Life history of *Bathyraja trachura* from the eastern Bering Sea, with evidence of latitudinal variation in a deep-sea skate species

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Although many skates possess life history characteristics that may make them vulnerable to exploitation, the detailed biological information needed to enact effective management schemes is lacking for most species. The objectives of this study were to provide age, growth, and maturity estimates for the roughtail skate, Bathyraja trachura, *from the eastern Bering Sea. Maximum age was estimated at 36 yr based on band pair counts in vertebral centra. Of the four growth models applied, the logistic model provided the best description of growth (asymptotic total length = 911 mm; growth coefficient = 0.131 yr^{-1}). There was no evidence of difference in growth between males and females. Females attained maturity at larger sizes and older ages than males. The median size-at-maturity was estimated at 741 mm total length (TL) for males and 796 mm TL for females; median age-at-maturity was estimated at 21.1 yr and 24.7 yr for males and females, respectively. The results of this study may indicate a latitudinal pattern in size and growth, with individuals from the eastern Bering Sea growing more slowly and reaching higher maximum ages than previously reported for specimens collected off the western coast of the continental United States.*

INTRODUCTION

In recent years, skates have received increased attention in light of population declines and local extirpations of once-common species (Brander, 1981; Dulvy *et al.*, 2000). While considerable research effort has been directed at commercially important, shelf-dwelling species, much less effort has been expended upon deep-sea skates. Deep-water species of some groups have been shown to attain greater maximum ages than their shallow-dwelling counterparts, which translates to lower productivity and hence greater susceptibility to overfishing (Cailliet *et al.*, 2001; García *et al.*, 2008). In combination with documented declines in skate stocks in several regions, the current trend of fisheries' expansion into deeper waters (Koslow *et al.*, 2000; Haedrich *et al.*, 2001; Roberts, 2002; Morato *et al.*, 2006) underscores the need to direct research effort towards the collection of basic life history information for poorly known, deep-dwelling members of skate assemblages.

Directed skate fisheries have developed in Alaskan waters in the past decade (Gburski *et al.*, 2007; Kenneth J. Goldman, Alaska Department of Fish & Game, personal communication), but the species-specific catch and life history data required to inform management are sparse. Until recently, skates in the eastern Bering Sea (EBS) were managed as a complex of 'other species' comprised several biologically discrete taxonomic groups, including sharks, sculpins, squid and octopus (Ebert *et al.*, 2009). Beginning in 2011, skates were removed from the 'other species' category and are currently managed as a separate aggregate complex (Ormseth *et al.*, 2010). Though this is an improvement over previous practices, results of studies conducted to date suggest that Alaskan skate species vary widely in maximum ages and ages-at-maturity, indicating high potential for shifts in assemblage structure in response to fishing pressure (McFarlane & King, 2006; Ebert *et al.*, 2007, 2008a, 2009; Gburski *et al.*, 2007; Matta & Gunderson, 2007). Life history parameter estimates are available for nine of the fifteen known members of the Alaskan skate assemblage (McFarlane & King, 2006; Ebert *et al.*, 2007, 2008a, 2009; Gburski *et al.*, 2007; Matta & Gunderson, 2007) but have yet to be produced for the deepest-dwelling species.

The roughtail skate, *Bathyraja trachura*, occurs in the EBS along the deep shelf and upper continental slope at depths of

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up to 2550 m (Ebert, 2003). The species has a relatively large geographical distribution in the eastern North Pacific (from northern Baja California to the Bering Sea) and is taken as by-catch in groundfish fisheries throughout its range, yet little information regarding the species is available in the literature. The only published age and growth study to date provided a maximum age estimate of 20 yr for specimens collected off the western coast of the continental USA (Davis *et al.*, 2007). Reproductive data are also limited (Ebert, 2005). While the estimates currently available do provide a rough estimate of the relative productivity of the species, its large range of distribution indicates a high probability of geographical variation in life history parameters (Lombardi-Carlson *et al.*, 2003; Frisk & Miller, 2006; Licandeo & Cerna, 2007; McPhie & Campana, 2009). Therefore, age estimates for *B. trachura* from the EBS are required to reliably assess the species' potential response to exploitation at the northern extent of its range.

This study addresses a gap in knowledge about the Alaskan skate assemblage by providing life history parameter estimates for *B. trachura*. Specifically, the objectives of this study were to determine the age and growth characteristics and estimate the size- and age-at-maturity of the species in the EBS. Results are compared with those previously reported for the species near the southern end of its range from the California Current (CC) ecosystem. Potential management implications are also discussed.

MATERIALS AND METHODS

Field sampling

Bathyraja trachura specimens were collected during fishery-independent surveys conducted in the EBS between June and August 2004 as part of the biannual National Marine Fisheries Service, Alaska Fisheries Science Center's (NMFS-AFSC) Eastern Bering Sea Continental Slope survey. The survey covered the EBS from an area north-west of Unalaska Island ($55^{\circ}95'$N $168^{\circ}92'$W) to the Navarin Canyon ($60^{\circ}16'$N $179^{\circ}68'$W) near the US–Russian border. Specimens were collected during 30 min bottom trawls (poly Nor'Eastern high-opening trawl equipped with mud-sweep roller gear and 127 mm stretched-mesh netting with a 32 mm mesh codend liner; Hoff & Britt, 2005) at depths of 624–1138 m. Trawl location was determined using a random stratified sampling design of the area with 83 pre-determined bottom trawl stations (Hoff & Britt, 2005). Location, depth of capture, and temperature were recorded for each haul. One additional sample was obtained from the same area during October 2007 by Jerry Hoff (Fishery Biologist, NMFS-AFSC).

Morphometric measurements taken at the time of collection included total length (TL, measured from the tip of the snout to the tip of the tail), disc width (DW), and total weight (W) when possible. All lengths and widths were recorded to the nearest mm. Total weights were recorded to the nearest 0.01 kg. For ageing, a minimum of ten vertebral centra was excised from a region posterior to the cranium between the 5th and 20th vertebrae and frozen at −20 to −23°C for future processing; vertebral centra were determined to be the most appropriate ageing structure for the species by using the methods of Davis *et al.* (2007).

