

# Age and growth characteristics of the Starry Skate, *Raja stellulata*, with a description of life history and habitat trends of the central California, U.S.A., skate assemblage

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**Abstract** Skates are prevalent in fisheries worldwide, but rarely are they identified to species. This is of conservation and management concern since skates exhibit a broad range of life history characteristics. The present study investigated the age and growth of the Starry Skate, *Raja stellulata*, and compared it to other regional skates inhabiting the U.S. West Coast. Age and growth parameters were determined using two vertebral preparation techniques: gross sectioning and histological sectioning. Gross section age estimates ranged from zero to 11 years and growth was described by the two parameter von Bertalanffy growth function (2 VBGF;  $L_{\infty}=915$  mm total length (TL) and  $k=0.13$  year<sup>-1</sup>;  $n=189$ ). Histological section age estimates ranged from zero to 15 years and growth was also described by the 2 VBGF ( $L_{\infty}=1092$  mm TL,  $k=0.06$  year<sup>-1</sup>;  $n=68$ ). Histological section results reflect a more conservative life history, specifically a lower von Bertalanffy growth coefficient, but had slightly biased results and a smaller sample size than the gross section results. An age and depth trend was found within the central California skate assemblage,

in which habitat depth and maximum age were positively correlated.

**Keywords** Age · Growth · Skates · Elasmobranchs · Life history · Central California

## Introduction

Skates (Chondrichthyes, Rajiformes), like many elasmobranchs, are generally characterized as having slow growth, late age at maturity, and extended longevity, making this group susceptible to targeted and incidental fishing pressures (Holden 1973; Stevens et al. 2000). Despite this commonly held axiom, considerable variation exists in life history characteristics within this group (Dulvy et al. 2000; Ebert et al. 2007, 2009). Recent research indicates skates can live between seven and 37 years and mature between three and 23 years (Cailliet and Goldman 2004; Gallagher et al. 2004; Ebert et al. 2009; Ainsley et al. 2011). Given this high degree of variability, a species-specific approach to studying all skate species is warranted to better understand the group as a whole.

The observed differences in life history characteristics among individual species may be driven in part by differences in habitat. It has been observed that in the eastern North Pacific skate species tend to segregate by depth (Ebert, unpubl. data). A recent study on Alaskan bathyrjids (Winton 2011) found that life history characters among species were correlated to habitat and depth; deeper-dwelling species exhibited increased maximum

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age. This trend could potentially be attributed to reduced metabolic rates of deep-sea fishes and has also been observed on a broader scale for both deep-sea chondrichthyans and bony fishes (Cailliet et al. 2001; Drazen and Seibel 2007; Garcia et al. 2008). By evolutionarily expanding into the deep-sea, chondrichthyans and bony fishes exhibit altered life history characters to cope with reduced availability of resources. If this relationship between life history and habitat is observed in other skate assemblages worldwide, it could be a useful convention in examining species-specific fishing impacts.

Despite evidence of inter-species variability, skates are often managed in aggregate categories such as ‘unspecified skate’ or ‘other species’ because they are predominantly landed as bycatch and are rarely sorted to species (Dulvy et al. 2000). Skates constitute a large percentage of bycatch in some regions, especially in bottom trawl fisheries, which raises concerns about the impacts of fishing pressure on skate populations (Matta et al. 2006). The use of aggregate categories can mask species-specific fishing impacts (Walker and Hislop 1998; Dulvy et al. 2000).

The skate assemblage off central California along the U.S. West Coast includes species in two families: Arhynchobatidae and Rajidae (Ebert 2003). The Arhynchobatidae, or softnose skates, generally occur on the upper continental slope below 200 m depth with the most common species being the Sandpaper Skate, *Bathyraja kincaidii*, and the Roughtail Skate, *B. trachura*. The Rajidae, or hardnose skates, generally occur less than 200 m depth on the continental shelf and upper slope with the most common species being the Big, *Beringraja binoculata*, California, *Raja inornata*, Longnose, *R. rhina* and Starry, *R. stellulata* Skates (Ebert 2003). *Raja stellulata* is a medium-sized skate with a maximum size of 761 mm total length (TL; present study). It occurs from Baja California, Mexico, to Barkley Sound, British Columbia, Canada, from near-shore to 982 m depth. It is most commonly found at about 100 m depth along the continental shelf. *Raja stellulata* occupies a different habitat than other skates, usually occurring on hard substrate near rocky reefs with some vertical relief. Its diet includes crustaceans, cephalopods, and teleosts including small Lingcod, *Ophiodon elongatus*, and rockfishes, *Sebastes* spp. (Ebert 2003).

