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Comparative age and growth of the Aleutian skate, *Bathyraja aleutica*, from the eastern Bering Sea and Gulf of Alaska

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Abstract The Aleutian skate (*Bathyraja aleutica*) is a large deep-water species that commonly occurs in bycatch of Alaskan trawl and longline fisheries. Although prominent in the skate biomass of the eastern Bering Sea (EBS) and Gulf of Alaska (GOA) ecosystems, minimal biological information exists. To increase our understanding of this potentially vulnerable species, and address the possibility of two separate populations in Alaskan waters, the age and growth of *B. aleutica* was studied. Vertebral centra were examined for age determination, and multiple growth models were evaluated to determine growth characteristics. Skates from the EBS attained maximum ages of 17 and 16 years for females and males, respectively, and the two-parameter von Bertalanffy growth functions generated estimates of k = 0.13 yr.-1 and L∞ = 162.1 cm for females, with similar results for males. Skates from the GOA reached 19 years in females and 18 years in males. Growth parameters of female skates from the GOA were estimated as k = 0.11 yr.-1 and L∞ = 160.0 cm, whereas males grew faster, with estimates of k = 0.15 yr.-1 and L∞ = 138.2 cm. The results of this study may indicate the presence of distinct populations of *B. aleutica* in the eastern North Pacific.

Keywords Age · Growth · Skate · *Bathyraja aleutica* · Gulf of Alaska · Eastern Bering Sea

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Introduction

In the eastern North Pacific, skates (Chondrichthyes, Rajiformes) are among the most commonly caught elasmobranchs in commercial groundfish fisheries (Camhi 1999). Skates represent the greatest proportion of incidental biomass landed, accounting for 51–78 % of the estimated totals of "other species" between 1992 and 2009 in the Bering Sea and Aleutian Islands (Ormseth et al. 2008). Species compositions and relative abundance of skate landings, however, remain unknown, as skates historically have been only identified to gross taxa (i.e. "skate unidentified"). This is of concern because many skates exhibit slow growth, low fecundity, and late age at maturity, which may severely restrict their ability to sustain fishing pressure or recover from overexploitation (Holden 1974; Walker and Hislop 1998; Reynolds et al. 2005). Population declines and local extirpations already have been reported for several North Atlantic species (Brander 1981; Casey and Meyers 1998; Dulvy and Reynolds 2002).

Skates have been managed as part of the "other species" category until 2004, when skates in the Gulf of Alaska were moved to a separate target species category. This management change was driven by the onset of directed fishing for skates in 2003 around Kodiak Island where big (*Beringraja binoculata*) and longnose (*Raja rhina*) skates were targeted with some minor harvest of bathyrajids (Mattes and Spalinger 2006). Directed fisheries for skates were prohibited in the Gulf of Alaska in 2005, due to the high levels of incidental catch and uncertainty in commercial catch data (Ormseth and Matta 2010). Incidental catch of skates from the Gulf of Alaska are still retained under big skate, longnose skate, and “other skate” categories (Ormseth and Matta 2010). Although the catch of skates from the Bering Sea and Aleutian Islands was separated from the “other species” category into a single skate complex in 2011, a lack of species-specific catch reporting remains (Ormseth 2012).

The Aleutian skate, *Bathyraja aleutica* (Gilbert 1895), is one of the largest skate species in the North Pacific, reaching about 161 cm total length (TL; Zenger 2004). Distributed throughout the eastern North Pacific, *B. aleutica* ranges from northern Japan to the Bering Sea to southeastern Alaska, and from northern British Columbia to Cape Mendocino (Love et al. 2005). A deepwater skate, it inhabits depths of 15–1602 m, but usually occurs at 100–800 m over the continental shelf and upper slope (Mecklenburg et al. 2002). Among the complex of 12 valid species of *Bathyraja* occurring in Alaska, *B. aleutica* dominates the biomass throughout the Gulf of Alaska (Ormseth and Matta 2010) and on the continental slope in the eastern Bering Sea (> 200 m depth; Ormseth et al. 2008). Essential life history components, including age and growth parameters, have not been estimated for *B. aleutica,* despite its common occurrence in the bycatch of Alaskan fisheries.

Skates are generally considered k-selected or equilibrium strategists, and exhibit variability in their life history parameters that may result in differential susceptibility to fishery exploitation (Walker and Hislop 1998; Agnew et al. 2000). In addition, intraspecific life history traits may be affected by latitude or local environmental conditions. Investigations reporting regional variability in batoids indicate that animals in higher latitudes have larger maximum sizes, slower growth rates and greater longevities than their conspecifics in lower latitudes (Frisk and Miller 2006; Licandeo and Cerna 2007). Regional differences were found in life history parameters for two deep-water rajids between the Gulf of Alaska, British Columbia, and US west coast (Zeiner and Wolf 1993; McFarlane and King 2006; Thompson 2006; Gburski et al. 2007), though these differences did not follow a latitudinal gradient. The eastern Bering Sea and Gulf of Alaska are two large marine ecosystems separated largely by the Aleutian Islands chain, therefore life history traits of *B. aleutica* may differ between regions. Populations in these large marine ecosystems experience differential temperature, ice extent, and productivity that may affect their growth characteristics (NRC 1996; Mundy 2005).

Objectives of this study were to assess the suitability of vertebral centra as appropriate ageing structures for *B. aleutica*; estimate age and growth parameters; and describe and compare growth patterns between the eastern Bering Sea and Gulf of Alaska. This study is the first to provide estimates of age and growth for *B. aleutica* from these two large Alaskan marine ecosystems.

Methods

Sample collection and preparation

Specimens of *B. aleutica* were collected from multiple sources in the eastern Bering Sea (EBS) and Gulf of Alaska (GOA). Skates were collected in the EBS from June to August 2004 during a research trawl survey conducted by the National Marine Fisheries Service Alaska Fisheries Science Center (NMFS-AFSC) along the EBS continental slope (ca. 54° N, 166° W to ca. 61° N, 180° W; Fig. 1) at depths of 194–1169 m (Hoff and Brit 2005). Additional EBS samples were collected during 2004–2006 by NMFS-AFSC staff and fisheries observers. In the GOA, skates were obtained from April 2005 to September 2007 during Alaska Department of Fish and Game (ADFG) and NMFS-AFSC surveys along the Alaskan Peninsula to Kamishak Bay and eastwards to the Kenai Peninsula (ca. 55° N, 160° W to ca. 61° N, 146° W; Fig. 1), at depths of 20–396 m, with much of the survey effort concentrated around Kodiak Island. Samples also were obtained from port sampling of direct and indirect fishery landings on Kodiak Island.