The TL of four skates could not be directly obtained due to tail damage. To estimate TL for those four specimens, a length conversion equation based on observed DW and TL values was derived. Initial scatterplots of TL and DW indicated a linear relationship. Since skates are sexually dimorphic (Ebert *et al.*, 2008b; Orlov *et al.*, 2010), this relationship may differ between sexes. Therefore, a linear regression model was applied, with TL as the response variable, DW as a linear explanatory variable and sex as a factor. An interaction term between DW and sex was also included to determine whether the slope of this relationship differed between sexes. All analyses were conducted in R (R Core Team, 2012).

Analysis of residuals from the initial regression indicated that variance increased with DW, violating the assumption of homogeneity. Therefore, generalized least squares (GLS) estimation in the R package 'nlme' (Pinheiro *et al.*, 2012) was used to allow for heterogeneity (Zuur *et al.*, 2009). The optimal regression model was identified from all possible model subsets as the model containing only significant terms ($P < 0.05$) with the smallest second-order Akaike information criterion value (AIC$_c$; Akaike, 1973; Burnham & Anderson, 2002). The AIC$_c$ difference (Δ_i) of each model was calculated based on the lowest observed AIC$_c$ value (AIC$_{c,min}$) as

$$\Delta_i = \text{AIC}_{c,i} - \text{AIC}_{c,min}.$$

Models with $\Delta_i < 2$ were considered indistinguishable (Burnham & Anderson, 2002).

Vertebral preparation and age determination

Vertebral centra were collected from 154 *B. trachura* (94 males, 59 females, and one of unknown sex). Histological preparation of vertebrae followed Natanson *et al.* (2007). Frozen vertebrae were thawed, cleaned of excess tissue with a scalpel, separated into individual centra, and fixed in 70% ethanol for a period of at least one month. Samples were then grouped by size and decalcified by immersion in RDO$^{\circledR}$ rapid decalcifying agent. Decalcification was considered complete when a scalpel blade could pass easily through the centrum with no remaining evidence of calcification in the centre. Decalcification times ranged from 47 to 185 min depending on centrum size. Following decalcification, centra were rinsed with flowing water for one hour and stored in 70% ethanol until processing. Decalcified vertebrae were embedded in paraffin wax following a nine-step dehydration process. Embedded centra were sectioned to a thickness of 80–100 μm with a sledge microtome. Sections were stained with Harris haematoxylin and adhered to microscope slides (see Natanson *et al.*, 2007 for details on the embedding and staining processes).

Vertebral sections were viewed and photographed under a dissecting microscope with transmitted light. The birthmark (age 0) was identified as the first distinct mark beyond the focus corresponding with a change in angle of the corpus calcareum (Casey *et al.*, 1985). Periodicity of band pair deposition could not be verified via centrum edge or marginal increment analysis because samples were primarily obtained during the summer. Therefore, each opaque and translucent band pair following the birth mark was interpreted as representing one year of growth, as has typically been assumed

for other skate species (McFarlane & King, 2006; Ebert *et al.*, 2007).

Age estimates were determined using three rounds of independent estimates by one reader (M.V.W.), without prior knowledge about specimen length, sex or previous band pair counts. The spacing and clarity of bands and inflections bordering the intermedialia were used to ensure that true band pairs, rather than 'checks' were being counted. The corpus calcareum arm exhibiting the most complete, distinct banding series was used for all reads; the other three arms were used to corroborate band pair counts in areas where resolution was poor. Individuals exhibiting growth beyond the birthmark but lacking the next subsequent band were aged at 0.5 years for purposes of growth curve fitting. Samples lacking banding patterns or too indistinct to produce consistent results were removed from analysis.

The first read was used as a practice read to familiarize the reader with the species' vertebral banding patterns and ensure that good ageing criteria had been established. Vertebrae for which the last two reads disagreed by more than 3 yr were recounted; if agreement was not achieved after a fourth read, the sample was discarded (Natanson *et al.*, 2007). Final age estimates were assigned based on the third read. To corroborate band pair interpretation, a subsample of 55 sections representative of the species' size range was independently aged by an experienced second reader (J.K.) following the above methodology. Consultation between readers was used to resolve discrepancies in age estimates.

Precision and error analysis

Age estimates were evaluated for reader consistency and repeatability of age assignment for each structure using the coefficient of variation (CV; Chang, 1982). Percentage agreement (PA = 100% × number of agreed reads/total number of reads) was also calculated to determine the precision of age estimates between independent ageing rounds and readers (Beamish & Fournier, 1981; Cailliet & Goldman, 2004). Age-bias plots (Campana *et al.*, 1995) and the Evans–Hoenig test of symmetry (Evans & Hoenig, 1998) were used to determine whether differences between reads were due to systematic bias or random error.

Growth parameter estimation

Length-at-age estimates based upon observed band pair counts were fitted using the Schnute (1981) growth model. The general model requires the specification of two reference ages, t_1 and t_2, and has the following four parameters: L_1, length at age t_1; L_2, length at age t_2; a, a constant (time^{-1}) describing the relative rate of the relative growth rate; and b, a dimensionless constant describing the incremental relative rate of the relative growth rate. Reference ages were set near the lower ($t_1 = 1$ yr) and upper end ($t_2 = 30$ yr) of the range observed.

The general model is specified as:

$$L_t = \left[L_1^b + (L_2^b - L_1^b) \frac{1 - e^{-a(t-t_1)}}{1 - e^{-a(t_2-t_1)}} \right]^{\frac{1}{b}},$$

where L_t = length at time t, $a \neq 0$, $b \neq 0$. The model takes

several forms based on the values of a and b. Not all of the forms (which include linear and exponential growth) were appropriate for our data; therefore we focused on the general model and three special cases, which are equivalent to the specialized von Bertalanffy (VBGF; von Bertalanffy, 1938), Gompertz (Ricker, 1975) and logistic growth models (Ricker, 1979) commonly reported in elasmobranch age and growth studies. The general model is equivalent to the VBGF when $a > 0$ and $b = 1$; it takes the logistic form when $a > 0$ and $b = -1$. When $a > 0$ and $b = 0$, it is equivalent to the Gompertz function and is expressed as:

$$L_t = L_1 e^{\ln\left(\frac{L_2}{L_1}\right) \frac{1 - e^{-a(t-t_1)}}{1 - e^{-a(t_2-t_1)}}}$$

Parameter estimates for each growth function were estimated using non-linear least-squares regression methods in R (R Core Team, 2012). Models with common parameter estimates between sexes were compared to those with separate parameter estimates to determine if there was evidence of difference. While this is typically presented as a two-part analysis in elasmobranch age and growth studies, it is really a question of overall model selection (i.e. does the inclusion of separate parameter estimates for each sex improve model fit, or can growth be sufficiently described using common parameter estimates for both sexes?). Therefore, if the inclusion of separate parameters produced a better fit than the model with common parameters, this was considered evidence of difference between males and females.