Life history characteristics, specifically age and growth data, are crucial for assessing population status and exploitation risk of a species. Various growth models

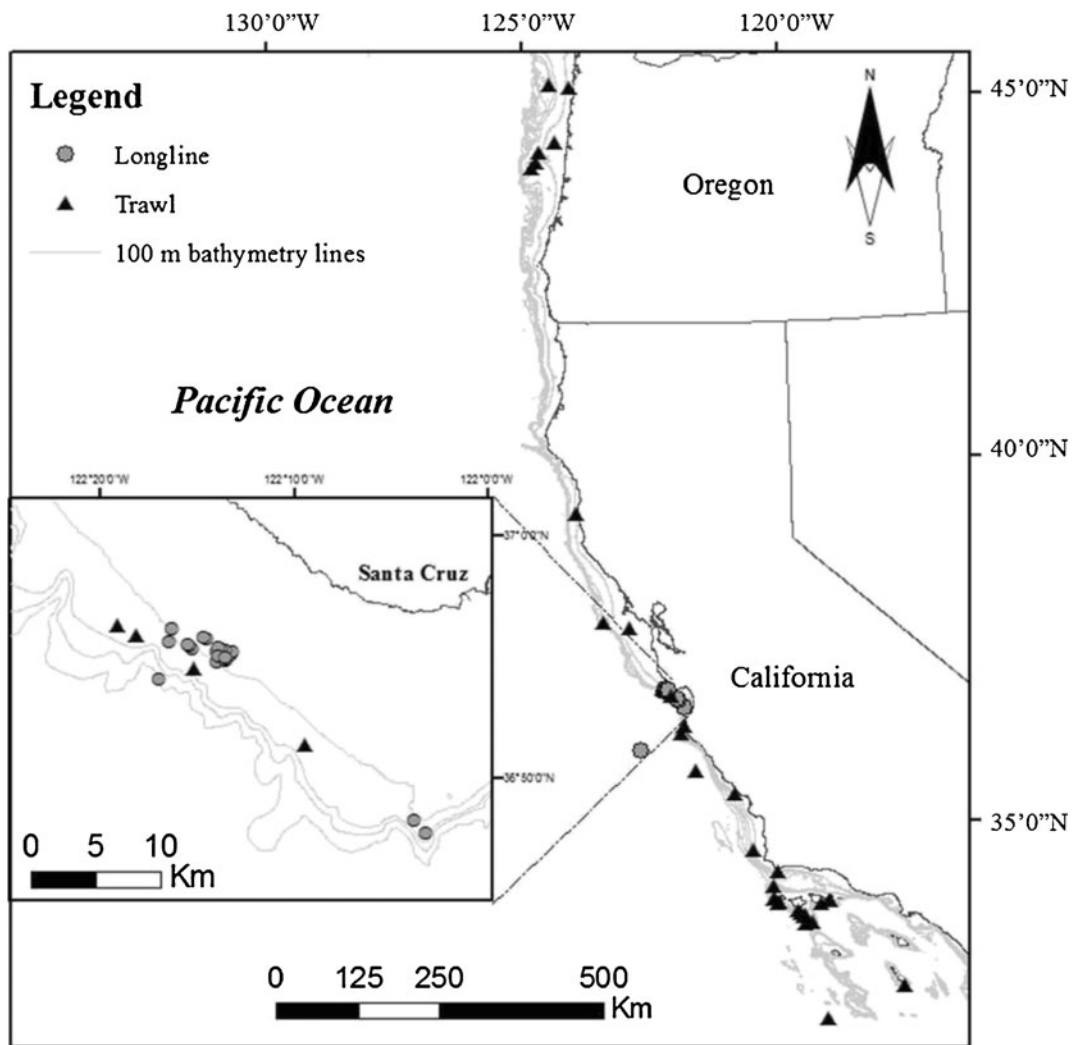
have been applied to elasmobranch length-at-age data (Cailliet and Goldman 2004). The three parameter von Bertalanffy (3 VBGF) is the most widely used for fishes including sharks, in part, because it models growth based on the biological premise that organism size directly depends on metabolic processes (Cailliet and Goldman 2004). However, the 3 VBGF does not estimate growth parameters well when sample size is low, especially lacking small or very large individuals (Cailliet and Goldman 2004). An alternate equation to the 3 VBGF replaces the biologically unrealistic variable  $t_0$  (theoretical time when TL is zero) with an estimate of size at birth,  $L_0$ , which is often well defined for elasmobranch populations. This alternate equation, the two parameter von Bertalanffy growth function (2 VBGF) provides more realistic growth parameter estimates with small sample sizes (Goosen and Smale 1997; Thorson and Simpfendorfer 2009). Additional growth models (i.e. Gompertz and logistic; Ricker 1979) are also used to describe elasmobranch age and growth especially if the volume of the organism better reflects growth than length (Cailliet and Goldman 2004).

The objectives of this study were to: (1) provide estimates of age and growth parameters for *R. stellulata*; (2) compare two band enhancement methods, gross sectioning and the histological technique; and (3) examine if there was a relationship between maximum observed age and habitat depth in the central California skate assemblage.