Skates were processed at the time of capture for total length (TL) from snout tip to tail tip (±0.1 cm), disc width (DW) from wing tip to wing tip (±0.1 cm), mass (kg), and sex, and maturity status was assessed following Ebert (2005). A section of at least eight vertebral centra was excised from the region posterior to the cranium between the 5th and 20th vertebral elements,

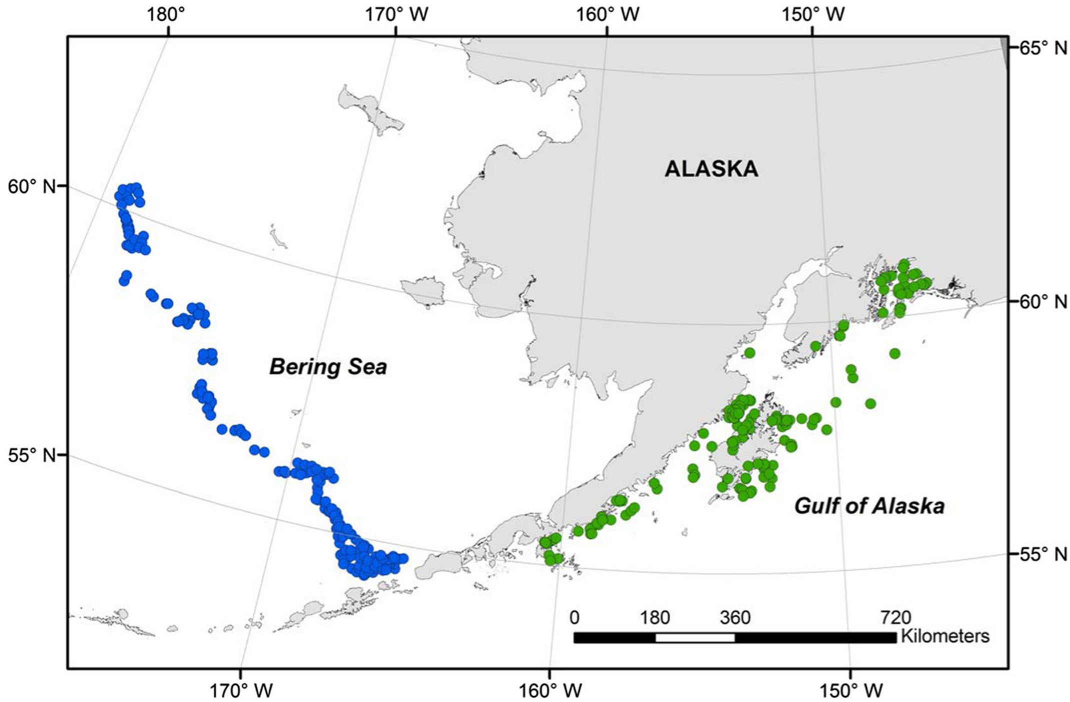


Fig. 1 Map of trawl locations where *Bathyraja aleutica* were collected in the eastern Bering Sea and Gulf of Alaska

and was frozen until processed at Moss Landing Marine Laboratories.

Vertebral sections were cleaned of tissue, soaked with 70 % ethanol, and air-dried. Centrum diameter was measured to the nearest 0.1 mm at two perpendicular axes, and the mean calculated. The mean centrum diameter (MCD) was plotted against TL, and a simple linear regression was performed to verify that vertebrae grew proportionally to body size. The regression was estimated for males and females separately from the EBS and GOA, and were compared using Analysis of Covariance (ANCOVA).

Vertebrae were mounted in polyester casting resin on waxed paper retail tags, and sectioned along the sagittal plane through the focus to a thickness of 0.4 mm using a Buehler® Isomet® 1000 precision saw with double diamond blades. Thin sections were mounted on slides with Cytoseal™ 60 and polished using wet sandpaper of successive grits (grades 600, 800, and 1200) to a thickness of 0.2–0.3 mm.

Age determination

Vertebral sections were examined for the birthmark (age 0) and number of band pairs. The birthmark was defined as the first distinct mark distal to the focus that coincided with an angle and density change in the corpus calcareum (Walmsley-Hart et al. 1999; Sulikowski et al. 2003), and band counts began subsequent to that point. A band pair consisted of a narrow translucent band and a wide opaque band when viewed under transmitted light (Fig. 2; Cailliet et al. 2006). Band pairs have typically been assumed to represent annual growth in skates (Zeiner and Wolf 1993; Sulikowski et al. 2005; Frisk and Miller 2006), and ages were estimated by counting the number of narrow translucent and associated opaque bands. A coat of mineral oil was used to enhance the banding patterns. Mean age estimates from anterior and posterior regions of the vertebral column were compared using a paired sample *t*-test (Zar 1999) to assess if banding patterns differed along the column.

Precision and bias

Analyses of precision and bias were used to assess reproducibility between reads and reader consistency. A single reader in three randomized trials made band counts for each specimen, with at least two weeks between successive reads, and no prior knowledge of sex, length, or previous counts. Final age estimates were assigned based on the agreement of two or more reads. If no agreement was reached in two of the first three

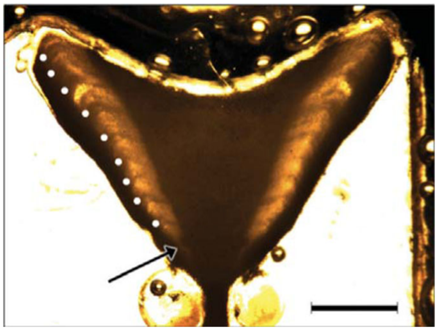


Fig. 2 Vertebral thin section from a 100 cm total length *Bathyraja aleutica* aged to 9 years. Arrow indicates the birthmark, signified by a change in angle and density of the corpus calcareum in the vertebral thin section. Band pairs (i.e. one opaque and one translucent band) are indicated by white dots. Bar =1 mm

reads, a fourth read was made to clarify age estimates. If no agreement could be made after the fourth read, the sample was omitted from further age analysis.

The readability of each sectioned vertebra was assessed with methods similar to Smith et al. (2007), with grade 1 being the lowest clarity and grade 5 the highest. For sectioned vertebrae given a grade 1 or 2, additional vertebrae were sectioned and reexamined. If the readability was still a grade 1, the specimen's vertebrae were excluded from further analysis.

