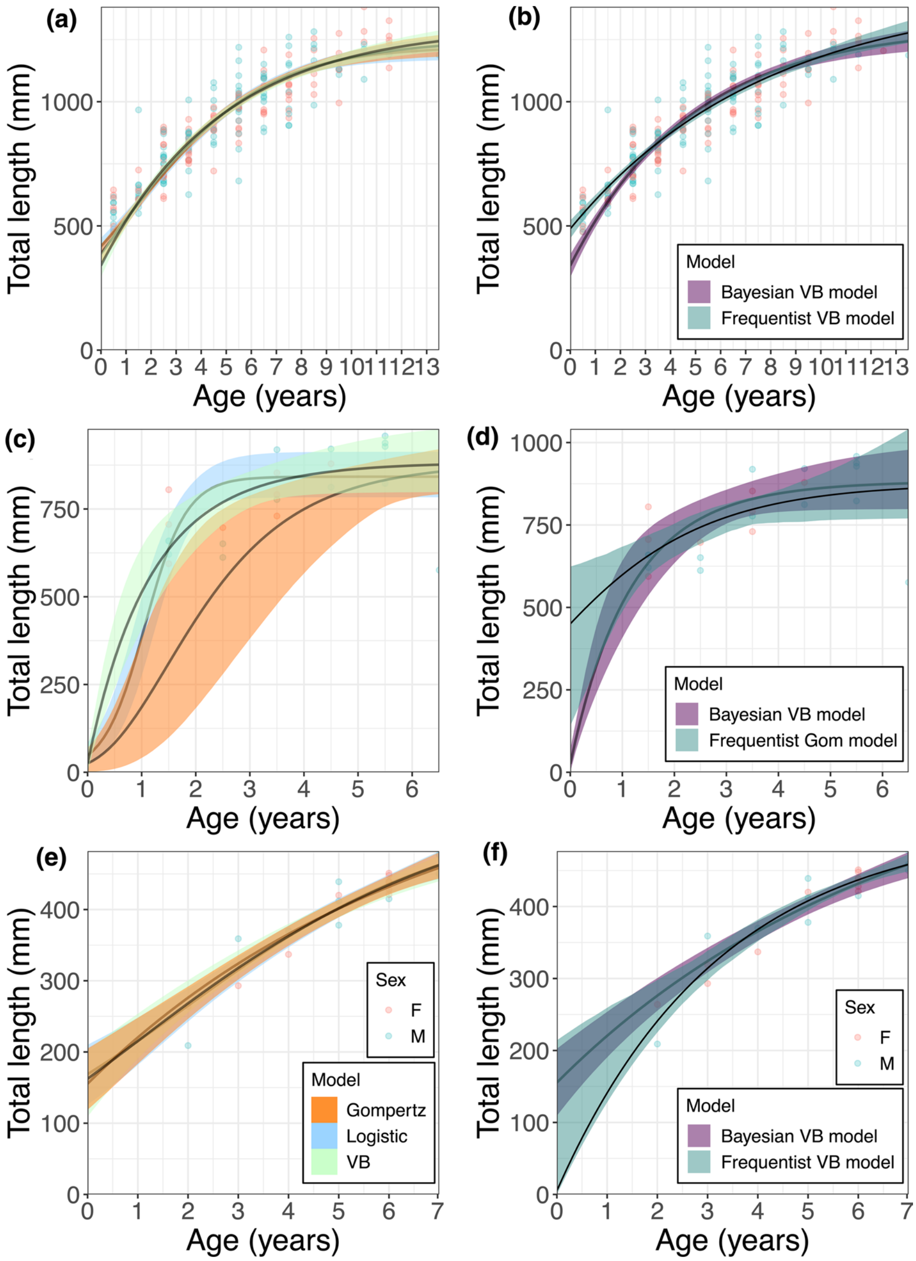

Fig. 4 Growth models for *Bathyraja* spp. Bayesian growth model comparison of observed combined sex data of **a** *Bathyraja irrasa,* **c** *Bathyraja eatonii* and **e** *Bathyraja murrayi*. Priors for the models were set at L_0 = 117 ± 29.25 mm and L_∞ = 1452 ± 132 mm, L_0 = 110 mm ± 30 SE and L_∞ = 1322 mm ± 132 SE, and L_0 = 209 mm ± 55 SE and L_∞ = 477 mm ± 132 SE, respectively; **b** Comparison of best fitting Frequentist von Bertalanffy (VB) model (AIC$_c$ = 2562.84; Table 7) and Bayesian VB model for *B.irrasa*, **d** best fitting Frequentist Gompertz (Gom) model (AICc = 196.39; Table 7) and Bayesian VB model for *B.eatonii* and **f** best fitting Frequentist Logistic model (AICc = 273.06; Table 7) and Bayesian VB model for *B. murrayi*. Males and females are represented by the blue and pink dots, respectively

be the best fitting frequentist model (Table 7). The Bayesian growth curve displayed an improved fit for younger and older individuals (Fig. 4d). This would largely be due to the absence of age zero samples which were accounted for in the Bayesian models but not the frequentist models.

The Bayesian models for *B. murrayi* displayed similar trends, with differences only noticeable for older ages (Fig. 4e). The models differed in both length-at-birth and asymptotic length, ranging from 155.40 mm TL to 168.84 mm TL; and 546.68 mm TL to 642.33 mm TL, respectively (Table 6). The frequentist von Bertalanffy growth model for *B. murrayi* was the best fitting frequentist model (Table 7). The Bayesian growth curve displayed an improved fit for younger and older individuals (Fig. 4f), similarly due to the absence of age zero samples accounted for in the Bayesian models.