## Methods

### Collection and preparation

Specimens of *R. stellulata* were obtained using longline and trawl gear from two National Oceanic and Atmospheric Administration (NOAA) Fisheries surveys, one from July through April 2002 to 2005 and the other from June through November 2006 to 2010, along the U.S Pacific Coast (ca. 48° 28' N, 124° 54' W to ca. 32° 31' N, 117° 11' W; Fig. 1). Specimens were processed at Moss Landing Marine Laboratories for TL, measuring to the nearest millimeter (mm) from snout tip to tail tip, disc width (DW) from wing tip to wing tip (mm), weight (kg), sex, and with maturity status noted following Ebert (2005). Relationships between TL and DW, and TL and mass were determined using regression analyses. A section of at least eight vertebrae was



**Fig. 1** Distribution of collection sites of *Raja stellulata* ( $n=58$ ). Grey circles were collection by longline and black triangles were collection by trawl. Inset is northwest Monterey Bay

excised from each specimen between the fifth and 20th vertebrae and a subsample of five to seven caudal thorns was excised from behind the tail insertion.

Four individual anterior vertebrae per specimen were cleaned of excess tissue. A vertebra from each specimen was randomly selected, and two perpendicular measurements of the centrum diameter (mm) were recorded. The mean centrum diameter (MCD) was calculated and plotted against TL and regression analyses were performed to verify that vertebral growth was in proportion to organismal growth. An ANCOVA was used to test for differences of MCD between sexes. Two centra were dried and stored in an airtight container for gross sectioning. The other two

were stored in 70 % ethanol for at least 2 months before histological preparation following Natanson et al. (2007).

For the gross sectioning technique, each vertebra was mounted on a merchandise tag with polyester casting resin. One vertebra from each specimen was cut sagittally through the focus using a low speed saw (Buehler Isomet®, Lake Bluff, IL, USA) with paired diamond-edged blades separated by a 0.4 or 0.6 mm spacer to a thickness of 0.4–0.6 mm. Sections were then mounted on microscope slides with Cytoseal™ 60 and polished to an optimal viewing thickness using 1,200 grit wet sandpaper. The methodology for the histological technique is detailed in Natanson et al. (2007).

## Ageing

Vertebral sections prepared using both techniques were photographed under a dissecting microscope with transmitted light. Photographs were analyzed using ImagePro Plus® 4.1.0 imaging software (Media Cybernetic, L.P. 1993–1999). The birthmark, age zero, was determined as the first fully-formed band pair beyond the focus that was associated with an angle change in the corpus calcareum (Cailliet and Goldman 2004). Each opaque and translucent band thereafter was considered a band pair.

Age was determined for each individual without knowledge of length, sex, collection date, or previous band pair count. Each section was counted for band pairs three times by the first author. The first read was used to become familiar with the banding pattern, and to confirm good ageing criteria so it was excluded from further analysis. If agreement within two band pairs among reads was not achieved, the vertebra was not used in this study (Smith et al. 2007). Age estimates were assigned from the last read.

## Caudal thorns

Caudal thorns were prepared for ageing as a possible non-lethal alternative to vertebral centra (Gallagher and Nolan 1999). In an attempt to resolve band pairs, a subsample of thorns was stained with a 1.0 % crystal violet solution (Schwartz 1983). Upon examination, no banding pattern was evident on the thorn surface of dried thorns or thorns stained with crystal violet, therefore no age estimates were obtained from caudal thorns.

## Precision and bias

Precision was determined using the following analyses: index of average percent error (IAPE; Beamish and Fournier 1981), coefficient of variation (CV), and index of precision (D; Chang 1982). Age zero individuals were excluded from calculations of IAPE, CV, and D because their inclusion would result in a value divided by zero, which is not possible. Precision values of 10 % or less were defined as acceptable (Campana 2001).

Age bias plots and contingency tables were used to determine the source of differences among reads, either systematic bias or random error. Contingency tables were analyzed using three chi-squared tests of symmetry: the Bowker's (Bowker 1948), Evans-Hoenig (Evans and

Hoenig 1998) and McNemar's (McNemar 1948). All the above precision and bias analyses were conducted to test for differences in age estimates among reads of the first author, and between preparation techniques.

## Indirect validation

Periodicity of band pair deposition was assessed using centrum edge analysis (CEA) and marginal increment analysis (MIA; Tanaka and Mizue 1979; Campana 2001; Cailliet and Goldman 2004; Cailliet et al. 2006). For CEA, the final band of each sample was examined and placed in two categories: opaque or translucent. The proportion of band types was plotted by month and band deposition periodicity was tested against no cycle, an annual cycle, or a biannual cycle (Okamura and Semba 2009). Goodness-of-fit for each model was determined using Akaike's Information Criterion adjusted for small sample size ( $AIC_c$ ; Burnham and Anderson 2002).  $AIC_c$  values were calculated from least squares regression statistics assuming normally distributed deviations. The  $AIC_c$  differences were calculated as:  $\Delta_i = AIC_c - AIC_{min}$ . Models with  $\Delta_i < 2$  have substantial support,  $2 < \Delta_i < 4$  have less support and  $\Delta_i > 10$  have essentially no support (Burnham and Anderson 2002).

The MIA was conducted using the marginal increment ratio (MIR), which was calculated as (Conrath et al. 2002):

$$MIR = \frac{MW}{PBW}$$

in which  $MW$  is the margin width of the forming band pair, and  $PBW$  is the width of the penultimate band pair. Mean MIR was calculated for each month, and plotted by month to determine periodicity of band pair deposition. Differences among months were tested using a non-parametric Kruskal-Wallis test (Simpfendorfer et al. 2000; Smith et al. 2007). Individuals of age zero or age one were excluded from indirect validation analyses because they do not have a penultimate band pair.