Precision was assessed using index of average percent error (IAPE; Beamish and Fournier 1981) and coefficient of variation (CV; Chang 1982). IAPE for the entire sample set was calculated as:

$$IAPE_j = 100\% * \frac{1}{N}\sum_{j=1}^{N}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{|X_{ij}-X_j|}{X_j}\right]$$

where N is the total number of samples, R is the number of reads per ageing structure, X_{ij} is the i^{th} age determination of the j^{th} ageing structure, and X_j is the mean age determination for the j^{th} ageing structure (Beamish and Fournier 1981). Coefficient of variation (CV) also was estimated for the entire sample set to facilitate comparison with other studies (Chang 1982). This was calculated as:

$$CV_j = 100\% * \frac{\sqrt{\sum_{i=1}^{R}\frac{(X_{i,j}-X_j)^2}{R-1}}}{X_j}$$

where CV_j represents a precision estimate for the j^{th} ageing structure (Chang 1982). Age 0 samples were excluded from precision calculations because they can distort APE estimates (Officer et al. 1996).

Chi-square tests of symmetry (McNemar 1947; Bowker 1948; Evans and Hoenig 1998) using contingency tables tested if differences between reads were due to bias or random error. Percent reader agreement (PA) was used to evaluate intra-reader consistency (Goldman 2004). Age bias plots modified after Campana et al. (1995) were produced to graphically examine variability among paired reads.

Indirect validation

Two methods were used to assess the temporal periodicity of growth band formation in the vertebrae. Marginal increment analysis was performed on vertebral thin sections following Conrath et al. (2002). The marginal increment ratio (MIR) was calculated as:

$$\mathrm{MIR} = \mathrm{MW}/\mathrm{PBW}$$

where the marginal band pair width (MW), or the distance from the last wide opaque band to the edge of the margin, is divided by previous band pair width (PBW). MIR measurements were conducted along the axis of the corpus calcareum using Image Pro Plus software (Media Cybernetics, Silver Springs, MD, USA). The resulting MIR values were plotted against month of capture. Differences in mean MIR among months were assessed using ANOVA (Zar 1999) to test for seasonality of band deposition.

Centrum edge analysis qualitatively compares the relative proportion of individuals with opaque or translucent centrum edges through time to discern seasonal changes in growth (Tanaka and Mizue 1979; Cailliet et al. 2006). The centrum marginal edge was graded into 4 categories, following Smith et al. (2007): narrow opaque band forming (O1), broad opaque band well-formed (O2), narrow translucent band forming (T1), and broad translucent band well-formed (T2). The proportion of edge types was compared for each sampled month to detect seasonal differences in growth. Because age-zero animals do not have fully formed growth bands, they were excluded from validation assessments.

Growth

Four growth models were fit to length-at-age data for males and females at each location. Growth model parameters were estimated using a non-linear least-squares regression and SigmaPlot 11.0 graphical software (SPSS Inc., Chicago, IL, USA). The three-parameter von Bertalanffy growth function (3VBGF; Beverton and Holt 1957) was fitted to the data with the following equation:

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

where L_t = length at age t; L_∞ = asymptotic or maximum length; k = growth coefficient; and t_o = age at theoretical length zero (Ricker 1979). Length at birth (L_0) was then calculated as:

$$L_0 = L_\infty\left(1 - e^{kt}\right)$$

to confirm whether the resulting value falls within the range of observed length at birth (Cailliet et al. 2006).

A two-parameter VBGF (2VBGF), which uses estimates of L_0 and does not require calculation of t_o, was fitted also to the data as it is more biologically meaningful and may provide more robust results (Cailliet et al. 2006; Goldman et al. 2012):

$$L_t = L_\infty - (L_\infty - L_0)e^{-kt}$$

where parameters are as previously defined.

The Gompertz growth function also was fitted to the data, as it has provided the best fit for some batoids (Mollet et al. 2002; Neer and Thompson 2005; Smith et al. 2007). Because of the limited weight data, the Gompertz parameters were estimated by substituting length-at-age data for weight variables using the following form:

$$L_t = L_\infty\left(e^{\left(-ke^{(-gt)}\right)}\right)$$

where L_t, L_∞ and t are as previously defined; k = a constant such that kg is the instantaneous growth rate when t = 0 and $L_t = L_0$; and g = instantaneous rate of growth when t = t_o (Ricker 1979).

Finally, a logistic model (modified from Ricker 1979) was fit to length-at-age data. Logistic parameters were estimated using:

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

where g = instantaneous rate of growth, to the inflection point, and other parameters as previously defined.

Growth model goodness-of-fit was assessed by comparisons of the coefficient of determination (r^2), significance level ($p < 0.05$), and residual mean square error (MSE; Carlson and Baremore 2005; Neer and Thompson 2005). Differences in growth parameters between sexes and locations were tested using Kimura's (1980) likelihood ratio test.

The oldest observed individuals provided initial longevity estimates, however, these are likely to be underestimates in a fished population. Theoretical longevity (ω) was also predicted using parameters derived from the 2VBGF following Taylor (1958); Ricker (1979) and Fabens (1965).

Results

Sample collection and preparation

Vertebral centra of 410 skates from the EBS and 247 skates from the GOA were used for age analysis. Specimens were collected during 10 months, although not from all months within each sampling year. Males from the EBS (n = 87) were 23.9 to 149.9 cm TL, and females (n = 223) 20.6 to 153.4 cm TL. Males from the GOA (n = 112) were 31.5 to 140.1 cm TL, and females (n = 135) 26.0 to 153.6 cm TL (Fig. 3).

The TL to MCD relationship was similar between the sexes within both the EBS (F = 0.600, p = 0.440, n = 157) and the GOA (F = 0.326, p = 0.569, n = 173). The TL to MCD relationship for each location was described by a linear function (EBS: TL = 6.593 + 14.671MCD, r^2 = 0.973; GOA: TL = 13.186 + 13.531MCD, r^2 = 0.967), indicating that centra grow proportionally to total length and were suitable as ageing structures (Fig. 4).

Age determination

Of the 410 centra prepared for ageing analysis from EBS skates, 325 (80 %) had suitable quality and agreement among age estimates for further analysis. Of the 247 centra examined from GOA skates, 186 (74 %) were of suitable quality and agreement for use in age analysis.