Discussion

This study provides the first species-specific life history information for *B. irrasa*, *B. eatonii* and *B. murrayi*. All three species exhibit a physical growth-limiting characteristic of being late-maturing relative to other skate species (Dulvy et al. 2000; Stevens et al. 2000; Nowara et al. 2017). Based on this life history characteristic, the three species

Table 7 Total length (mm) estimates for *Bathyraja irrasa*, *Bathyraja eatonii* and *Bathyraja murrayi* from Heard and McDonald Islands

Species	Model	L_0 (±SE)	L_∞ (±SE)	*k/g* (±SE)	AIC_c
B. irrasa	Gompertz	347.35 ± 13.99	1236.67 ± 25.49	0.28 ± 0.017	2948.80
	VBF	317.39 ± 24.53	1328.62 ± 39.53	0.17 ± 0.015	2936.46
	Logistic	384.32 ± 12.92	1193.36 ± 20.34	0.40 ± 0.021	2963.15
B. eatonii	Gompertz		850.87 ± 38.07	0.83 ± 0.14	270.62
	VBF	280.80 ± 578.55	878.60 ± 112.03	0.50 ± 0.59	273.31
	Logistic		837.27 ± 32.49	1.17 ± 0.15	271.40
B. murrayi	Gompertz	296.83 ± 15.27	450.06 ± 29.37	2.00 ± 1.17	218.98
	VBF	5.23 ± 92.47	517.91 ± 49.51	0.31 ± 0.11	196.39
	Logistic	296.83 ± 15.27	449.41 ± 27.77	2.21 ± 1.15	218.98

TL estimates were for combined sexes and generated by three Frequentist growth models: Gompertz, von Bertalanffy (VBF) and Logistic. L_0 length-at-birth, L_∞ asymptotic length, *k/g* growth coefficient, AIC_c Akaike information criterion

have a high probability of being susceptible to overexploitation, even when taken as by-catch (Dulvy et al. 2000; Stevens et al. 2000; Nowara et al. 2017).

