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SPECIAL ISSUE-SKATES

Age, growth, maturity, and mortality of the Alaska skate, *Bathyraja parmifera*, in the eastern Bering Sea

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Abstract The Alaska skate, *Bathyraja parmifera*, is the most abundant species of skate on the eastern Bering Sea shelf, accounting for over 90% of total skate biomass. However, little is known regarding the life history of this species despite its common occurrence as bycatch in several Bering Sea fisheries. This is the first study to focus on the age and growth of *B. parmifera*. From 2003 to 2005, more than one thousand specimens were collected by fisheries observers and on scientific groundfish surveys. Annual banding patterns in more than 500 thin sections of vertebral centra were examined for age determination. Caudal thorns were tested as a potentially non-lethal ageing structure. Annual band pair deposition was verified through edge and marginal increment analyses. A three-parameter von Bertalanffy growth function and a Gompertz growth function were fit to observed length-at-age data. Both models provided significant fits, although the Gompertz function best described the overall pattern of growth in both males and females, based upon statistical criteria and parameter estimates. Age and size at 50% maturity were 9 years and 92 cm TL for males and 10 years and 93 cm TL for females. The maximum observed ages for males and females were 15 years and 17 years, respectively. Estimates of natural mortality (M) ranged from 0.14 to 0.28, and were based on published relationships between M and longevity, age at maturity, and the von Bertalanffy growth coefficient. Due to these life history characteristics and a lack of long-term species-specific stock data, a conservative management approach would be appropriate for *B. parmifera*.

Keywords Elasmobranch · Rajidae · Life history · Natural mortality · Caudal thorns

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Introduction

The Alaska skate, *Bathyraja parmifera*, is a large-bodied species (111 cm maximum total length (TL); Ebert 2005) that is widely distributed across the eastern Bering Sea (EBS) and typically found at depths from 50 m to 200 m (Stevenson 2004). While its range extends to the eastern Aleutian Islands and the Gulf of Alaska, *Bathyraja parmifera* is the dominant skate species across the EBS shelf, accounting for over 90% of total skate biomass there (Matta et al. 2006). Despite the abundance of *B. parmifera*, little is known regarding its life history. Additionally, no long-term species-specific catch data are available, since skate catch in the EBS is officially reported in aggregate, and fishery observers have only been

identifying skates to species since 2003 (Matta et al. 2006).

While there is currently no directed fishery for *B. parmifera* in the EBS, the formation of one is possible due to its large body size and abundance. Skates already make up a large part of the observed incidental catch in several EBS groundfish fisheries, approximately 30% of which is retained (Matta et al. 2006). Declines of large-bodied skate species have been documented in other parts of the world and have often been attributed to overfishing (Brander 1981; Walker and Heessen 1996; Casey and Meyers 1998; Dulvy et al. 2000). Certain species of skate may have particularly low resilience to exploitation and increased vulnerability to extinction due to their life history characteristics (Walker and Hislop 1998; Dulvy and Reynolds 2002), highlighting the need for species-specific data when making management decisions.

Skates belong to the taxonomic group Elasmobranchii, which also includes sharks and rays. As a group, elasmobranchs can be classified as equilibrium (K-selected) strategists and typically share the biological characteristics of low fecundity, late maturity, high juvenile survivorship, slow body growth, and long life span (Hoenig and Gruber 1990; Winemiller and Rose 1992; Camhi et al. 1998; King and McFarlane 2003). Equilibrium strategists tend to have low reproductive rates and slow population growth and generally cannot sustain high levels of fishing pressure (Holden 1974; Adams 1980; Hoenig and Gruber 1990). King and McFarlane (2003) suggested that due to their life history characteristics, equilibrium strategists should only be harvested at low to moderate rates.

Life history studies are necessary for stock assessment, as the resulting parameters are often incorporated into fishery models. Age at maturity may be an especially good indicator of a population's resilience to fishing pressure, since it is negatively correlated with population growth rate (Cortés 2002). Furthermore, age at maturity, the von Bertalanffy growth coefficient, and longevity may be useful predictors of the instantaneous rate of natural mortality (Hoenig 1983; Jensen 1996). Such information is essential to understanding the biology and dynamics of a given population.

Ageing elasmobranchs is a complicated process, as there are few available calcified structures and difficulties in validation. However, in recent years researchers have successfully developed accurate ageing methods for skates (Cailliet and Goldman 2004). Skates are generally aged by counting vertebral annuli, although caudal thorns are semi-calcified structures that have been aged successfully in several species (Gallagher and Nolan 1999). Caudal thorns are external modified spines that are thought to aid in protection; the benefit of using caudal thorns as ageing structures is that they can presumably be obtained non-lethally.

The aims of this study were to: (1) determine whether vertebral thin sections and caudal thorns are appropriate ageing structures for *B. parmifera*; (2) describe the pattern of growth for both sexes; (3) verify age estimates through edge analysis and marginal increment analysis (MIA); (4) estimate size and age at maturity; and (5) estimate the instantaneous rate of natural mortality (M) from empirical longevity, von Bertalanffy growth coefficients, and age at maturity estimates. This study is the first to provide estimates of age and growth, age at maturity, and natural mortality for *B. parmifera* in the eastern Bering Sea.