There was no detectable bias in centrum banding patterns from anterior and posterior regions of the vertebral column. Differences between paired age estimates

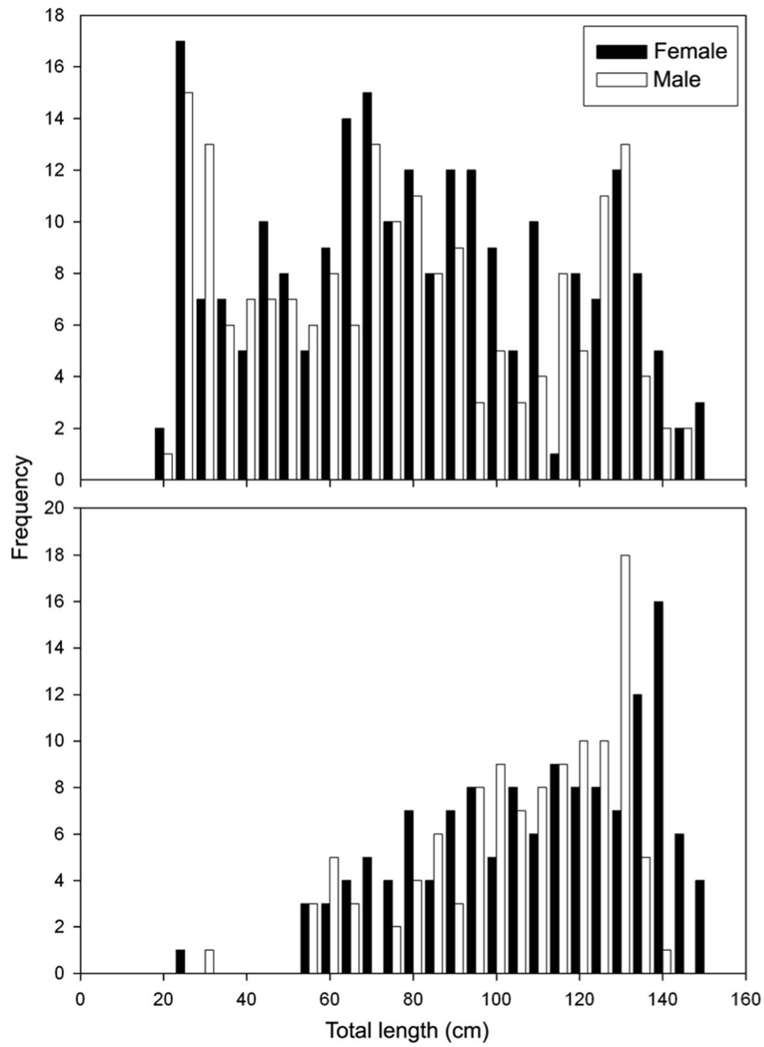


Fig. 3 Length frequencies of *Bathyraja aleutica* used for age analysis. Top: Females (n = 223) and males (n = 187) from the eastern Bering Sea; and bottom: females (n = 135) and males (n = 112) from the Gulf of Alaska

from anterior and posterior vertebrae were not significant ($t = -1.564$, $p = 0.130$, $n = 27$), therefore, all age estimates were based on anterior vertebral centra as they generally are larger in size.

Precision and bias

Overall precision among the three age estimates from vertebral thin sections was good for both EBS (IAPE = 8.91 %, CV = 11.45 %) and GOA (IAPE = 8.08 %, CV = 10.50 %) samples. Results of contingency table tests indicated no differences between reads of EBS vertebrae (reads 2 versus 3: Bowker's: $\chi^2 = 20.2$, df = 29, $p = 0.886$; Evans-Hoenig: $\chi^2 = 0.947$, df = 2, $p = 0.623$; McNemar's: $\chi^2 = 0.530$, df = 1, $p = 0.465$). All reads of GOA vertebrae indicated a bias (second vs. third reads: Bowker's: $\chi^2 = 57.49$, df = 41, $p = 0.045$; Evans-Hoenig: $\chi^2 = 32.419$, df = 3, $p < 0.001$; McNemar's: $\chi^2 = 27.59$, df = 1, $p = <0.001$), except reads 1 versus 3. Since the final age estimate is based on the agreement of two or more reads, this bias did not impact the final age estimates. In addition, percent agreement analysis indicated good precision among vertebral reads, with a high proportion of all ages within three years for the EBS (99.4 %) and GOA (97.3 %). Age bias plots demonstrated no appreciable bias between vertebral reads (Fig. 5).

Indirect validation

An annual pattern of band deposition could not be validated using applied marginal increment and edge

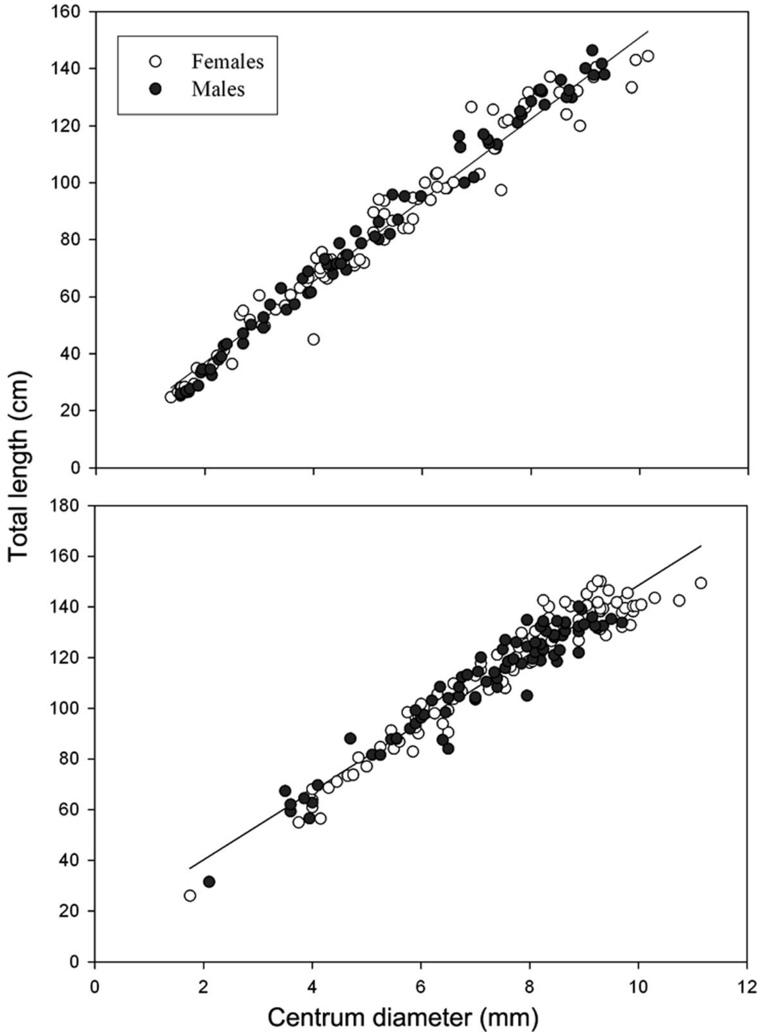


Fig. 4 Relationship between mean centrum diameter and total length for combined sexes of *Bathyraja aleutica* from a) the eastern Bering Sea (n = 157) and b) the Gulf of Alaska (n = 173)