Final model selection was based on statistical fit and compatibility with known biological parameters. Model goodness-of-fit was evaluated by the small-sample, bias-corrected form of the AIC$_c$ (Akaike, 1973; Burnham & Anderson, 2002). The AIC$_c$ provides a measure of model fit and complexity and allows for the simultaneous comparison of growth models and their subsets, with the model with the smallest AIC$_c$ value the 'best' out of the suite of models considered. The AIC$_c$ difference (Δ_i) of each model was calculated based on the lowest observed AIC$_c$ value (AIC$_{c,\min}$) as

$$\Delta_i = \text{AIC}_{c,i} - \text{AIC}_{c,\min}$$

to provide an estimate of the magnitude of difference between each model and the best model in the set. Models with values of $\Delta_i < 2$ were considered to have strong support; those with $\Delta_i > 10$ had essentially no support and were omitted from further consideration. Models that differed by less than 2 were considered indistinguishable in terms of fit. To approximate model likelihood, the Akaike weight (w_i) of each model was also calculated (Burnham & Anderson, 2002).

Ninety-five per cent confidence intervals were constructed for parameter estimates via bootstrap methods using the 'nlstools' package in R (Baty & Delignette-Muller, 2011). Residual plots were inspected to ensure the assumptions of homoscedasticity and normality of the error terms were met (Zuur *et al.*, 2009). Parameter estimates typically reported (e.g. asymptotic size, L_∞; theoretical size at birth, t_0) were calculated following Schnute (1981) for comparison with other studies. Length-at-birth (L_o) was estimated from the resulting equation for each growth model.

Table 1. Determination of maturity stages by visual inspection for male and female *Bathyraja trachura*. Modified from Ebert (2005).

Stage	Male	Female
(1) Embryo	In egg case	In egg case
(2) Immature	Claspers flexible and do not extend beyond pelvic fins Undifferentiated testes No coiling of epididymis	Undifferentiated ovaries with no visible follicles No differentiation between oviducal gland and uterus Uterus thin (width <1% of total length), transparent
(3) Maturing	Claspers at or beyond pelvic fins and partly calcified Testes differentiated but not vascularized Somewhat coiled epididymis	Slightly differentiated ovaries with small whitish follicles Some differentiation between oviducal gland and uterus Oviducal gland not well defined in shape or color
(4) Mature	Claspers extend past pelvic fins (>20% of total length) and are highly calcified Testes differentiated, lobular and vascularized Highly coiled epididymis	Vascularized ovaries with yellow, vitellogenic follicles (>12 mm in diameter) Oviducal gland opaque, kidney-shaped, and well differentiated (>5% of total length) from uterus Uterus extended
(5) Gravid	N/A	Egg case(s) present

Maturity

Sex and maturity status were determined in the field by visual inspection of reproductive organs based on Ebert (2005) (Table 1). Embryos in egg cases were assigned to stage 1. Stages 2 and 3 individuals were classified as immature and maturing, respectively. Specimens identified as maturity stages 4 or 5 were considered mature adults. For males, inner clasper length was measured from the insertion of the clasper near the pelvic fin to the tip. Oviducal gland widths of females were measured at the widest point. Yellow, vitellogenic follicles were identified as mature.

Size- and age-at-maturity were estimated using maturity ogives fit to binomial maturity data (0 = embryo/immature/maturing; 1 = mature/gravid). A logistic regression of the following form was fit to binomial maturity data using iteratively reweighted least squares in R (R Core Team, 2012):

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

where Y = the probability of being mature and x = TL in mm or age in years. The median size (TL_{50}) and age (Age_{50}) at which 50% of the population was mature was calculated from the resulting regression parameters as $-a/b$. Ninety-five per cent confidence intervals were also calculated. Sex was incorporated as a factor with or without an interaction term to examine its effect on the probability of maturity. All possible model subsets were evaluated using the AIC_c as described above.

RESULTS

A total of 187 *Bathyraja trachura* specimens were collected for this study (111 males, 75 females, 1 sex unknown). Skates ranged in size from 182 to 942 mm TL (Figure 1). The smallest female was 204 mm TL and the smallest male 182 mm TL. The largest female was 942 mm TL and the largest male 918 mm TL.
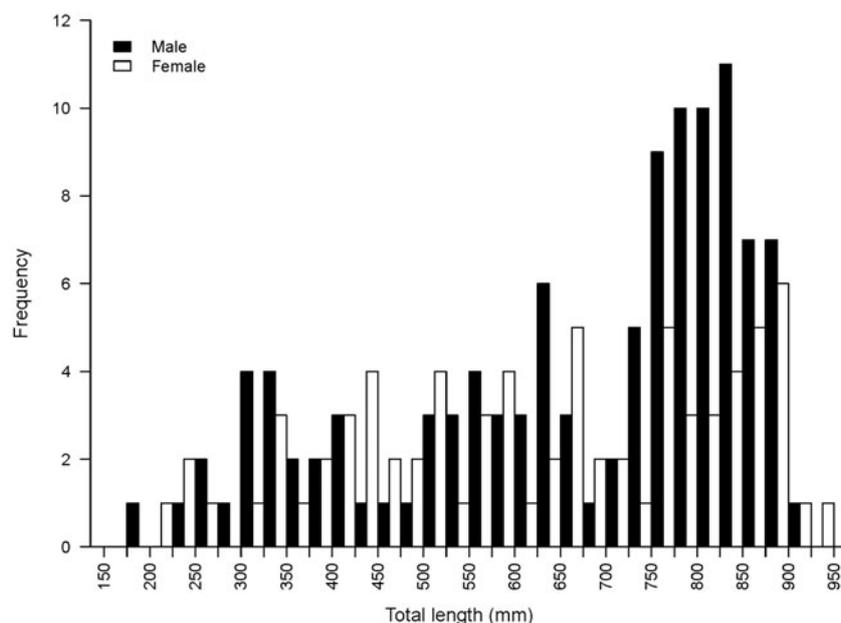
Fig. 1. Size–frequency histogram of male ($N = 111$) and female ($N = 75$) *Bathyraja trachura* sampled from the eastern Bering Sea.