Methods

Specimen collection and preparation

Skates were collected from NOAA Fisheries EBS groundfish trawl surveys during the summers of 2003 and 2004, and throughout 2004 and 2005 by the North Pacific Groundfish Observer Program (NPGOP) on flatfish trawlers and Pacific cod longline vessels. Due to morphological similarities between Bering Sea skates, fishery observers were specially trained in species identification prior to sampling. Samples were obtained every month of the year excluding March, April, and May. Each skate was sexed, and weighed when possible, and TL and disc width (DW) measurements were recorded to the nearest centimeter. Maturity stage was determined at sea using the modified criteria of Zeiner and Wolf (1993; Table 1) and later confirmed in the laboratory through visual inspection of the gonads. A length

of vertebral column was removed from the thoracic (mid-dorsal) region of the body and frozen until further processing was possible. Caudal thorns were removed from the base of the tail where it joins the disc and stored frozen. Three to five vertebrae from each specimen were individually separated with a sharp blade, rinsed in tap water, and allowed to soak in 70–95% ethanol for at least 24 h. After air-drying, vertebrae were cut through the centrum with a double-bladed low-speed saw to create sagittal thin sections approximately 0.3 mm thick, which were then mounted on glass slides. Caudal thorns were cleaned by boiling in tap water for 10–20 min, and excess tissue was thereafter gently wiped away using a piece of tissue-paper and forceps.

Age estimates and verification

Vertebral band pairs, or annuli, were viewed against a dark background with reflected light using a dissecting microscope. Mineral oil was applied to the thin section surface to clarify the banding pattern. A band pair consisted of one wide opaque band of growth that appeared lightly colored and one narrow translucent band that appeared darkly colored (Fig. 1). Age estimates were generated by counting translucent bands. Each translucent band was considered to represent one year of growth if it accompanied an opaque band and if it could be detected across the corpus calcareum. The birthmark increment, assumed to correspond to the event of hatching from the egg case, was evident from a change in the angle of the corpus calcareum relative to the intermedialia (Goldman 2004) and was not included in the age estimate. In some cases, faint checks were present within the larger bands. These checks were distinguished from growth zones by their lack of continuity throughout the ageing structure, irregular spacing, and faint appearance.

The annuli in caudal thorns were also viewed with a dissecting microscope, using reflected light and a dark background (Fig. 2). As in vertebral thin sections, each band pair consisted of one translucent band and one opaque band, together assumed to represent one year of growth. Age estimates were generated by counting each translucent band with reference to a protothorn (birthmark increment) located at the apex of each caudal thorn (Gallagher and Nolan 1999). The protothorn was evident by an angle change relative to the next fully formed translucent band. Each translucent band had a ridge-like appearance and was considered to represent one year if it accompanied an opaque band and extended around the circumference of the thorn. Age estimates generated from caudal thorns and vertebrae were compared by means of a paired-sample *t* test and an age-bias plot.

Vertebral thin sections were aged three independent times by a primary reader, and a subset of 72 samples was aged three times by a second reader with experience in ageing skates. Several

Table 1 Criteria used to define maturity stages in male and female *B. parmifera*, adapted from Zeiner and Wolf (1993)

Stage	Male characteristics	Female characteristics
1 Juvenile (Immature)	No coiling of vas deferens Testes small and undeveloped Claspers do not extend past posterior edge of pelvic fin No alar thorns present	Small undeveloped ovaries and shell glands No differentiated ova present
2 Adolescent (Maturing)	Some coiling of vas deferens Testes enlarging Claspers extend past pelvic fin edge but are only somewhat calcified Alar thorns may be present	Ovaries beginning to enlarge and differentiate Ova white, distinguishable but smal Shell glands widening but still gelatinous in appearance
3 Adult (Mature)	Complete coiling of vas deferens Large developed testes Calcified claspers Prominent alar thorns	Large yellow (yolked) ova, greater than 2.0 cm in diameter Large, solid, functional shell glands

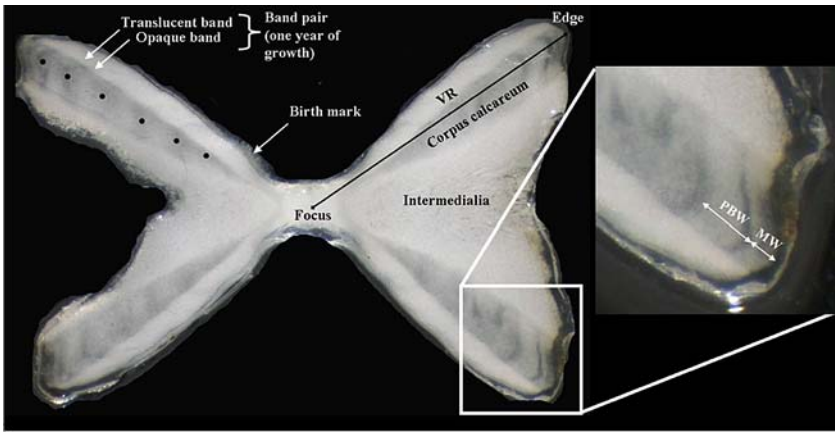

Fig. 1 Digital photograph of a vertebral thin section from a 75 cm TL female skate, viewed with reflected light against a dark background. The birthmark increment is indicated by the angle change in the corpus calcareum relative to the intermedialia. VR is vertebral radius. Inset shows measurements used for marginal increment analysis (MIA), where PBW is penultimate band pair width and MW is margin width. Translucent bands, indicated by solid black circles, were counted to give an age estimate of 6 years old for this specimen. Photographs were not digitally enhanced

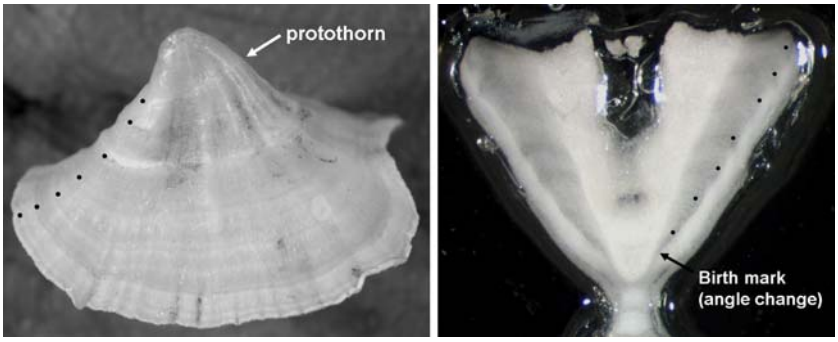

Fig. 2 Caudal thorn (left) and vertebral thin section (right) from a 7 year old, 82 cm TL skate. Translucent bands are indicated by solid circles

measures of precision were used to evaluate the consistency of inter- and intra-reader age estimates, including average percent error (APE; Beamish and Fournier 1981), the coefficient of variation (CV), and percent reader agreement (PA). Additionally, bias between readers was visually assessed using an age-bias plot.