## Growth modeling

Size-at-age estimates were adjusted based on the date of capture relative to a theoretical birth date. *Raja stellulata* does not display a seasonal peak in egg deposition (James 2011), therefore January 1st was chosen as the theoretical birth date. Setting a theoretical birth date, even for a species with aseasonal reproduction, allows

for a more biologically realistic age estimate since individuals with the same band pair count caught in different months are unlikely to all be exactly the same age. Date of capture, in Julian day, was divided by 365.25 and added to the band pair count to obtain a fractional age. Multiple growth functions were fit to fractional age estimates for each sex and sexes combined. Growth model parameters were estimated with non-linear least-squares regression methods in SigmaPlot version 12.0 (SPSS Software Inc., 2011). The four growth models applied were the 3 VBGF (von Bertalanffy 1938), the 2 VBGF (von Bertalanffy 1960), the Gompertz growth function, and the logistic growth function (both modified from Ricker 1979). The size at birth,  $L_0$ , for the 2 VBGF was 140 mm TL, based on the midpoint of the estimated birth size (120–160 mm; Ebert 2003). Likelihood ratio tests also were applied to determine differences in growth parameters between sexes (Kimura 1980; Haddon 2001). Relative goodness-of-fit for each model was determined using Akaike's Information Criterion adjusted for small sample size ( $AIC_c$ ; Burnham and Anderson 2002). Model selection was based on  $AIC_c$ , residual analysis, and model performance given the sample size (Thorson and Simpfendorfer 2009).

#### Age and depth analysis

To examine if a relationship was present between life history and habitat, maximum age and average depth were determined for the most common central

California skates species, *B. kincaidii*, *B. trachura*, *B. binoculata*, *R. inornata*, *R. rhina* and *R. stellulata*. Maximum estimated age was attained from this study and the literature (Zeiner and Wolf 1993; Davis et al. 2007; Perez et al. 2011; W. Smith and D. Ebert, unpubl. data). Gross section age estimates were used because this technique was common to all species. Average depth was calculated from NOAA Fisheries survey collection data. Estimated ages were plotted against average depth and the trend was examined using regression analysis.

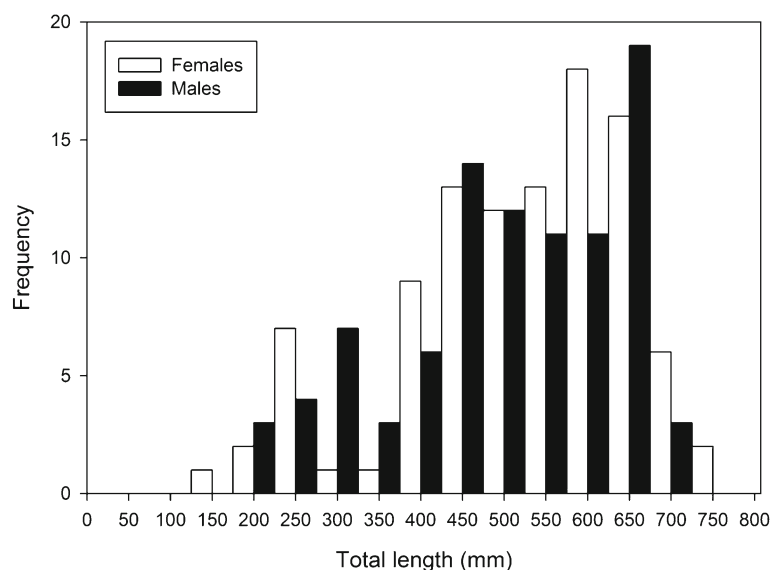
## Results

### Collection and preparation

Specimens collected ( $n=193$ ) were representative of the size range of this species, from 151 to 761 mm TL (Fig. 2). The number of females ( $n=101$ ) to males ( $n=92$ ) was nearly equal. The TL to DW relationship was described, based on the coefficient of determination,  $r^2$ , by a linear function ( $r^2=0.981$ ,  $DW=4.68+0.62\cdot TL$ ,  $n=192$ ). The TL to mass relationship was described, based on  $r^2$ , by a power function ( $r^2=0.937$ ,  $Mass=1.02\cdot 10^{-9}\cdot TL^{3.31}$ ,  $n=187$ ).