Based on AIC_c values, regression analysis indicated that the optimal DW–TL relationship included DW, sex and the DW–sex interaction term ($N = 182$; Table 2). The AIC_c difference between the optimal model and the regression including only DW as an explanatory variable ($\Delta_{DW} = 28.16$) suggested an effect of sex on this relationship and was indicative of sexual dimorphism in disc shape, with males becoming more 'bell-shaped' than females upon maturation. The DW–TL relationship was described for both sexes as follows:

$$\text{Female: TL} = 1.61(\text{DW}) - 28.38$$

$$\text{Male: TL} = 1.52(\text{DW}) - 5.79$$

Age determination

Final age estimates were determined from 142 specimens (86 males, 55 females, 1 sex unknown). Of the original 154 samples collected and prepared for ageing, 12 sections (7.8%) were excluded from analysis due to problems with processing, indiscernible banding patterns or lack of agreement of independent age estimates. Growth bands consisted of wide translucent bands separated by narrow opaque bands

Table 2. Parameter estimates for the regression model describing the relationship between disc width (DW) and total length (TL) ($N = 182$).

Parameter	Value	SE	*t* value	*P* value
Intercept	−28.38	6.00	−4.72	<0.001
DW	1.61	0.02	103.36	<0.001
Sex (female = 0; male = 1)	22.59	7.80	2.90	0.004
DW*sex	−0.09	0.02	−4.47	<0.001

SE, standard error; *, indicates interaction term.

(Figure 2). Banding patterns were not visible across the intermedialia in most specimens; therefore, band counts were based on the corpus calcareum. Observed ages ranged from 0 to 36 yr, with a maximum age estimate of 35 yr (827 mm TL) for males and 36 yr (889 mm TL) for females. The largest male (918 mm TL) and female (942 mm TL) had 34 and 31 band pairs, respectively.

Precision and error analysis

Precision among age estimates was deemed acceptable (CV = 4.5%). Overall percentage agreement was high, with 95.1% of all reads falling within ±3 yr. An age-bias plot indicated no appreciable bias between reads until age 20, after which age estimates became more variable and read 3 produced consistently lower estimates (Figure 3A); the Evans–Hoenig test of symmetry also suggested bias ($\chi^2 = 35.36$, df = 5, $P < 0.001$). Though differences in age estimates were generally small, they occurred in the same direction, with read 3 producing slightly lower band pair counts than read 2.

Inter-reader agreement among age estimates indicated consistency in band pair interpretation (CV = 5.5%). Most reads (92.7%) agreed within ±3 yr and all within ±5 yr. Both age bias plots (Figure 3B) and the Evans–Hoenig test of symmetry ($\chi^2 = 7.11$, df = 4, $P = 0.13$) provided no evidence of appreciable bias between readers.

Growth parameter estimation

The general form of the Schnute model and the logistic model with common parameter estimates for both sexes were well supported based on the available data ($\Delta_i < 2$; Table 3). Both versions of the von Bertalanffy as well as the Gompertz including separate parameter estimates for each sex had little to no support ($\Delta_i > 10$). Incorporating separate parameter estimates for males and females did not improve fit over the model using common parameter estimates for any
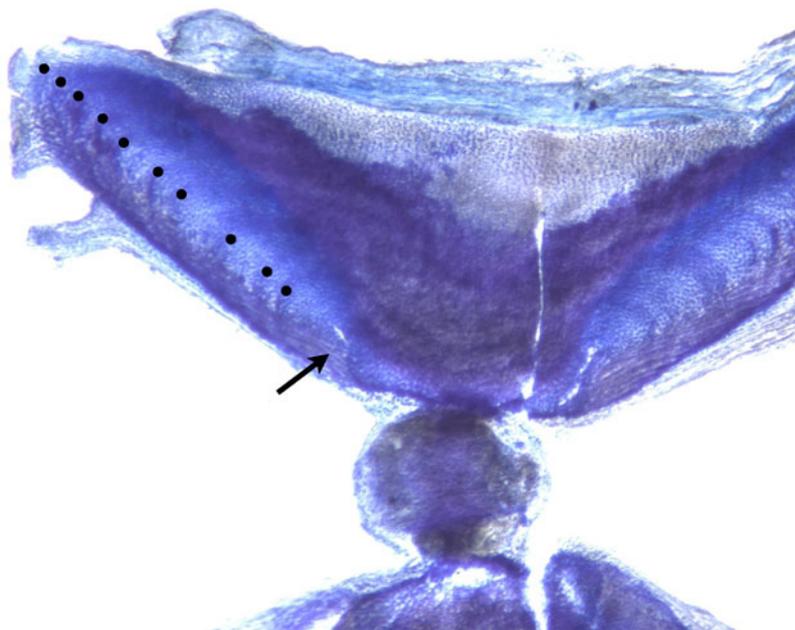
Fig. 2. Vertebral section from a *Bathyraja trachura* specimen. The arrow signifies the birthmark (age 0). Subsequent black circles indicate opaque bands. This 430 mm female had an estimated age of 10 years.
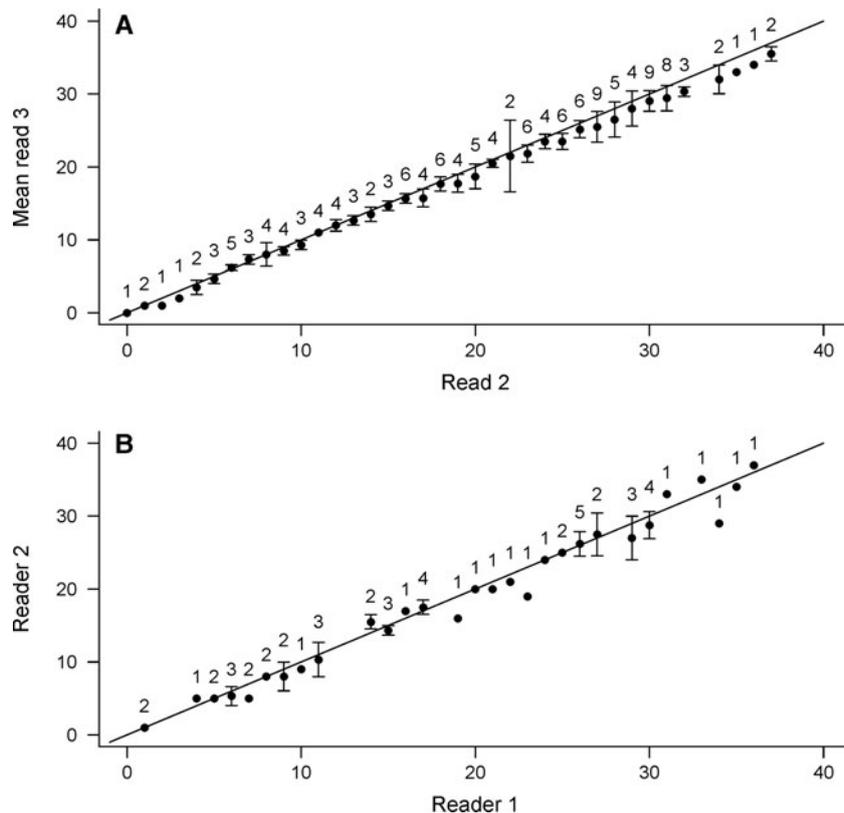
Fig. 3. Age bias plot between (A) independent reads of *Bathyraja trachura* vertebral sections ($N = 142$) by the primary study reader and (B) between readers ($N = 55$). The 45° line represents 1:1 agreement between band counts. Error bars indicate 95% confidence intervals. Sample sizes are indicated above each age-class.