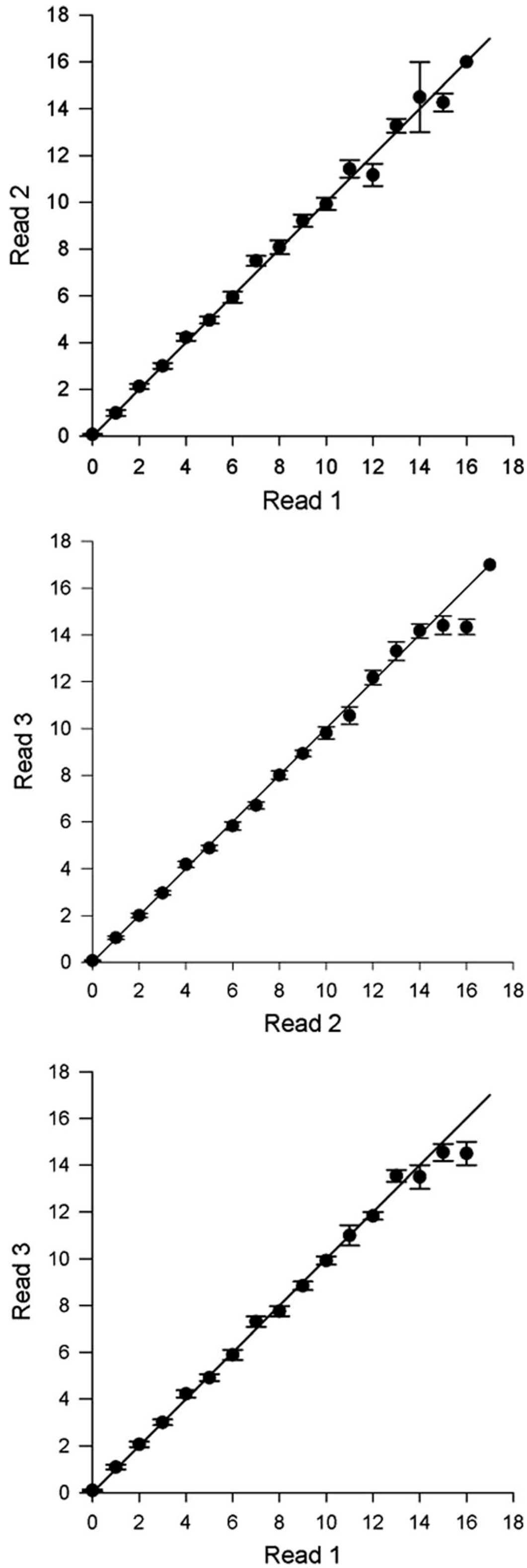
analysis methods. Among vertebral samples from the EBS, 109 were considered usable for marginal increment analysis. The greatest mean MIR value (0.80) occurred in January and the least (0.42) in March. Differences in mean MIR values among months were not significant (F = 1.824, p = 0.081). Comparison of centrum edge types from 125 vertebral samples demonstrated that translucent bands were present most frequently at the edge during January and opaque bands during July.

Among the 175 vertebral thin sections from GOA skates that were examined, there was no evident pattern of centrum edge types among months. The greatest mean MIR value (0.82) occurred in July and the lowest (0.45) in March. Mean MIR values did not differ significantly among months (F = 1.415, p = 0.214; Fig. 6).

Growth

Age estimates for skates from the EBS were 0 to 16 years for males (n = 149) and 0 to 17 years for females (n = 176). Skates from the GOA attained greater ages, and were 0 to 18 years for males (n = 83) and 0 to 19 years for females (n = 103; Table 1).

All growth models fit the length-at-age data well and were highly significant in both locations, though models fit the EBS data better (Table 2). For skates in the EBS, all growth models were biologically reasonable, but the 3VBGF had the best goodness-of-fit. Growth model parameters were generally similar for GOA skates, however, the theoretical maximum length estimated by the 3VBGF was biologically unrealistic, and likely was skewed by the lack of length-at-age data for small skates



◀ **Fig. 5** Age bias plots of age estimates between independent reads of vertebral thin sections from *Bathyraja aleutica* from the eastern Bering Sea ($n = 325$). Plots demonstrated no biases between reads. The 45° line represents 1:1 agreement between band counts. Bars represent one standard error

(<50.0 cm TL). Further age and growth results, therefore, were compared using the 2VBGF.

Male skates from the EBS reached a lesser maximum size ($L_\infty = 158.9$ cm) and had a slightly larger growth coefficient ($k = 0.14$) than females ($L_\infty = 162.1$ cm, $k = 0.13$); differences in growth were not significant between sexes ($\chi^2 = 0.47$, $p = 0.791$). Similarly, GOA males attained a lesser maximum size ($L_\infty = 138.2$ cm) and had a larger growth coefficient ($k = 0.15$) than females ($L_\infty = 160.0$ cm, $k = 0.11$). Male and female growth curves, however, were significantly different ($\chi^2 = 11.13$, $p = 0.0038$). Significant differences in 2VBGFs between the EBS and GOA occurred for both females and males (Fig. 7; females $\chi^2 = 34.25$, $p < 0.0001$; males $\chi^2 = 44.62$, $p < 0.0001$).

Discussion

Age and growth studies must ensure that the calcified structures used to estimate age represent continuous growth of the animal (Casselman 1983). Vertebral centra have become the predominant elasmobranch ageing structure after Ridewood (1921) first documented calcified growth bands in shark and ray centra. In *B. aleutica*, the strong positive relationship between CD and TL indicated vertebral centrum size increased proportionally with somatic growth, and centra were suitable structures for age and growth analysis. In addition, the measures of precision were reasonable for *B. aleutica* age estimates, and were consistent with other elasmobranch studies. Estimates of APE and CV were better than those found for *B. trachura* (Davis et al. 2007) and *Raja rhina* (Thompson 2006). In most shark ageing studies, CV values typically exceed 10 % (Campana 2001); therefore, precision of age estimates was considered acceptable for each structure in *B. aleutica*.