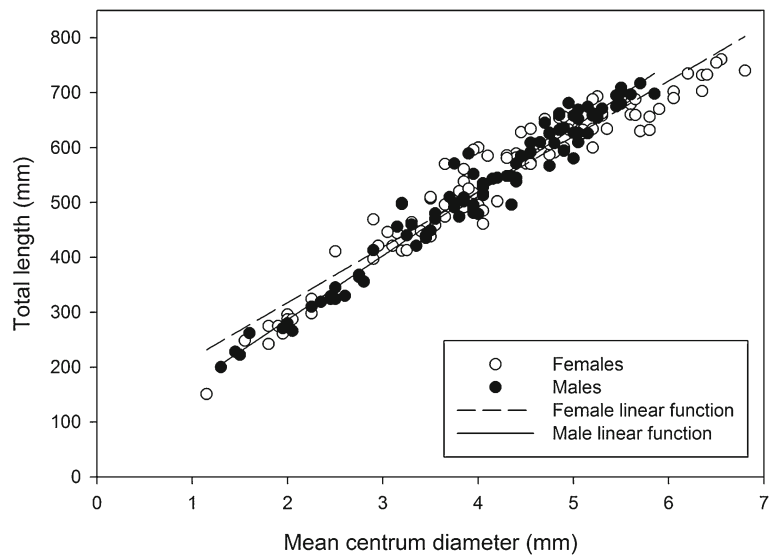
Centra grew proportionally to body length, indicating that centra were an appropriate structure to use for ageing (Fig. 3). An ANCOVA detected a significant difference between sexes ( $F=22.401$ ,  $df=1$ ,  $p<0.001$ ) therefore sexes were plotted separately. The MCD to TL for both sexes was described, by a linear function

**Fig. 2** Size frequency distribution by sex of *Raja stellulata* specimens ( $n=193$ ). Open bars are females and black bars are males





**Fig. 3** Linear relationship of mean centrum diameter (MCD) and total length (TL) by sex (Females:  $TL=115.5+100.99 \cdot MCD$ ,  $n=101$ ; Males:  $TL=55.14+116.60 \cdot MCD$ ,  $n=91$ )



(Females:  $r^2=0.926$ ,  $TL=115.5+100.99 \cdot MCD$ ,  $n=101$ ; Males:  $r^2=0.963$ ,  $TL=55.14+116.60 \cdot MCD$ ,  $n=91$ ).

### Ageing

In total, 193 vertebral centra were prepared for ageing using the gross sectioning technique. Four gross sectioned vertebrae were deemed unreadable and were excluded from further analysis, leaving age estimates for 189 individuals. Due to time and financial constraints, only 71 centra (35 females and 36 males) were prepared using the histological technique. Three histologically sectioned vertebrae were deemed unreadable and were excluded from further analysis, leaving age estimates for the remaining 68 vertebrae.

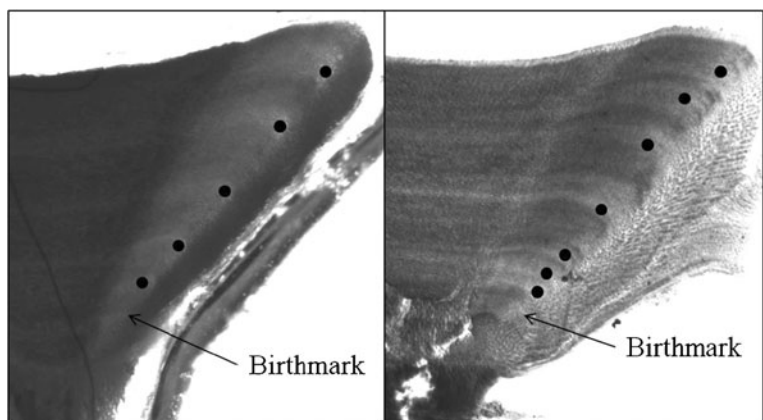
Histological sections were consistently assigned greater age estimates than gross sections (Fig. 4).

Female gross section age estimates were zero to 11 years ( $n=99$ ; 151–761 mm TL) and male age estimates were zero to 10 years ( $n=90$ ; 200–717 mm TL). Female histological section age estimates were zero to 15 years ( $n=34$ ; 151–755 mm TL) whereas males were two to 14 years ( $n=34$ ; 271–717 mm TL). Age zero was assigned to a 151 mm TL female for both preparation techniques, which falls within estimated birth size range of 120–160 mm TL (Ebert 2003).

### Precision and bias

Age estimates among reads were similar in precision for each processing method, but the gross sectioning technique had less bias than the histological sectioning technique. Precision among reads was good for both techniques (Gross sections: IAPE=5.74 %,

**Fig. 4** Comparison of gross section (on left) to histological section (on right). Both centra are from the same *R. stellulata* individual, a 485 mm total length female. The individual was estimated as five years old from the gross section and seven years old from the histological section



CV=8.03 %, D=5.38 %; Histological sections: IAPE=6.58 %, CV=9.01 %, D=5.78 %). For gross sectioned samples, an age bias plot indicated no bias between the second and final reads. The Bowker's, Evans-Hoenig, and McNemar's  $\chi^2$  tests of symmetry detected no bias between the second and final reads (Bowker's:  $\chi^2=26.6$ ,  $df=20$ ,  $p=0.150$ ; Evans-Hoenig:  $\chi^2=4.38$ ,  $df=2$ ,  $p=0.112$ ; McNemar's:  $\chi^2=1.71$ ,  $df=1$ ,  $p=0.191$ ). However, for histologically sectioned samples, an age bias plot indicated bias between the second and final read. All three tests of symmetry detected the same bias (Bowker's:  $\chi^2=41$ ,  $df=23$ ,  $p=0.01$ ; Evans-Hoenig:  $\chi^2=32.57$ ,  $df=2$ ,  $p<0.001$ ; McNemar's:  $\chi^2=31.87$ ,  $df=1$ ,  $p<0.001$ ).