individual growth curve (Table 3); therefore sexes were pooled for final curve fitting (Table 4). While the Gompertz model did produce biologically reasonable estimates (Table 4), it was not as strongly supported based on AIC$_c$ values ($\Delta_{\mathrm{Gompertz}} = 6.21$).

The general Schnute model was technically the best fitting with the absolute lowest AIC$_c$ value (Table 3). However, it produced less realistic parameter estimates than the logistic model, which was indistinguishable in terms of fit ($\Delta_i < 2$; Burnham & Anderson, 2002). The Schnute model produced an inflated estimate of $L_o = 213$ mm TL. The reported birth size of the species is approximately 160 mm TL (Ebert,

Table 3. Relative goodness-of-fit for each candidate growth model for *Bathyraja trachura* from the eastern Bering Sea. Models are ranked from best to worst fitting. +Sex indicates the incorporation of separate parameter estimates for males and females; all other models included common parameter estimates for both sexes.

Model	k	AIC$_c$	Δ_i	w$_i$	LL
Schnute	5	1,567.02	0.00	0.48	−778.29
Logistic	4	1,567.51	0.48	0.38	−779.61
Schnute + Sex	9	1,571.19	4.17	0.06	−775.91
Logistic + Sex	7	1,571.39	4.37	0.05	−778.28
Gompertz	4	1,573.23	6.21	0.02	−782.47
Gompertz + Sex	7	1,577.99	10.97	0.00	−781.57
von Bertalanffy	4	1,584.40	17.38	0.00	−788.05
von Bertalanffy + Sex	7	1,590.17	23.14	0.00	−787.66

k, total number of regression parameters; AIC$_c$, second-order Akaike information criterion; Δ_i, Akaike difference; w$_i$, Akaike weight; LL, log likelihood.

2003), and the sole specimen with an estimated age of 0 yr in this study had a TL of 182 mm. It also resulted in the lowest estimate of $L_\infty = 871$ mm TL. While the confidence bounds of the parameter estimates did include more reasonable values, parameter estimates for the logistic model were closer to known values. Therefore, the logistic model was deemed the most appropriate description of growth based on both statistical fit and biological plausibility (Figure 4).

Maturity

Maturity status was assigned to 111 males at the time of collection. Roughly half of the males sampled were mature ($N = 52$; 46.8%). The smallest mature male measured 710 mm TL and the largest immature male 821 mm TL. Inner clasper lengths ranged from 9 to 231 mm ($N = 111$; TL: 182–918 mm); all mature males had inner clasper lengths greater than 160 mm.

A little more than a quarter of the 75 females collected were mature ($N = 20$; 26.7%), six of which were gravid. The TL of the smallest mature and largest immature female was 740 mm and 880 mm, respectively. Oviducal gland widths ranged from 3 to 71 mm ($N = 63$; TL: 249–942 mm); all mature females had oviducal widths greater than 22 mm.

According to the optimal logistic regression model based on AIC$_c$ values ($N = 186$; Table 5), the probability of maturity-at-size and -age depended on sex, suggesting difference between males and females. Males matured at smaller sizes and ages than females (Table 6; Figure 5). Based on maturity ogives, TL$_{50}$ was estimated at 741 mm (95% CI:

Table 4. Growth model parameters for *Bathyraja trachura* based on age estimates from vertebral sections. All models were parameterized as special cases of the general Schnute (1981) growth model. More commonly presented parameter estimates are also included. Ninety-five per cent bootstrap confidence intervals for each parameter are indicated in parentheses below when relevant. All lengths presented are given in mm.