Quality, or readability, was recorded by the primary reader on a scale of one to five, based on criteria described by the Committee of Age Reading Experts (CARE 2000). A quality rating of '1' was considered poor, with considerable variation expected between readings due to inaccurate band visualization. A quality of '5' corresponded to a very clear growth pattern, with an excellent chance of reproducing the same age in subsequent readings. By recording quality, samples with vague or 'checky' patterns could be omitted from the analysis if necessary, reducing the possibility of inaccurate age estimation. Only samples with APE less than 15% (Sulikowski et al. 2003) and a quality rating greater than '2' were used to estimate growth parameters.

TL was plotted against vertebral radius (VR) and against caudal thorn base length (TBL) to ensure that the growth of each ageing structure was proportional to the growth of the skate. In vertebral thin sections, this relationship was used to generate a back-calculation function:

$$TL_i = \left(\frac{VR_i}{VR_c}\right)^v TL_c$$

where TL_i = total length (cm) at time of formation of growth increment i, VR_i = vertebral radius (mm) at time of increment formation, TL_c = total

length at time of capture, VR_c = vertebral radius at time of capture, and v = the slope parameter derived from the allometric TL–VR relationship (Francis 1990). The back-calculation function was used to determine the average length at time of birthmark increment formation (TL_{BM}). Length at birth was estimated independently from late-stage embryos and from the smallest free-swimming individual observed during this study; the actual length at birth was assumed to fall within this range of values. By comparing TL_{BM} with the independent estimates of length at birth, it was possible to verify the accurate identification of the birthmark when generating age estimates from vertebral thin sections.

Edge analysis and MIA were performed to verify the annual nature of band deposition. Edge type was assessed without knowledge of collection date by using digital photographs of caudal thorns and vertebral thin sections from fish of all age classes. The criteria for determining edge type were adapted from Yudin and Cailliet (1990) and Gallagher and Nolan (1999). Edge types were defined as follows: (1) translucent band (or ridge in caudal thorns) forming at the marginal edge; (2) narrow opaque band beginning to form on the marginal edge; and (3) broad opaque band well-formed on the marginal edge. 'Broad' and 'narrow' opaque bands were defined based on the relative width of the previous fully formed opaque band (Cailliet et al. 2006). MIA was performed on vertebral thin sections following the methodology of Conrath et al. (2002). A digital photograph was taken of each specimen and all measurements were made using Image-Pro Plus 5.1 software (Media Cybernetics). Margin width (MW) was divided by penultimate band pair width (PBW) to yield the marginal increment ratio (MIR; Fig. 1). Mean MIR was calculated from at least four 5–8 year-olds during each month of collection. Edge type and mean MIR were both compared against month of collection to determine the seasons of opaque and translucent growth zone deposition and to confirm the annual nature of band pair formation. Differences between months in MIR were assessed using a non-parametric Kruskal–Wallis analysis of variance by ranks test and examined post-hoc with Dunn's test for multiple comparisons (Zar 1999).

Growth estimates

Two different models were fit to observed length-at-age data from males, females, and both sexes combined using the Levenberg–Marquardt routine for nonlinear least squares parameter estimation in the statistical software SPSS (v. 12.0.1 SPSS, Inc). The first model fitted was a three-parameter von Bertalanffy growth function in the form:

$$L_t = L_\infty (1 - e^{-k(t-t_0)})$$

where L_t = total length at age t, L_∞ = theoretical asymptotic length, k = growth rate coefficient, and t_0 = theoretical age at zero length (Quinn and Deriso 1999; Haddon 2001). After fitting the von Bertalanffy model, the theoretical average length of an age zero fish (L_0) was estimated from the model parameters by the equation: $L_0 = L_\infty\ (1 - e^{kt_0})$, and compared to the independent estimates of length at birth to verify the biological appropriateness of using the von Bertalanffy model (Cailliet and Goldman 2004; Cailliet et al. 2006).

A modified form of the Gompertz growth function was also fit to the data as:

$$L_t = L_0 * e^{G(1 - e^{-gt})}$$

where G is the instantaneous rate of growth at time t, g is the rate of decrease of G, and L_0 is defined as above (Goldman 2004; Bishop et al. 2006). Asymptotic length (L_∞) was estimated by the equation: $L_\infty = L_0\ e^G$ using the parameters obtained by fitting the Gompertz model and was then compared to maximum observed length (Mollet et al. 2002).

Model goodness-of-fit was assessed by comparisons of significance level ($P < 0.05$), coefficient of determination (r^2), and residual mean squared error (MSE; Carlson and Baremore 2005; Neer and Thompson 2005), and by the production of reasonable biological estimates (Cailliet et al. 2006). Independent estimates of length at birth and maximum observed length were compared with the values of L_0 and L_∞ predicted by each of the growth functions. Potential differences between males and females were examined for

each model through Kimura's (1980) likelihood ratio test as described by Haddon (2001).

Maturity

Size at 50% maturity (L_{50}) was estimated for each sex separately by fitting a logistic model to paired maturity and length data using a weighted non-linear least squares parameter estimation routine in the statistical software R v.2.0.1 (R Dev Core Team 2004). A logistic model of the form:

$$P = \frac{1}{1 + e^{-(a+bx)}}$$

was fit to the data, where P is the proportion of mature individuals in each 1 cm size interval, x is total length (cm), and a and b are parameters. Following parameter estimation, length at 50% maturity was calculated by setting P equal to 0.5 and solving for x. Variance and confidence intervals for length at 50% maturity were calculated after Ashton (1972). Age at 50% maturity (T_{50}) was directly estimated for each sex from paired age and maturity data using the methods above.