Age estimates used in this study were based on the assumption of annual band deposition, although validation was inconclusive in *B. aleutica.* In skates from the EBS, the proportion of centrum edge

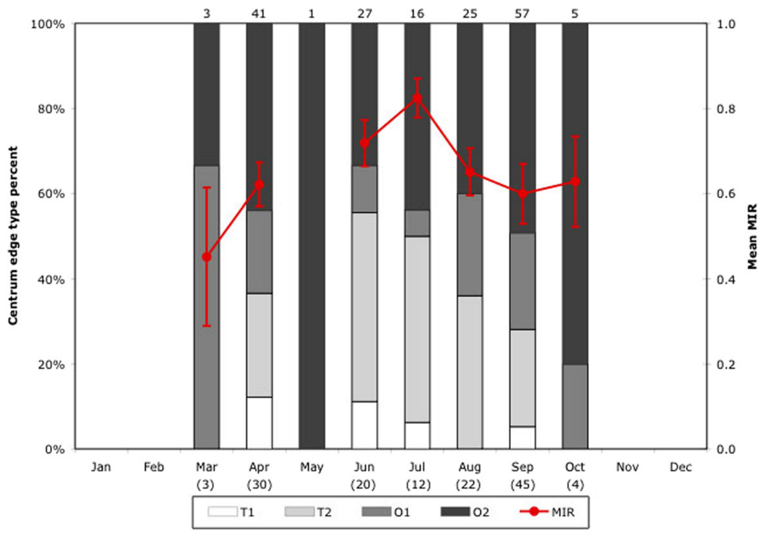


Fig. 6 Monthly variation in centrum edge type ($n = 175$) and mean marginal increment ratio (MIR) ± 1 standard error ($n = 136$) determined for skates from the Gulf of Alaska. Values listed above the histogram represent the number of samples used in centrum edge analyses. Sample sizes included in MIR analyses are depicted below month in parentheses. T1, narrow translucent edge; T2, broad translucent edge; O1, narrow opaque edge; O2, broad opaque edge

types was consistent with the expected pattern of greatest opaque edges in the summer (fast growth) and translucent edges in the winter (slow growth; Waring 1984), as was found in *B. parmifera* (Matta and Gunderson 2007). The resolution of an annual banding pattern may have been precluded by inconsistent samples available for each month, as well as limitations in edge clarity due to reduced calcification, overpolishing, or photographic resolution. However, edge analyses have supported the annual deposition pattern of one opaque and one translucent band for several other skate species, including *A. radiata* (Sulikowski et al. 2005), *Raja texana* (Sulikowski et al. 2007), and *Bathyraja parmifera* (Matta and Gunderson 2007). In addition, age validation using oxytetracycline injection (Holden and Vince 1973; Natanson 1993; Cicia et al. 2009) and bomb radiocarbon (McPhie and Campana 2009) has been successful in skates, therefore a pattern of annual band deposition was assumed for *B. aleutica*. Because of the possibility of over or underestimation of ages in this study, however, estimates for fisheries management must be used cautiously (Campana 2001).

Table 1 Size and estimated age for the largest and oldest specimens

	Size (cm TL)	Estimated age (years)
Eastern Bering Sea		
Largest male	149.9	13
Largest female	153.4	15
Oldest male	132.4	16
Oldest female	144.4	17
Gulf of Alaska		
Largest male	140.1	15
Largest female	153.6	15
Oldest male	130.6	18
Oldest female	140.6, 149.4, 152.5	19

Among batoids, maximum ages vary widely, from 3 years in the coastal species *Himantura imbricata* (Tanaka and Ohnishi 1998) to 37 years in *Bathyraja minispinosa* (Ainsley et al. 2011). Maurer (2009) determined *B. lindbergi* and *B. maculata* both reached 32 years using histological methods. This method can result in greater band counts than gross sectioning, but also may yield too much detail and overestimate age (Maurer 2009). Nonetheless, histology has been accepted for *B. interrupta* and *B. trachura* (Winton et al. 2013; Ainsley et al. 2014), and should be investigated for *B. aleutica* in the future.

The maximum ages estimated for *B. aleutica* (EBS 17 years, GOA 19 years) were similar to some of the deep-water, smaller sized skates from the eastern North Pacific, with reported maximum ages of 18 years for *B. kincaidii* (Perez et al. 2010), 17 years for *B. parmifera* (Matta and Gunderson 2007), and 20 years for *B. trachura* (Davis et al. 2007). Although *Beringraja binoculata* from British Columbia attained larger sizes and older ages (204 cm TL, 26 years), *B. binoculata* the GOA reached approximately the same size classes as

Table 2 Parameters for each growth model for females and males of *Bathyraja aleutica* by location. 3VBGF = three-parameter von Bertalanffy growth function; 2VBGF = two-parameter von Bertalanffy growth function using set L_o; L_∞ = asymptotic total length in cm; *k* and *g* = growth coefficients; t_0 = theoretical age at 0 length; L_0 = total length at birth in cm

	Model	L_∞	k	t_0	L_0	g	r^2	MSE	SEE	p
Eastern Bering Sea										
Females	3VBGF	174.4	0.10	1.86	30.3	-	0.9545	63.38	7.96	<0.0001
	2VBGF	162.1	0.13	-	23.0	-	0.9455	75.59	8.69	<0.0001
	Gompertz	150.4	1.54	-	32.2	0.21	0.9535	64.85	8.05	<0.0001
	Logistic	142.3	-	3.56	-	0.32	0.9495	70.41	8.39	<0.0001
Males	3VBGF	170.5	0.11	1.69	29.0	-	0.9569	60.41	7.77	<0.0001
	2VBGF	158.9	0.14	-	23.0	-	0.9497	70.04	8.37	<0.0001
	Gompertz	147.6	1.55	-	31.3	0.22	0.9566	60.92	7.81	<0.0001
	Logistic	140.1	-	3.45	-	0.34	0.9531	65.84	8.11	<0.0001
Gulf of Alaska										
Females	3VBGF	211.8	0.05	4.55	44.0	-	0.8860	95.33	9.76	<0.0001
	2VBGF	160.0	0.11	-	23.0	-	0.8620	114.27	10.69	<0.0001
	Gompertz	176.3	1.31	-	47.6	0.10	0.8859	95.40	9.77	<0.0001
	Logistic	162.7	-	5.14	-	0.16	0.8859	95.37	9.77	<0.0001
Males	3VBGF	158.3	0.09	3.41	41.4	-	0.8554	83.22	9.12	<0.0001
	2VBGF	138.2	0.15	-	23.0	-	0.8351	93.71	9.68	<0.0001
	Gompertz	147.3	1.16	-	46.1	0.14	0.8521	85.12	9.23	<0.0001
	Logistic	141.7	-	3.34	-	0.19	0.8489	86.90	9.32	<0.0001

Bathyraja aleutica yet reached a lesser maximum age of 15 years (McFarlane and King 2006; Gburski et al. 2007). Overall, *B. aleutica* generally falls within the mid-range of longevity estimates for skates (Sulikowski et al. 2005).