Model	a	b	l_1	l_2	L_∞	L_o	t_o
Schnute	0.205	−2.642	230	844	871	213	–
	(0.112–0.356)	(−5.770–−0.618)	(192–260)	(823–864)	(836–945)	(172–245)	
Logistic	0.131	−1	207	847	911	186	–
	(0.11–0.151)		(179–234)	(830–866)	(875–962)	(159–214)	
Gompertz	0.086	0	187	850	975	162	–
	(0.070–0.101)		(158–220)	(832–869)	(919–1,057)	(132–195)	
von Bertalanffy	0.038	1	170	854	1193	130	−3.030
	(0.025–0.050)		(127–213)	(836–872)	(1060–1487)	(79–181)	(−5.148–−1.572)

a, a constant (yr^{-1}) describing the relative rate of the relative growth rate; b, a dimensionless constant describing the incremental relative rate of the relative growth rate; l_1, estimated length at age 1; l_2, estimated length at age 30; L_∞, asymptotic total length; L_o, length at birth; t_o, theoretical time at which the fish would have a length of 0 mm.
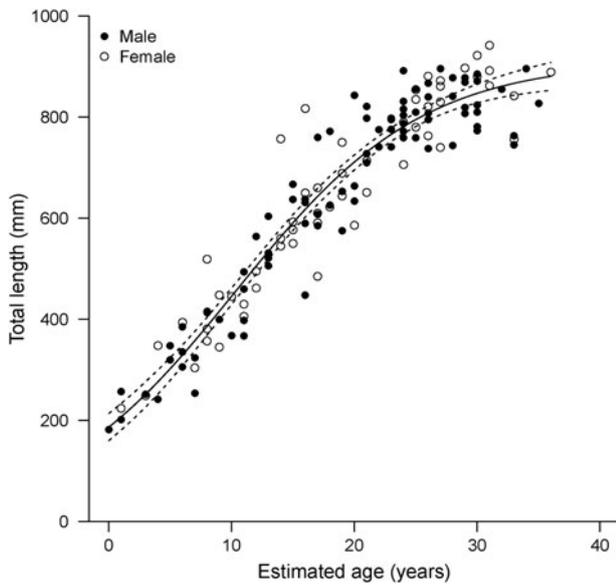
Fig. 4. Logistic growth model fitted to length-at-age data derived from band pair counts in vertebral sections ($N = 142$) for combined sexes of *Bathyraja trachura* from the eastern Bering Sea. Dotted lines indicate 95% bootstrap confidence intervals.

Table 5. Relative goodness-of-fit for each candidate size-at-maturity model based on (A) total length (TL) and (B) age. Models are ranked from best to worst fitting.

Model	k	AIC_c	Δ_i	w_i	LL
(A)					
TL + Sex	3	84.93	0.00	0.69	−39.40
TL*Sex	4	86.86	1.93	0.26	−39.32
TL	2	90.52	5.59	0.04	−43.23
(B)					
Age*Sex	4	76.19	0.00	0.83	−33.95
Age + Sex	3	79.60	3.40	0.15	−36.71
Age	2	83.96	7.76	0.02	−39.93

k, number of parameters; AIC_c, second-order Akaike information criterion; Δ_i, AIC_c difference; w_i, Akaike weight; LL, log likelihood; +, indicates incorporation of a factor; *, indicates incorporation of an interaction term.

Table 6. Parameter estimates for the optimal model describing the relationship between maturity and (A) total length (TL) and (B) age.

Parameter	Value	SE	z value	P value
(A)				
Intercept	−23.91	4.33	−5.52	<0.001
TL	0.03	0.01	5.59	<0.001
Sex (female = 0; male = 1)	1.66	0.63	2.65	0.01
(B)				
Intercept	−7.15	1.91	−3.74	<0.001
Age	0.29	0.08	3.70	<0.001
Sex (female = 0; male = 1)	−7.41	4.35	−1.70	0.09
Age*sex	0.40	0.20	2.04	0.04

SE, standard error; *, indicates interaction term.

710–764 mm) for males and 796 mm (95% CI: 762–828 mm) for females. In terms of age, males and females attained maturity at 21.1 yr (95% CI: 19.4–22.5 yr) and 24.7 yr (95% CI: 21.6–28.3 yr), respectively.

DISCUSSION

The maximum age estimate for *Bathyraja trachura* from the EBS (36 yr) is among the highest reported for a skate species to date, with corresponding growth coefficients among the lowest (Cailliet & Goldman, 2004; Gallagher *et al.*, 2005; Gedamke *et al.*, 2005; Sulikowski *et al.*, 2005; Frisk & Miller, 2006; Licandeo *et al.*, 2006; Davis *et al.*, 2007; Ebert *et al.*, 2007, 2009; Gburski *et al.*, 2007; Natanson *et al.*, 2007; Arikhipkin *et al.*, 2008; Ainsley *et al.*, 2011). Overall, age estimates and growth coefficients for *B. trachura* are most similar to those reported for other deep-dwelling bathyrajid species from the EBS (Table 7). Several studies have suggested that size is linked with life history correlates in skates and therefore may be indicative of a species' potential susceptibility to overexploitation (Dulvy *et al.*, 2000; Frisk *et al.*, 2001; Dulvy & Reynolds, 2002). In terms of the Alaskan skate assemblage, it appears that longevity, and hence vulnerability, may scale with depth rather than species' size. This trend has been previously observed among deep-water bony fish and chondrichthyans (Cailliet *et al.*, 2001; García *et al.*, 2008) and may be related to the
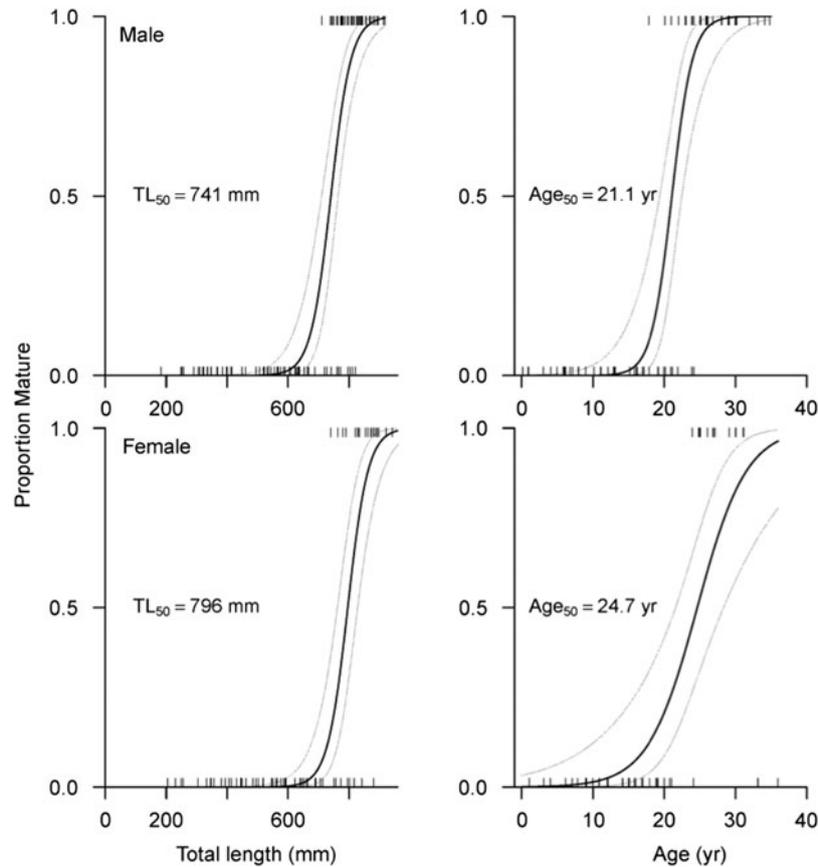
Fig. 5. Estimated probability of maturity-at-size and -age based on maturity ogives for male and female *Bathyraja trachura* from the eastern Bering Sea. Rug plots indicate individual skates. The median size- (TL_{50}) and age-at-maturity (A_{50}) for each sex is indicated. Dashed lines correspond to 95% confidence intervals.