Pairwise comparisons between processing methods showed that more band pairs were counted using the histological technique than the gross sectioning technique. An age bias plot indicated a strong bias, in which histological sections consistently produced older age estimates than gross sections (Fig. 5). This bias was also detected by all three tests of symmetry (Bowker's:  $\chi^2=58.3$ ,  $df=36$ ,  $p=0.01$ ; Evans-Hoenig:  $\chi^2=57.67$ ,  $df=6$ ,  $p<0.001$ ; McNemar's:  $\chi^2=57.07$ ,  $df=1$ ,  $p<0.001$ ). Histological age estimates were consistently greater than gross section age estimates in 93 % of samples by one to seven band pairs.

#### Indirect validation

The results of the CEA of gross sections plotted by month exhibited more opaque edge types from

February to August and translucent edge types from October to January (Fig. 6a). Annual, biannual, and no cycle in band deposition periodicity all had similar support from Okamura and Semba's method ( $2009$ ;  $\Delta_i<2$ ). A biannual cycle had the lowest AIC<sub>c</sub> value ( $\Delta_i=0$ ), followed by an annual cycle ( $\Delta_i=1.52$ ) and no cycle ( $\Delta_i=1.90$ ), but one periodicity is not supported above the others using AIC<sub>c</sub>.

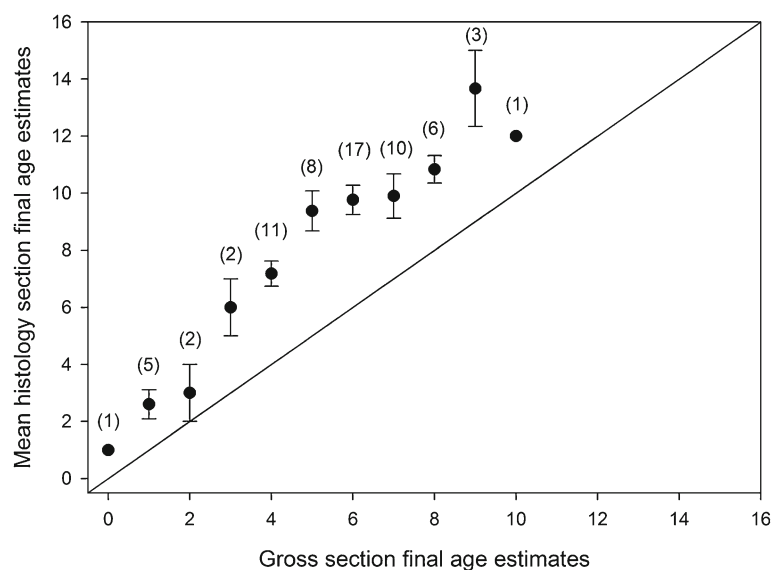
The results of the MIR plotted by month displayed an annual band pair pattern with values approaching one in July and August and values markedly less from October to January (Fig. 6b). The MIR values of gross sections were tested over months with a non-parametric Kruskal-Wallis test and a significant difference among months was detected ( $K=18.74$ ,  $df=10$ ,  $p=0.044$ ,  $n=172$ ).

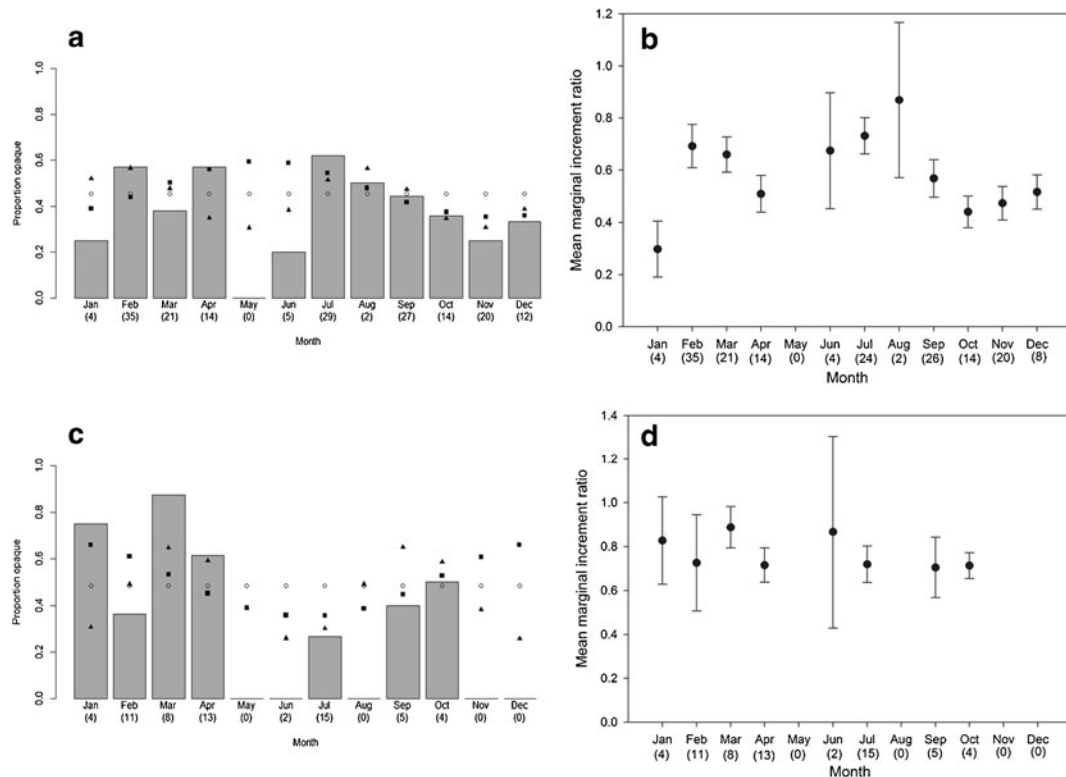
The results of the CEA of histological sections marginally supported a biannual or no cycle band deposition periodicity ( $\Delta_i=0$ ;  $\Delta_i=1.03$ ; Fig. 6c), over an annual cycle ( $\Delta_i=2.08$ ). One-way ANOVA of MIR for histological sections was not significantly different among months (MIR  $F=0.63$ ,  $df=7$ ,  $p=0.889$ ; Fig. 6d).