Theoretical longevities were estimated for comparison to the maximum band count, which is likely an underestimate of longevity in a fished population (Natanson et al. 2002). Fabens' (1965) estimates, based on the time it takes to reach 99 % of L_∞, were generally twice the maximum band counts (44 years for GOA females), and may not be the best method for *B. aleutica*. Taylor's (1958) estimate, reaching 26 years for GOA females, was closest to vertebral ages, and considered the most biologically reasonable method. McPhie and Campana (2009) also found Taylor's estimates nearest maximum observed ages for four North Atlantic skate species.

Researchers of chondrichthyan age and growth primarily apply the 3VBGF to age-at-length data. However, based on the criteria of statistical fit, biological relevance, and convenience (Roff 1980; Moreau 1987; Cailliet et al. 2006), the 2VBGF best fit the length-at-age data of *B. aleutica*. Growth parameters estimated by the 3VBGF were the least biologically reasonable in size at birth (L_o) and asymptotic length (L_∞). Teshima and Tomonaga (1986) estimated L_o as 19.6–26.3 cm TL, whereas Hoff (2009) determined *B. aleutica* embryos at 23.5–25.8 cm TL had completely internalized their yolk and were near egg-case emergence. In EBS skates, the L_o predicted by the 3VBGF (29.7 cm TL) was greater than the smallest free-swimming individuals (23.9 cm TL male, 20.6 cm TL female); estimates of L_o for GOA skates were much greater (41.4 cm TL male, 44.0 cm TL female). These overestimates may indicate the limited ability of the 3VBGF to describe early growth (Gamito 1998). This also may reflect the use of whole ages, as prescribing ages with half-year increments may have provided more precise model fits, especially during initial growth (Frisk and Miller 2006; Smith et al. 2007). In addition, the L_∞ estimated by the 3VBGF for females from the GOA (211.8 cm TL) was much greater than the largest *B. aleutica* reported (161 cm TL; Zenger 2004), and likely resulted from the lack of small skates (<50.0 cm TL) in the sample. L_∞ estimates from the 2VBGF were closest to the maximum observed sizes for all skates except males from the GOA, which were influenced by

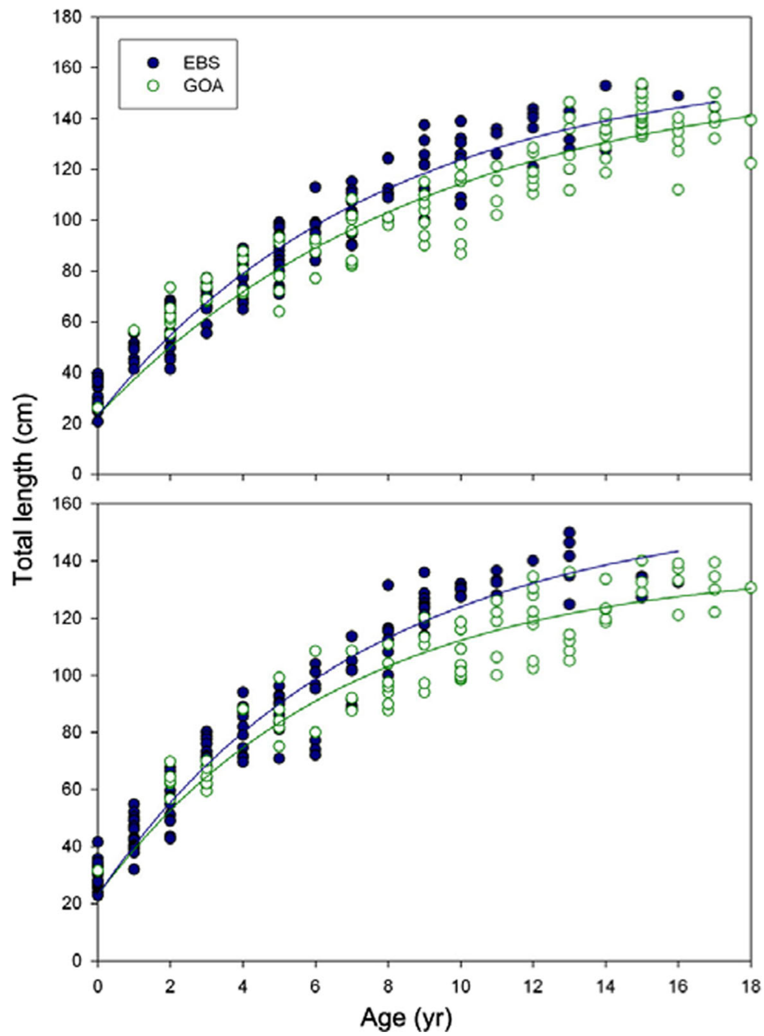


Fig. 7 Two-parameter von Bertalanffy growth functions fitted to observed length-at-age data for a) female and b) male *Bathyraja aleutica* from the eastern Bering Sea and Gulf of Alaska

the lack of samples greater than 140.0 cm. Because the 2VBGF best fit the growth of skates from the GOA, and fits well for skates from the EBS, this function was used to compare growth between locations.

The von Bertalanffy growth coefficient (k) is commonly used to compare life history strategies and address the potential vulnerability of a population. Although the conventional view has been that most elasmobranchs exhibit slow growth in comparison with bony fishes (Camhi et al. 1998), a wide range of growth rates has been found in deep-water batoids. Estimates of k values among deep-water skates are quite broad (Musick 1999; Calliet and Goldman 2004), with reported growth coefficients ranging from 0.05 yr.$^{-1}$ for *Dipturus pullopunctata* (Walmsley-Hart et al. 1999) to 0.50 yr.$^{-1}$ for *Raja miraletus* (Abdel-Aziz 1992). Growth coefficients for *Bathyraja aleutica* were similar to those in the smaller sized *B. parmifera* (Table 3; Matta and Gunderson 2007). Likewise, growth rates were greater than in comparably sized *Raja rhina* (k = 0.037–0.056 yr.$^{-1}$), but within the range of estimates for the larger species, *R. binoculata* (k = 0.080–0.152 yr.$^{-1}$; Gburski et al. 2007), from the GOA. *Bathyraja aleutica*, therefore, is considered a moderately slow growing, large bodied species.