reduced metabolic rates of deep dwellers (Childress, 1995). For Alaskan bathyrajids that have been aged to date, slope-dwelling species live longer and mature later than those that inhabit the shelf.

Banding patterns in *B. trachura* were relatively difficult to interpret due to the poor vertebral calcification typical of deep-water elasmobranch species (Cailliet *et al.*, 2001; Gennari & Scacco, 2007). The full histological approach has been used in only a handful of studies due to equipment, time and cost requirements (Ishiyama, 1951; Natanson &

Cailliet, 1990; Natanson, 1993; Natanson *et al.*, 2007). However, the enhancement of banding patterns and subsequent reduction in the difficulties associated with ageing rendered the more time- and cost-intensive histological process worthwhile for *B. trachura*.

Despite the difficulties experienced with vertebral interpretation, age estimates were comparable between readers and precision was high. The lack of bias between study readers indicated consistency of band pair interpretation in vertebral sections. The bias exhibited by the

Table 7. Summary of available age, growth and maturity data for members of the Alaskan skate assemblage. Three parameter von Bertalanffy growth function parameters are presented for the sake of comparison. Habitat type was based on Ormseth *et al.* (2010). All lengths presented are in cm; ages are in yr. Median size- and age-at-maturity estimates are presented separately for each sex (female estimate/male estimate).

Species	Habitat	TL_{max}	Age_{max}	TL_{50}	Age_{50}	L_{∞}	k	t_o	Reference
Bathyraja aleutica	Shelf/Slope	150	17	124/123	10/10	173	0.11	−1.78	Ebert *et al.* 2007
B. lindbergi	Slope	102	33	79/80	19/17	119	0.04	−2.63	Ebert *et al.* 2009
B. maculata	Shelf/Slope	134	36	95/93	23/21	170	0.02	−5.41	Ebert *et al.* 2009
B. minispinosa	Slope	90	37	67/70	24/23	147	0.02	−5.76	Ainsley *et al.* 2011
B. parmifera	Shelf	111	17	93/92	10/9	135	0.10	−1.60	Matta & Gunderson, 2007
B. taranetzi	Shelf/Slope	77	14	63/58	9/10	78	0.13	−1.90	Ebert *et al.* 2009
B. trachura	Slope	94	36	80/74	25/21	119	0.04	−3.03	This study
Beringraja binoculata	Shelf	214	26	90/72	8/6	293	0.04	−2.01	McFarlane King, 2006; Ebert *et al.* 2008a
Raja rhina	Shelf	125	26	83/65	10/7	134	0.07	−1.92	McFarlane King, 2006; Ebert *et al.* 2008a
Rhinoraja interrupta	Shelf/Slope	86	13	70/68	8/7	126	0.08	−2.32	Ebert *et al.* 2007

TL_{max}, maximum observed total length; Age_{max}, maximum observed longevity; TL_{50}, median total length at maturity; Age_{50}, median age at maturity; L_{∞}, theoretical asymptotic length; k, von Bertalanffy growth coefficient; t_o, theoretical age at zero length.

primary study reader (M.V.W.) was likely due to the reader becoming increasingly familiar with the species' banding patterns with subsequent reads. Inter-reader precision and bias analyses and final age estimates for the EBS population were based on the primary reader's third count; therefore, the observed bias was deemed inconsequential in light of the lack of bias between readers.

Maturity

Bathyraja trachura matures relatively late in life, with females maturing at greater sizes and ages than males, a pattern often reported among skates (Gallagher *et al.*, 2005; Gedamke *et al.*, 2005; McFarlane & King, 2006; Licandeo & Cerna, 2007). Both sexes reached TL_{50} at over 70% of their maximum observed size, which falls within the range observed for other skates (Ebert, 2005; Ebert *et al.*, 2008b; Frisk, 2010; Ainsley *et al.*, 2011). Median age-at-maturity occurred at approximately 69% of the observed maximum age for females and 59% for males. This supports the results of other studies suggesting that skates have a protracted juvenile stage in comparison with most other elasmobranchs (Cortés, 2000; Ebert, 2005; Frisk, 2010).

Median size-at-maturity estimates reported in this study for *B. trachura* were similar to those previously reported for males, but were larger for females. Ebert (2005) determined that females ($TL_{50} = 735$ mm TL) matured at smaller sizes than males ($TL_{50} = 755$ mm TL) in the EBS. However, sample sizes of both sexes were considerably smaller than in the present study. In both studies, maturity classifications were made at sea and based solely on visual assessment; as a result, the potential for misclassification of maturity cannot be excluded. For example, the largest immature female from this study was the oldest observed specimen and may have been reproductively inactive rather than immature (Ebert, 2005). Future studies should incorporate histological assessment of reproductive tracts to avoid misclassifications, which may cumulatively skew estimates of the size- and age-at-maturity.