#### Growth models

Likelihood ratio tests for all growth functions, using both gross and histological sections, indicated no evidence of significant difference between sexes; therefore, sexes were pooled ( $p>0.654$ ). All gross section growth functions had substantial support ( $\Delta_i<2$ ) using AIC<sub>c</sub> values (Table 1; Fig. 7a) therefore no one model can

**Fig. 5** Age bias plot of gross section age estimates versus mean histological age estimates ( $n=66$ ). Sample sizes in parentheses. Error bars represent one standard error





**Fig. 6** Monthly variation in centrum edge analysis (CEA) for **(a)** gross sections with a biannual band pair deposition cycle in black triangles, an annual cycle in black squares, and no cycle in open circles ( $n=183$ ) and **(c)** histological sections with a biannual band pair deposition cycle in black triangles, an annual cycle in

black squares, and no cycle in open circles ( $n=62$ ) and mean marginal increment ratio (MIR) for **(b)** gross sections ( $n=172$ ) and **(d)** histological sections ( $n=62$ ). Samples sizes for are below each month in parentheses. Grey bar represents the proportion edges that are opaque. Error bars represent one standard error

be chosen above the others simply from  $AIC_c$  values. For gross sections, the 2 VBGF was chosen to describe *R. stellulata* growth based on  $AIC_c$  value, residual analysis and better model performance at small sample sizes ( $n < 200$ ; Thorson and Simpfendorfer 2009). For histological sections, the 2 VBGF was chosen to describe the growth of *R. stellulata* based on  $AIC_c$ , residual analysis, and model performance given the small sample size (Fig. 7b; Thorson and Simpfendorfer 2009). The other three growth functions for histological sections had moderate support ( $\Delta_i > 2$ ; Table 1).

#### Age and depth analysis

Age was significantly correlated with depth among central California skate species and the relationship was well described by a power function ( $r^2=0.812$ ,  $\text{Age}=4.30 \cdot \text{Depth}^{0.23}$ ,  $p < 0.02$ ) where an increase in habitat depth coincided with an increase in maximum estimated age (Fig. 8). Maximum estimated gross section

ages from this study and the literature were 11, 12, 13, 13, 18 and 20 years for *R. stellulata*, *B. binoculara*, *R. inornata*, *R. rhina*, *B. kincaidii*, and *B. trachura* (Zeiner and Wolf 1993; Davis et al. 2007; Perez et al. 2011; W. Smith and D. Ebert, unpubl. data). Average depths were 65 m (SE=4.05;  $n=239$ ) for *B. binoculara*, 105 m (SE=2.46,  $n=303$ ) for *R. inornata*, 114 m (SE=4.31,  $n=271$ ) for *R. stellulata*, 247 m (SE=4.49,  $n=1106$ ) for *R. rhina*, 382 m (SE=12.31,  $n=251$ ) for *B. kincaidii*, and 956 m (SE=12.58,  $n=182$ ) for *B. trachura*.

#### Discussion

The vertebrae of *R. stellulata* exhibited a clear banding pattern when processed with the gross sectioning technique, but by using the histological technique, the same individuals had up to seven additional band pairs than their gross section counterparts. The goal of band enhancement of chondrichthyan vertebrae is to make ageing



**Table 1** Growth model parameters and goodness-of-fit for females, males and sexes pooled of the four growth functions for a) gross sections ( $n=189$ ), and b) histological sections ( $n=68$ ).  $L_{\infty}$  is the asymptotic total length (TL) in mm;  $L_0$  is the estimated TL at birth in mm,  $k$  is the von Bertalanffy growth coefficient per year

or a dimensionless parameter for the Gompertz function;  $t_0$  is the theoretical time when the TL would be zero;  $g$  is the growth coefficient per year;  $AIC_c$  is the small-sample, bias corrected form of the Akaike's information criterion;  $\Delta_i$  is the Akaike difference;  $n$  is the number of parameters fitted to each model