Several examples exist where skate populations have collapsed due to fishing mortality (Brander 1981; Dulvy et al. 2000), demonstrating the vulnerability of this taxon to overfishing. The three species in this study have previously been managed using a by-catch limit based on a population assessment without species-specific growth estimates. Instead, inferences from other closely related species were used (Nowara et al. 2017). This poses an undefined level of risk if their management is not sufficiently precautionary. Accurate stock assessments are built on a foundation of species-specific life history information, which is required to understand population productivity. This study has addressed this for *B. irrasa, B. murrayi* and *B. eatonii*, providing additional information to support evidenced-based decision-making by fisheries managers to help reduce the risk of overexploitation of these species.

In many species, vertebrae grow isometrically with respect to the rest of the body (Gburski et al. 2007), therefore age estimates obtained by observing the growth bands within the vertebral centra of *Bathyraja* spp. were assumed to be reliable. Similarity in the growth banding structures supported the assumption that a single growth band was produced each year (Perez et al. 2010). However, many species of elasmobranchs exhibit asynchronous reproduction throughout the year (Harry et al. 2010), with previous studies of skate reproduction supporting year-round egg deposition in *Bathyraja* species (Ainsley et al. 2011b). This assumption was made in this study for all three species as their reproductive patterns remain unknown. To maximise the accuracy of the results, the effects of asynchronous reproduction must be accounted for in the growth analyses, as the first growth increment could reflect any number of months growth, depending on when the individual was born. Age determination of most chondrichthyans, including skates, relies on counts of regularly deposited growth increments on the vertebrae that are regularly deposited, which has been validated for several other closely related species (e.g., Cailliet and Goldman 2004; Okamura et al. 2013). It is, however, important to acknowledge that no validation has previously been attempted for these species due to the lack of sample specimens. The age of asynchronously reproducing animals is uncertain (within 12 months) due to the unknown age at first increment formation (Harry et al. 2010). To account for this uncertainty, we performed age adjustments of 0.5 years to the observed age classes (Harry et al. 2010). The models for all three species should be reassessed should information regarding the reproductive biology, specifically those regarding their reproductive cycles, becomes known through future studies.

Bathyraja irrasa was found to mature at around 6 and 8 years of age for males and females, respectively. This is younger than that of the graytail skate, *B. griseocauda* (males 14 years, females 18 years), and the whitebrow skate, *B. minispinosa* (males 23 years, females 24 years; Arkhipkin et al. 2008; Ainsley et al. 2011a), which are species of similar size and occupy a similar habitat, although it should still be considered as a late maturing skate species when compared to species of other genera (S9 in Online Resource 1). *Bathyraja eatonii* matures at 5 and 6 years of age for males and females, respectively, while *B. murrayi* matures at 5 years for both males and females. Estimating the age of *B. eatonii and B. murrayi* also proved to be difficult due to the smaller size of the vertebrae. The challenges posed in preparation and interpretation of such small samples included inconsistent growth patterns and faint growth band pairs (Gburski et al. 2007). This resulted in inconsistencies in the age estimates as defined by the intra-reader variability having larger APE values. Coupled with the small sample sizes, the true age-at-maturity of these species remain elusive. While future studies could improve accuracy with a larger sample size, ideally a minimum of 200 (Smart et al.

2013; Thorson and Simpfendorfer 2009), consisting of a wider spread of different age- and size-classes, this study still provides a useful advancement from the previously used proxy species.

Bathyraja irrasa was also found to mature at larger sizes compared to other skate species. In comparison, the Antarctic starry skate, *A. georgiana*, from the Ross Sea reaches sexual maturity at smaller sizes of 640 mm and 690 mm TL for males and females, respectively (Francis and Maolagáin 2005; S2 and S10 in Online Resource 1). Information from past studies show most other *Bathyraja* spp. reach sexual maturity at smaller sizes, except for the Aleutian skate, *B. aleutica*, which matures at 1210 mm and 1330 mm TL for males and females, respectively (S2 in Online Resource 1). Elasmobranch species with late maturity at larger sizes may be more susceptible to the effects of fishing as a larger proportion of those captured may be comprised of immature individuals (Ainsley et al. 2011a, b). This is even more problematic for skates, which were found to mature at 75–90% of their maximum TL (Ainsley et al. 2011a). With later maturity, such as that seen with *B. irrasa*, a high rate of survival is necessary for an individual to reach maturity and subsequently reproduce.