Longevity and natural mortality

Longevity (T_{max}) was estimated from the oldest vertebral age estimates observed during this study. Three methods were used to indirectly estimate natural mortality. Hoenig's method (1983) is based on the empirical relationship between mortality and longevity. Hoenig demonstrated that for fishes, the general relationship between the instantaneous rate of mortality (Z) and maximum age is: $\ln(Z) = 1.46–1.01*\ln(T_{max})$. Because Hoenig's data came from unexploited or lightly exploited stocks, Z approximates M, the instantaneous rate of natural mortality.

Jensen (1996) demonstrated theoretically that the von Bertalanffy growth coefficient (k) should be a good predictor of M. We used the relationship derived from Pauly's (1980) database ($M = 1.6k$) to obtain a second estimate of M, with approximate confidence intervals for M estimated after Gunderson et al. (2003).

The theoretical relationship between mortality and age at maturity was used to obtain a third estimate of natural mortality with the equation: $M = 1.65/T_{50}$ (Jensen 1996), where T_{50} is age at 50% maturity.

Results

Age estimates and verification

A total of 1356 skates was collected between July 2003 and December 2005. Males ranged in size from 22 to 118 cm TL, and females ranged from 21 cm to 119 cm TL. Vertebral thin sections from 546 specimens were prepared and aged blindly three independent times. Of these, 431 thin sections, or approximately 79%, had low enough APE (< 15%) and adequate quality (>'2') to be considered suitable for use in growth modeling. Acceptable vertebral thin section age estimates came from 200 males, ranging in size from 22 to 114 cm TL, and 231 females ranging in size from 21 to 116 cm TL, during each month of collection (Fig. 3a, b). Age estimates generated from vertebral thin sections and used in growth models ranged from 0 to 15 years for males and 0 to 17 years for females.

Independent estimates of length at birth were generated to verify birthmark increment identification in vertebral thin sections and to assess the adequacy of growth models in describing the early years of growth. The mean size of late-stage embryos, excluding the embryonic tail filament, was approximately 19.8 cm TL (SE = 0.20; $n = 39$; Hoff[1]) and the smallest observed free-swimming individual in this study was 21 cm TL; therefore the actual length at birth was assumed to fall within 19.8–21 cm TL.

The relationship between TL and VR was nearly linear but was best described by a power function of the form: $TL = 27.166VR^{0.867}$ ($P < 0.0001$; $r^2 = 0.97$; $n = 311$). The relationship between TL and caudal TBL was also best described as a power function, of the

[1] G. Hoff. 2006. Personal communication, unpublished data. Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115.

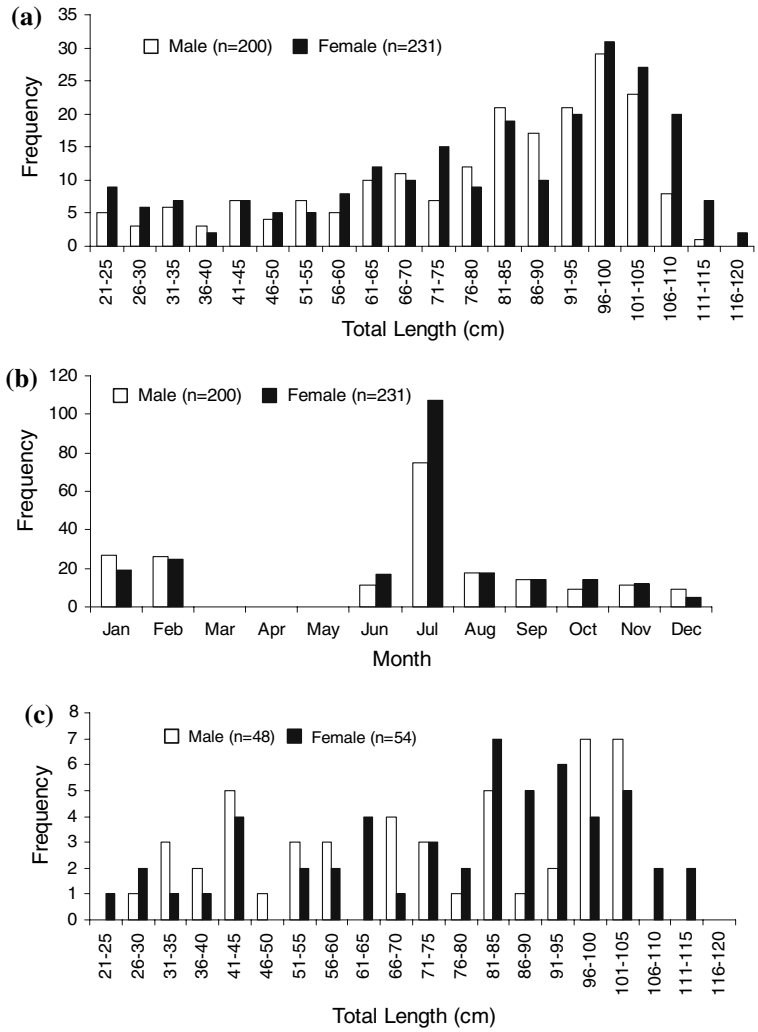

Fig. 3 Frequency histograms of vertebral thin section samples used in growth models by (**a**) length and (**b**) month of collection, and (**c**) length frequency histogram of caudal thorn samples

form: $TL = 10.342TBL^{0.9703}$ ($P < 0.0001$; $r^2 = 0.93$; $n = 100$). Through back-calculation, the average TL at vertebral birthmark increment formation (TL_{BM}) was estimated as 22.14 cm TL ($n = 310$; 95% CI = 21.87, 22.41), very close to the independent estimates of size at birth (19.8–21 cm TL), thus verifying the correct identification of the birthmark increment.