Growth parameters differed between sexes of *Bathyraja aleutica*. Female skates reached larger sizes and grew more slowly than males in both locations; however, growth curves were significantly different only between sexes from the GOA. Male GOA skates were the only specimens collected that did not reach 150.0 cm TL, which likely contributed to differences in 2VBGF

Table 3 Comparison of age and growth parameters for several species of deep-water eastern North Pacific skates. Max L_{obs}, observed maximum length; L_∞ and k, von Bertalanffy growth parameters; Max Age_{obs}, observed maximum age. Parameters are from the three-parameter von Bertalanffy function to facilitate comparisons between studies

Species	Source	Max L_{obs} (cm)	L_∞ (cm)	k	Max Age_{obs}	Location
Bathyraja aleutica	This study	153.4 (F) 149.9 (M)	174.4 170.5	0.10 0.11	17 16	E. Bering Sea
Bathyraja aleutica	This study	153.6 (F) 140.1 (M)	211.8 158.3	0.05 0.09	19 18	Gulf of Alaska
Bathyraja interrupta	Ainsley et al. (2014)	86 (F) 80 (M)	112.5	0.06	19	E. Bering Sea
Bathyraja interrupta	Ainsley et al. (2014)	87 (F) 82 (M)	119.2	0.05	21	Gulf of Alaska
Bathyraja lindbergi	Maurer (2009)	102.1 (F) 93.2 (M)	131.9	0.04	32	E. Bering Sea
Bathyraja kincaidii	Perez et al. (2010)	61.0 (F) 63.5 (M)	56.0	0.21	18	E. North Pacific
Bathyraja maculata	Maurer (2009)	114.5 (F) 114.4 (M)	155.6	0.04	32	E. Bering Sea
Bathyraja minispinosa	Ainsley et al. (2011)	89.5 (F) 83.7 (M)	146.9	0.02	37	E. Bering Sea
Bathyraja parmifera	Matta and Gunderson (2007)	119.6 (F) 118.0 (M)	135.4	0.10	17	E. Bering Sea
Bathyraja taranetzi	Ebert et al. (2009)	72.5 (F) 66.3 (M)	78.1	0.13	14	E. Bering Sea
Bathyraja trachura	Winton et al. (2013)	94.2 (F) 91.8 (M)	119.3	0.04	36	E. Bering Sea
Bathyraja trachura	Davis et al. (2007)	86.5 (F) 91.0 (M)	112.1	0.06	20	E. North Pacific
Beringraja binoculata	Gburski et al. (2007)	178 (F) 141 (M)	189.6	0.11	15	Gulf of Alaska
Beringraja binoculata	McFarlane and King (2006)	203.9 (F) 183.6 (M)	293.4	0.04	26	British Columbia
Raja rhina	Gburski et al. (2007)	140 (F) 129 (M)	203.8	0.04	25	Gulf of Alaska
Raja rhina	McFarlane and King (2006)	124.6 (F) 122.0 (M)	133.8	0.07	26	British Columbia

parameters between sexes from the GOA. Slower growth rates and larger sizes in females have been reported for several skates McFarlane and King (2006); Gburski et al. 2007; Licandeo and Cerna 2007). This pattern is likely a result of differing reproductive biology, with females attaining larger body size to accommodate egg production and storage, while males grow faster to reach sexual maturity (Walmsley-Hart et al. 1999).

In comparing growth between locations, EBS male and female skates attained greater lengths at age than hose from the GOA, and skates from the GOA reached greater maximum ages. Estimates of L_∞ and k were greater in the EBS, with the exception of a lesser growth coefficient for males from the EBS ($k = 0.14$) than the GOA ($k = 0.15$). Ainsley et al. (2014) also found that *B. interrupta* from the GOA attained older ages than those from the EBS. Regional variability in size and growth was also documented in *B. trachura* between the BS and California Current ecosystem (Winton et al. 2013).

Apparent differences in growth between regions may be attributed to sampling methods or environmental factors. A temporal effect may have occurred, as the majority of EBS samples were collected in 2004, whereas skates from the GOA were captured during 2005–2007. Sampling depth also may have attributed to variability in growth parameters. All skates from the EBS were collected in the continental slope region, between 194 and 1169 m (mean 510 m), whereas skates from the GOA were taken from shallower shelf areas between 20 and 396 m (mean 123 m). Though life history patterns have been linked with size in some skate assemblages (Dulvy and Reynolds 2002), longevities of Alaskan skate species may scale with depth (Cailliet et al. 2001; Winton et al. 2013). This association has also been observed in deepwater chondrichthyans (Garcia et al. 2008). In addition, skates inhabiting the slope may shift from deeper to shallower waters with size (Orlov et al. 2006; Hoff 2010). Temperature, a factor of region and sampling depth, also may have attributed to variation in growth between skates from EBS and GOA. In tows where *B. aleutica* were captured, during the 2004 EBS survey bottom temperatures ranged from 2.3 to 4.3°, whereas during the 2005 GOA survey, temperatures were about two degrees greater, ranging from 4.0 to 6.7 °C. Though temperature may have a significant effect on banding patterns in elasmobranchs (Goldman 2004), no effects were apparent on vertebral band deposition in *Leucoraja erinacea* (Natanson 1993; Sagarese and Frisk 2010).

Geographic variations in life history parameters have been documented in several elasmobranchs, but do not exhibit discrete patterns. Several researchers discussing variation by latitude have found that animals in higher latitudes are larger and grow more slowly to older ages than their conspecifics at lower latitudes (Carlson and Parsons 1997; Yamaguchi et al. 1998; Frisk and Miller 2006; Licandeo and Cerna 2007). However, deep-water *Raja undulata* had faster growth in higher latitudes (Moura et al. 2007). Conversely, western Atlantic rays, *Rhinoptera bonasus*, were larger but grew faster and had lesser longevities than rays from the Gulf of Mexico (Neer and Thompson 2005). Although *B. aleutica* were collected from both the EBS and GOA in an overlapping range of ~55–61° N latitude in this study, growth characteristics were still significantly different, and may indicate the presence of distinct populations of *B. aleutica* in the eastern North Pacific.

Conclusion

The continued presence of skates as bycatch in trawl and longline fisheries emphasizes the importance of conservative management. Several species primarily taken as commercial bycatch have experienced dramatic declines in population size (Ebert and Winton 2010). Of particular concern is unevaluated rajids that could become targets of developing fisheries, as fishers look to alternative and bycatch species in the face of declining stocks of traditional species (Ebert et al. 2007). Also, in mixed-species fisheries, long-lived animals would suffer the greatest threats as they could become depleted as the more productive species continues to be fished (Musick 1999). As several chondrichthyan species have proven unsustainable in the past, data from this study should be considered in augmenting current management strategies or developing new fishery management plans.

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Compliance with ethical standards

Ethical approval All applicable institutional guidelines for the care and use of animals were followed. This research was conducted under Institutional Animal Care and Use Committee (IACUC) protocol #801.

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