Accuracy of the growth models applied relies on the inclusion of both the smallest and largest sizes of individuals in the population (Francis and Francis 1992). The absence of these size classes may result in problems with the estimation of growth parameters: missing smaller age groups will overestimate L_∞, while missing larger age groups will underestimate L_∞ (Francis and Francis 1992). This could happen for *B. eatonii* in this study, as the maximum size of an individual sampled was 958 mm TL, which is considerably smaller than the reported maximum size of 1100 mm TL (Francis 2006). No age zero individuals (i.e., below one year of age) were sampled, indicating the smallest size class of the population was absent. This resulted in the use of hypothetical L_0 values from similar-sized *Bathyraja* spp. for *B. eatonii* when setting the priors for the Bayesian growth models. Therefore, while the Bayesian modelling approach was able to better account for missing older individuals (Smart and Grammer 2021) and provided the best available information, further work is needed to improve the accuracy of these growth models, which can be achieved through inclusion of actual biological information obtained from age zero individuals.

The Bayesian growth model comparison resulted in the same growth function, the Gompertz growth model, being selected as the best fitting model for all three species, although all three models provide very similar quality of fit for the data. We chose the von Bertalanffy growth models for inferences in this study so that our findings are easier to be included in future analyses such as mortality estimation, especially since many current modelling software requires von Bertalanffy parameter inputs (Kenchington 2013). Using the von Bertalanffy growth curve combined for sexes, the asymptotic length is larger for *B. irrasa* (1241.03 mm) than *B. eatonii* (907.49 mm) and *B. murrayi* (642.33 mm), along with other similar Antarctic skate species such as *A. georgiana* (1013 mm; Francis and Maolagáin 2005) and other *Bathyraja* spp. with asymptotic lengths ranging from 597 to 3652 mm (S2 in Online Resource 1). *Bathyraja irrasa* can therefore be considered to mature at relatively large sizes.

The findings support the assumptions that *B. irrasa* have slow growth rates and mature late, indicating their increased vulnerability to exploitation. Although scientific surveys have suggested that populations of the three species have remained stable over time, with the exception of a substantial increase between 2009 and 2011, a risk of localised depletion exists (Nowara et al. 2017). Furthermore, the phasing out of trawl fishing in the HIMI Patagonian toothfish fishery and increase in longline effort at the HIMI fisheries may alter the impacts on skates, which would thereby require a timely review on their population status, especially for *B. irrasa* which forms the majority of longline by-catch and therefore may face an increased risk of overexploitation (Nowara et al. 2017). The estimates of age and growth parameters, will help improve the management of these species by providing more certainty in a fundamental component of future population assessments. Therefore, our results represent valuable information on these *Bathyraja* spp. and subsequently serve as a foundation to further refine and develop future management strategies and conservation efforts.

Supplementary material

The following supplementary material is made available in Online Resource 1:

Summaries of known length-at-maturity and age-at-maturity information of *Bathyraja* spp.; posterior density plots and trace plots for the best fitting Bayesian growth models for each species; length-frequency distribution plots of samples; age-bias plots and comparison of von Bertalanffy growth curves of skate species from previous studies.

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Author contributions DW and JR conceived and designed the research. JC, PY and PZ advised on the study and provided all samples used. DW, JB and JR conducted sample processing and data collection. DW, JS and JR performed data analysis. DW wrote the first draft of the manuscript, and all authors edited/commented on previous versions of the manuscript. All authors read and approved the final manuscript. JR and JS supervised the study.

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Data availability The datasets generated and/or analyzed during the study are available from the corresponding author on reasonable request, if not already included in this published article and its supplementary information files.

Declarations

Conflict of interest All authors have no competing interests to declare that are relevant to the content of this article.

Ethical approval No approval of research ethics committees was required for this study as no live animals were used throughout.

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