In total, 102 caudal thorns were aged blindly three independent times and were compared with vertebral thin sections from the same specimens (Fig. 3c). Precision between thorn and vertebral age estimates was generally high (APE = 7.92%, CV = 11.20%), and there was no detectable bias between estimates from the two structures (Fig. 4a). A paired t test demonstrated no significant difference between mean age estimates from caudal thorns and vertebral thin sections after samples with poor quality and APE were excluded ($t = -1.372$, $P > 0.10$, $n = 70$).

Overall precision between the primary reader's three age estimates from vertebral thin sections was generally high (APE = 8.08%, CV = 10.89%, $n = 546$). Precision between the second reader's estimates was slightly lower (APE = 14.49%, CV = 19.19%, $n = 72$), and inter-reader precision was considered acceptable (APE = 9.99%, CV = 14.13%, $n = 72$). Thirty-five percent of the two readers' age estimates were in complete agreement, 76% agreed within 1 year, and 94% of age estimates agreed within 2 years. Furthermore, an age bias plot demonstrated no

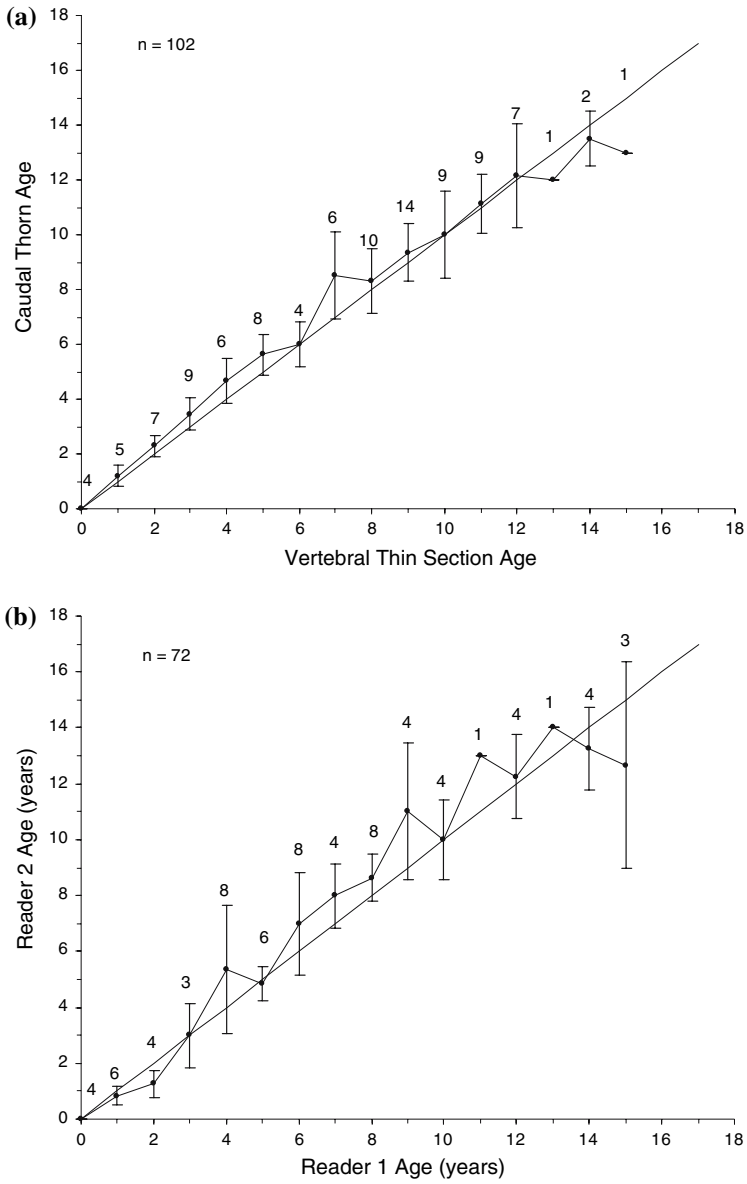

Fig. 4 Age-bias graphs showing (**a**) mean caudal thorn age estimates relative to vertebral thin section age estimates, and (**b**) the mean vertebral age estimates of Reader 2 relative to the age estimates of Reader 1. Sample sizes are listed above each age, error bars represent 95% confidence intervals around mean caudal thorn or Reader 2 age estimates, and the 1:1 equivalence line is given

appreciable bias between vertebral age estimates from the two readers (Fig. 4b).

The results of edge analysis and MIA of vertebral thin sections support annual band pair formation (Fig. 5). Translucent bands at the edge (Type 1) were present most frequently during the months of January and February, narrow opaque bands (Type 2) during the months of June through October, and broad opaque bands (Type 3) during November and December, suggesting a seasonal progression in band formation. A significant difference in MIR between months was detected with a Kruskal–Wallis test (KW $\chi^2 = 43.783$, $P < 0.001$). The lowest mean MIR occurred during the month of February (mean MIR = 0.044, SE = 0.026), after which an increasing trend was apparent, resulting in the highest mean MIR during the month of November (mean MIR = 0.662, SE = 0.071). Significant differences in MIR between the month of February and the months of August ($P < 0.005$), September ($P < 0.005$), November ($P < 0.001$),

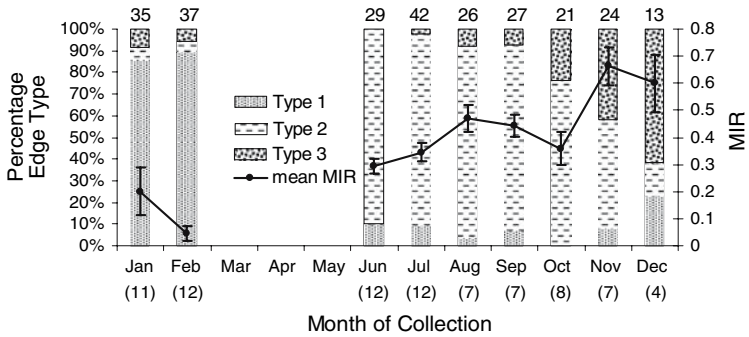

Fig. 5 Percentage edge type (columns) and mean marginal increment ratio (MIR; line) during each month of collection. Edge analysis sample sizes are listed above the columns, and marginal increment analysis sample sizes are listed along the *x*-axis in parentheses. Error bars represent mean MIR ± 1 SE

and December ($P < 0.005$), and between the months of January and November ($P < 0.01$), were detected with Dunn's post hoc test for multiple comparisons. Thus vertebral translucent band formation appears to occur during the winter months, followed by formation of the opaque band in summer and fall, supporting the assumption that each band pair represents one year of growth.