Latitudinal variability

The results of this study may indicate a latitudinal pattern in size and growth for the species, with individuals from the EBS reaching higher maximum ages and growing more slowly than previously reported for specimens collected from the CC (Davis *et al.*, 2007). The maximum observed age estimate based on vertebral sections for specimens collected from the EBS was 16 yr older than that reported for the CC by Davis *et al.* (2007). Based on the resulting growth curves derived in the two regional studies, *B. trachura* in the CC have a higher growth rate and consequently reach larger sizes-at-age than in the EBS (Figure 6). Such latitudinal and regional patterns in life histories have often been documented in chondrichthyan fish (Yamaguchi *et al.*, 1998; Lombardi-Carlson *et al.*, 2003; Neer & Thompson, 2005; Frisk & Miller, 2006; Licandeo & Cerna, 2007; McPhie & Campana, 2009).

The results presented do provide evidence of difference in growth between ecosystems; however, it is important to note that these estimates are not directly comparable due to the different vertebral preparation techniques used in both studies. Vertebral sections in this study were prepared using a histological technique; sections from the previous study were examined unstained. Given the difficulties associated with ageing this species, histological preparation of samples used
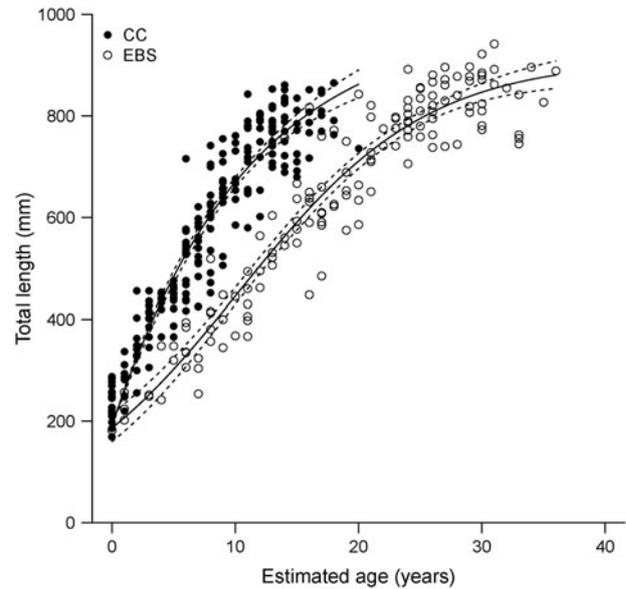

Fig. 6. Regional growth models fitted to length-at-age data derived from band pair counts in vertebral sections for *Bathyraja trachura* from the eastern Bering Sea (EBS, $N = 142$; this study) and California Current ecosystems (CC, $N = 214$; Davis *et al.*, 2007). Dotted lines indicate 95% bootstrap confidence intervals.

in the earlier study would likely result in slightly higher age estimates; age estimates based on histological sections were 5 yr higher, on average, than those based on unstained sections from the same individuals for EBS specimens (M. Winton, unpublished data). Although the differences reported herein may be inflated as a result, maximum age estimates based on unstained sections from the EBS (M. Winton, unpublished data) were still 10 yr older than those reported by Davis *et al.* (2007). Observed regional differences were also unlikely to be due to interpretation error. Comparison of band pair counts for a subset of vertebrae used in the earlier study (Davis *et al.*, 2007) indicated no bias between the two study readers (M. Winton, unpublished data).

Previously reported spatial differences in life history parameters of marine species have been attributed to differences in environmental factors such as temperature (Parsons, 1993; Yamaguchi *et al.*, 2000; Walker, 2007), prey availability (Yamaguchi *et al.*, 2000), exploitation rates (Sosebee, 2005) and discrete breeding populations (Tovar-Ávila *et al.*, 2007). Of the potential factors listed above, environmental differences are likely the most plausible for this species, although the possibility of genetically discrete populations cannot be excluded due to lack of available data. Temperature is strongly related to growth in fish (Neuheimer & Taggart, 2007); long-term but small-scale changes in temperature have been linked to corresponding changes in the growth rate of several deep-dwelling teleost species (Thresher *et al.*, 2007). Bottom temperature values at the depths *B. trachura* inhabits are 4–5°C higher in the CC than the EBS (Keller *et al.*, 2007a, b, 2008; Lauth, 2011), suggesting that temperature may play some role in the differences observed between regions.

Management implications

Given that several elasmobranch species exhibit seemingly random banding patterns that are not directly related to

time (Natanson & Cailliet, 1990; Natanson et al., 2008), demographic analyses and management actions based on the age estimates reported herein will be inherently characterized by a high degree of uncertainty until validation of age estimates is achieved. The use of incorrect ages and resulting growth rates in demographic analyses can lead to errors in estimates of natural mortality rates, population growth rates and management actions based upon those estimates (Beamish & McFarlane, 1983). Therefore, longevity estimates and any models or management actions based upon unvalidated age estimates should be interpreted with caution.

Cortés (2002) proposed a 'fast–slow' continuum of shark life-history characteristics based on the results of age-structured life table and Leslie matrix analyses. Species at the fast end of the continuum were characterized by fast growth, early maturity, short life span and high productivity. Species at the slow end exhibited slow growth, late maturity, high longevity and consequently low productivity. *Bathyraja trachura* is among the longest-lived, latest maturing and slowest growing species reported in the Alaskan skate assemblage to date (Table 7; McFarlane & King, 2006; Ebert et al., 2007, 2008a, 2009; Gburski et al., 2007; Matta & Gunderson, 2007; Ainsley et al., 2011). Thus, in relative terms, *B. trachura* falls near the slow end of the spectrum proposed by Cortés (2002) and will likely be less resilient to fishing pressure than its shelf-dwelling congeners at the faster end of the continuum. Differences in growth parameters observed between the CC and EBS may indicate the presence of distinct populations of *B. trachura* in the eastern North Pacific and should be taken into account when developing regional skate management plans. Future studies should seek to produce validated age and maturity estimates throughout the species' range in the eastern North Pacific to obtain a more complete idea of intra-specific variability in these essential fisheries parameters.

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