It was not possible to perform a full marginal increment or edge analysis on caudal thorns, as they were only collected during June and July. However, it should be noted that the majority of these thorns (94%) had a narrow opaque band (Type 2) beginning to form at the edge, suggesting that ridges (translucent bands) are deposited earlier in the year, consistent with our findings for vertebral thin sections.

Growth estimates

Overall, both the von Bertalanffy and Gompertz growth models fit the observed length-at-age data well (Fig. 6; Table 2). Each model provided highly significant ($P < 0.0001$) and reasonable fits with similar MSE and r^2. Independent estimates of length at birth (19.8–21 cm TL) were very close to L_0 (average length at age zero) predicted by the von Bertalanffy model (19–20 cm TL) and the Gompertz model (22–23 cm TL), indicating that both models adequately describe the early years of growth. However, the Gompertz model had slightly lower MSE and higher r^2 than the von Bertalanffy model for both sexes (Table 2). Furthermore, asymptotic length (L_∞) estimated from the Gompertz parameters (111 and 121 cm TL for males and females, respectively) is closest to the observed maximum length of this species (118 and 119 cm TL for males and females respectively.)

Significant differences between the sexes in overall growth were detected with likelihood ratio tests for both the von Bertalanffy model ($\chi^2 = 11.54$, df = 3, $P < 0.01$) and the Gompertz model ($\chi^2 = 16.48$, df = 3, $P < 0.01$). Using likelihood ratio tests on single parameters, significant differences between the sexes were determined for the von Bertalanffy model in terms of the L_∞ parameter ($\chi^2 = 5.78$, df = 1, $P < 0.05$) and k parameter ($\chi^2 = 6.23$, df = 1, $P < 0.05$), and for the Gompertz model in terms of the g parameter ($\chi^2 = 6.55$, df = 1, $P < 0.05$).

Maturity

The smallest observed mature male and female were 85 and 87 cm TL, respectively. The largest immature male and female were 98 and 101 cm TL, respectively. Length at 50% maturity (L_{50}) occurred at 91.75 cm TL in males ($n = 555$; 95% CI = 90.94, 92.57) and at 93.28 cm TL in females ($n = 642$; 95% CI = 92.52, 94.04; Fig. 7a). Females had a slightly later age at maturity (T_{50}) than males (Fig. 7b). Males were estimated to mature at an age of 8.97 years ($n = 200$; 95% CI = 8.60, 9.33) and females matured at 9.71 years ($n = 231$; 95% CI = 9.38, 10.04).

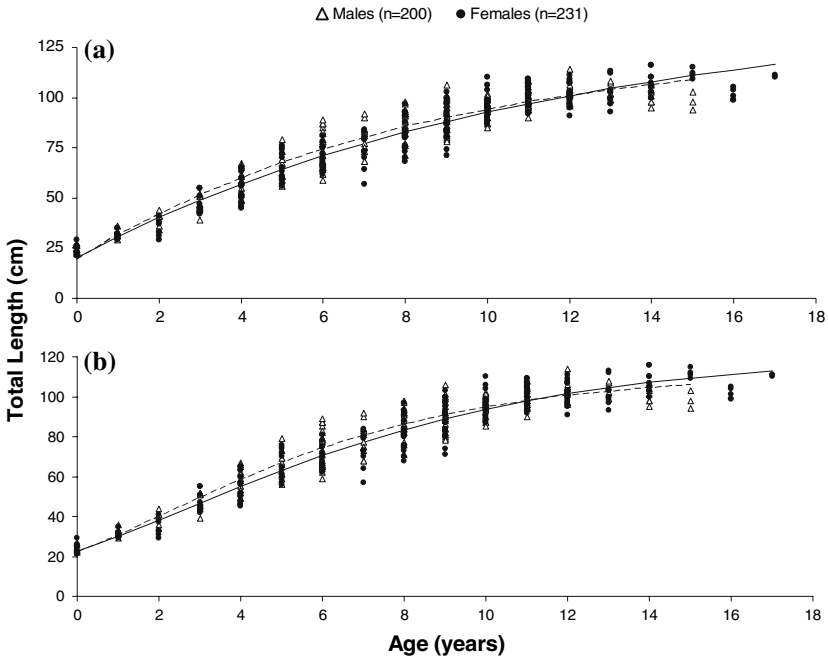

Fig. 6 Three parameter von Bertalanffy (**a**) and Gompertz (**b**) growth functions fit to observed length-at-age data for male (dashed lines) and female (solid lines) *B. parmifera*

Table 2 Parameter estimates and measures of goodness-of-fit from von Bertalanffy and Gompertz growth functions, fit to length-at-age data from males (n = 200), females (n = 231), and both sexes combined (n = 431)

Von Bertalanffy model						
	L_∞ (cm TL)	k (year^{-1})	t_0 (year)	L_0 (cm TL)	r^2	MSE
Males	126.29	0.12	–1.39	19.33	0.916	43.98
	[116.92–135.66]	[0.098–0.14]	[–1.78–(–0.98)]			
Females	144.62	0.087	–1.75	20.48	0.928	46.17
	[131.31–157.93]	[0.070–0.10]	[–2.18–(–1.33)]			
Both sexes	135.39	0.10	–1.60	20.02	0.921	46.05
	[127.44–143.34]	[0.088–0.11]	[–1.90–(1.30)]			
Gompertz model						
	L_0 (cm TL)	g (year^{-1})	G	L_∞ (cm TL)	r^2	MSE
Males	21.90	0.23	1.63	111.26	0.922	40.56
	[19.03–24.76]	[0.20–0.26]	[1.51–1.74]			
Females	22.54	0.19	1.68	120.51	0.935	42.05
	[20.09–24.98]	[0.17–0.21]	[1.59–1.77]			
Both sexes	22.50	0.21	1.64	115.99	0.927	42.67
	[20.62–24.38]	[0.19–0.22]	[1.57–1.71]			

Numbers in brackets are 95% confidence intervals for parameter estimates, and MSE is mean squared error of the residuals for each model fit. Predicted average length at age zero (L_0) and asymptotic length (L_∞) were estimated after fitting the von Bertalanffy and Gompertz functions, respectively

Longevity and natural mortality

Observed estimates of maximum age (T_{max}) were 15 years for males and 17 years for females. Using Hoenig's method (1983), estimates of natural mortality (M) based on T_{max} were 0.25 for females and 0.28 for males. Estimates of M based on the von Bertalanffy growth coefficients (Jensen 1996; Gunderson et al. 2003) were 0.14 for females (approximate 95% CI = 0.11, 0.17) and 0.19 for males (approximate 95% CI = 0.15, 0.23). Estimates of natural mortality using Jensen's method (1996) and

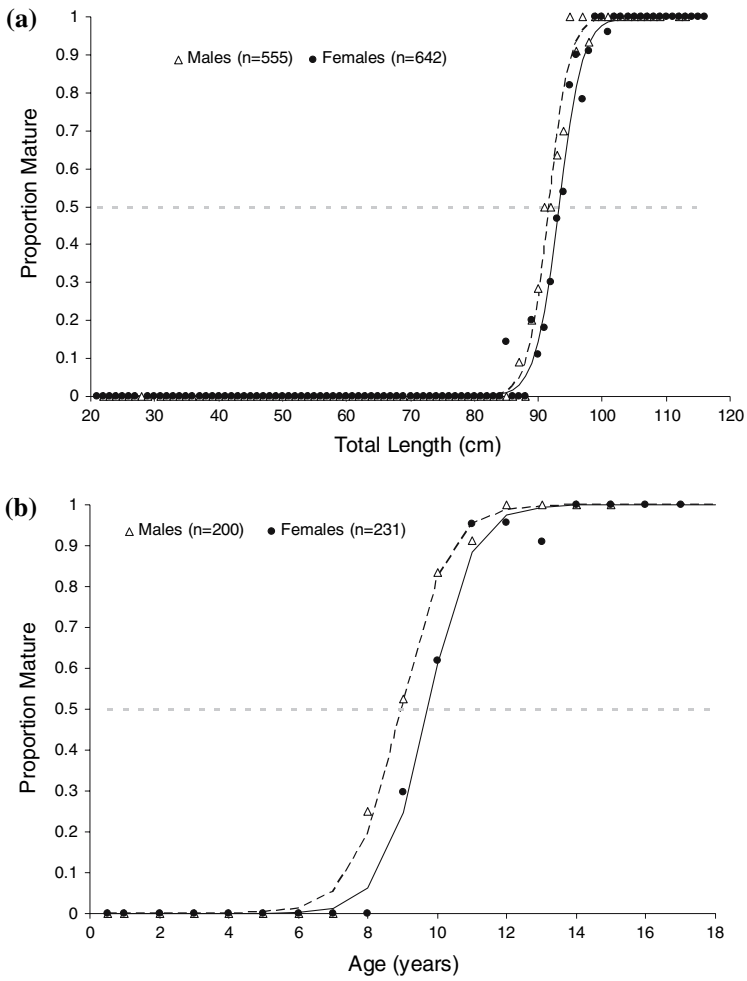

Fig. 7 Maturity ogives for (**a**) length and (**b**) age of male (dashed lines) and female (solid lines) *B. parmifera*

age at 50% maturity were similar: *M* was 0.17 for females and 0.18 for males.

Discussion

The appropriateness of using both vertebrae and caudal thorns as ageing structures for the Alaska skate is supported by the strong relationships between TL and VR and between TL and TBL. The average TL back-calculated from the birthmark increment in vertebral thin sections was very close to independent estimates of length at birth derived from the smallest free-swimming individuals and from late-stage embryos. Identification of the birthmark increment thus appeared to be accurate and consistent across specimens.

Agreement between age estimates generated from caudal thorns and vertebral thin sections was high, suggesting that thorns may be a suitable alternative to vertebrae as an ageing structure for *B. parmifera*. Thorns are much easier and faster to collect at sea, and require little storage space aboard a vessel and less processing time in the laboratory. Additionally, their removal likely causes minimal mortality, although the potential of thorns as truly non-lethal ageing structures must be studied in more detail. Caudal thorns may have application to other skate age and growth studies, and their usefulness should be tested on a species-by-species basis.

The measures of precision reported here, specifically the values of APE and CV, were consistent with other elasmobranch studies. Campana (2001) reported that CVs from shark age studies rarely fall below 10%; thus the precision of our age estimates was considered acceptable.

Both readers found interpretation of ageing structures to be moderately difficult, and a long training period was required for readers to feel confident in their age estimates. Nevertheless, bias between readers was not evident from visual inspection of the age bias plot.

Edge and marginal increment analyses indirectly validated vertebral age estimates by supporting the assumption of annual band pair deposition in *B. parmifera*. The assumption of predictable and temporally regular band deposition must be tested in elasmobranch ageing studies, as at least one species has been shown to lay down bands inconsistently (Natanson and Cailliet 1990). Edge and marginal increment analyses are among the simplest ways to indirectly validate age estimates, at least for younger fish, since direct methods such as tagging studies and captive rearing often require a great deal of time and funding to obtain results. MIA is generally more successful when applied to specimens that are still in a rapid state of growth (Campana 2001). For this study, MIA was performed on immature specimens from only a few age classes (5–8 years) due to the difficulty associated with quantitatively measuring vertebral growth in mature individuals; however, edge analysis was possible for all age groups. Since edge analysis and MIA yielded similar results, it was assumed that older individuals follow a similar pattern of growth to younger individuals. However, validation of absolute age, using methods such as mark-recapture or captive rearing of fish from hatching, should remain a goal of future research (Campana 2001; Cailliet and Goldman 2004).

Approximately half of the skates included in this analysis were collected through fishery-dependent sources (longliners). Consequently, the sample length distribution is biased, likely due to gear selectivity or to selective retention of larger, more commercially valuable individuals. However, age estimates were generated for a number of very small skates, including young-of-the-year, and both growth models had intercepts that passed very close to the known size at hatching. Thus the skewed length distribution is not believed to present a problem with regard to estimates of growth. The maximum length observed in this study for male and female Alaska skates (118 and 119 cm TL, respectively) is greater than the maximum length previously reported (Ebert 2005). There was little difference between males and females in terms of maximum observed length, although there were generally more large females than males.

The von Bertalanffy and Gompertz models both provided highly significant and reasonable fits to the observed length-at-age data. Many authors have pointed out weaknesses in the von Bertalanffy function and its application to fish growth, yet due to its prevalence in the literature, it still has some utility for comparison with other studies (Haddon 2001). An increasing number of elasmobranch studies are using forms of the Gompertz model to describe growth, especially for batoids (Cailliet and Goldman 2004; Carlson and Baremore 2005; Neer and Thompson 2005). Biologically meaningful parameters can be derived from both the Gompertz function and the von Bertalanffy function, including length at age zero (which approximates length at birth) and asymptotic length. In the case of the Alaska skate, both models appear to describe the early years of growth similarly, passing through the *y*-axis very close to the independent estimates of length at birth. However, the Gompertz model had the best overall fit to the data, based upon statistical criteria (r^2 and MSE) and reasonable parameter estimates. For both models, the differences in parameter estimates between the sexes appear to be very small based upon visual examination of the curves and are most likely related to the slight difference in maximum observed age for males and females.

Length at 50% maturity (L_{50}) occurred at approximately 78% of the maximum observed TL for both males and females. There was no significant difference between males and females with respect to size at maturity, as evidenced by overlapping confidence intervals for L_{50}. Age at maturity (T_{50}) occurred at approximately 60% of the observed maximum age for both males and females, falling within but near the late end of the continuum for batoids (Zeiner and Wolf 1993; Walmsley-Hart et al. 1999; Francis et al. 2001; Neer and Cailliet 2001; Sulikowski et al. 2003, 2005; Neer and Thompson 2005; McFarlane and King 2006). Maximum observed age also fell

within the observed range for skates (Cailliet and Goldman 2004), suggesting that *B. parmifera* has moderate longevity when compared with other species. It is possible that older individuals are present within the population; however, our sample included large individuals, including some larger than the previous maximum reported size. Thus, we feel it is not likely that maximum age would increase substantially with additional sampling.

The methods of Hoenig (1983) and Jensen (1996) produced estimates of natural mortality ranging from 0.18 to 0.28 for males, and from 0.14 to 0.25 for females. These estimates are based on maximum age, von Bertalanffy growth coefficients, and age at maturity observed in this study. In this case, M should be interpreted with caution, as the assumed relationships from which M has been indirectly derived are based primarily on teleost fishes. Future studies should strive to obtain direct estimates of M, possibly through mark-recapture studies or from catch curves.

This study is among the first to describe the biology of *Bathyraja parmifera* in detail. As our knowledge of this species continues to improve, it will be possible to assess demography, stock structure, and population dynamics. Genetic studies have been planned to determine whether multiple populations of *B. parmifera* exist across its range (Michael Canino, Alaska Fisheries Science Center, personal communication) and if this is indeed the case, examination of potential differences in life history parameters among stocks will be necessary.

This species currently experiences relatively low exploitation rates since it is only caught incidentally in the EBS, although it could potentially become the target of a directed fishery in the future, owing to its abundance and large body size. Relative biomass of this species in the EBS has averaged around 400,000 metric tons over the past eight years (Matta et al. 2006). While it is difficult to determine the actual annual catch rate of *B. parmifera* in the EBS, since species composition of the skate catch must be derived from fishery observer estimates, it likely does not exceed 6% of biomass estimates (Matta et al. 2006). Ecosystem model simulations indicate that fishing pressure is a greater source of mortality for *B. parmifera* than predation, as this species has few natural predators in the EBS (Gaichas et al. 2005). Additionally, the mortality of discarded skates is unknown and likely varies with the handling process. Future work may elucidate potential ecosystem effects related to *B. parmifera* removal, sources of natural and human-induced mortality, and levels of fishing mortality required for sustainability.

Charnov (2002) showed that relative age at maturity (T_{50} relative to T_{max}) is one of the three critical life history variables differentiating major vertebrate taxa. Relative age at maturity clearly distinguishes elasmobranchs from teleosts. Stock assessment and management methods that have traditionally been used for teleosts may not be appropriate for elasmobranchs due to the differences in life history patterns. The Alaska skate, like most elasmobranchs, appears to have moderate longevity, late maturity relative to T_{max}, and slow to moderate growth. These life history characteristics, coupled with other aspects of the reproductive biology of the Alaska skate (Matta 2006), suggest that this species could only support a directed fishery with limited catch rates, should one develop (Hoenig and Gruber 1990; Musick et al. 2000; King and McFarlane 2003).

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