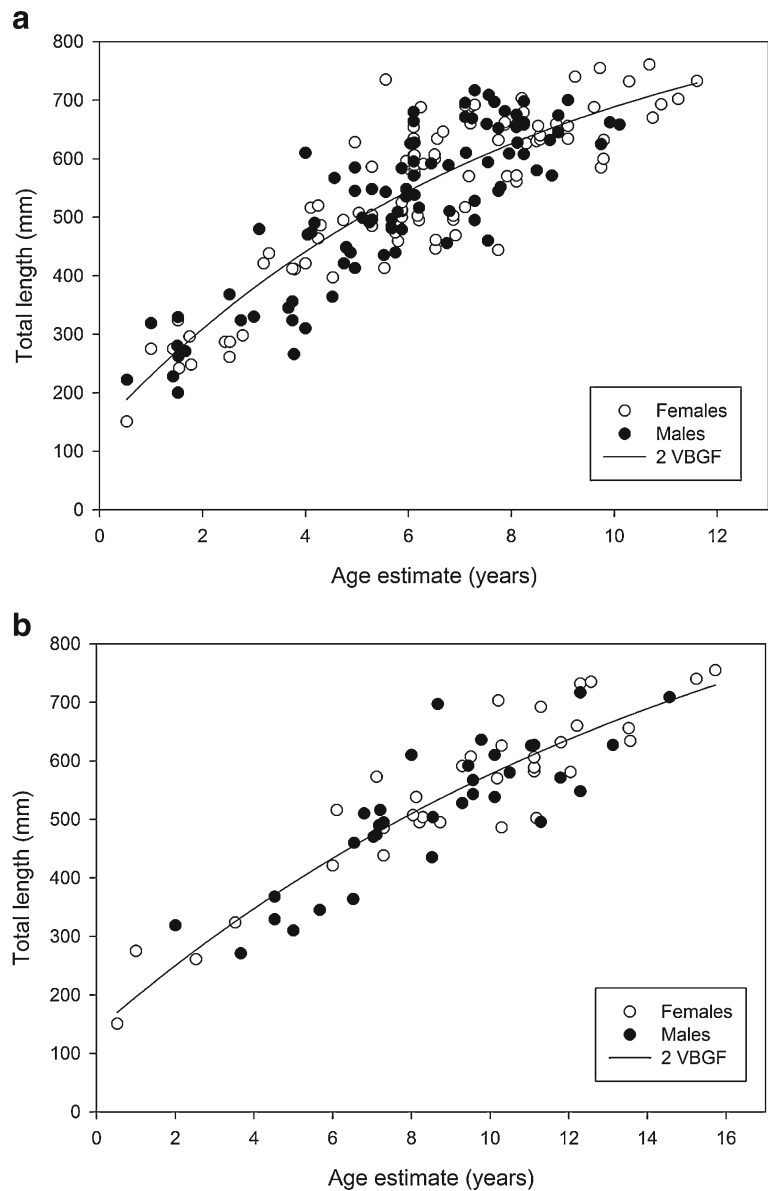
Growth model		$L_{\infty}$	$L_0$	$k$	$t_0$	$g$	adj $r^2$	$AIC_c$	$\Delta_i$	$n$
3 Parameter VBGF	Pooled	886	126	0.13	-1.14		0.761	693.70	1.97	4
	Females	836	107	0.16	-0.88		0.771			
	Males	993	146	0.11	-1.51		0.744			
2 Parameter VBGF	Pooled	915	140	0.13			0.762	691.73	0	3
	Females	884	140	0.13			0.772			
	Males	972	140	0.11			0.747			
Gompertz	Pooled	770	158	1.58		0.26	0.764	692.75	1.02	4
	Females	754	151	1.61		0.27	0.772			
	Males	799	167	1.56		0.23	0.749			
Logistic	Pooled	725	362		2.97	0.38	0.765	692.43	0.70	4
	Females	719	359		0.39	0.39	0.770			
	Males	733	366		0.37	0.37	0.752			
3 Parameter VBGF	Pooled	1165	154	0.05	-2.61		0.801	247.58	2.20	4
	Females	1162	163	0.05	-2.78		0.847			
	Males	969	116	0.08	-1.67		0.717			
2 Parameter VBGF	Pooled	1092	140	0.06			0.803	245.37	0.00	3
	Females	1049	140	0.07			0.851			
	Males	1059	140	0.06			0.725			
Gompertz	Pooled	859	172	1.61		0.14	0.802	247.39	2.02	4
	Females	884	183	1.58		0.13	0.845			
	Males	771	142	1.69		0.18	0.724			
Logistic	Pooled	772	386		5.07	0.23	0.801	247.47	2.09	4
	Females	802	401		5.28	0.21	0.842			
	Males	704	352		4.50	0.28	0.729			

both more precise and accurate. The gross sectioning technique requires basic sectioning equipment and is relatively inexpensive. Many skates, however, do not exhibit strong banding patterns and require band enhancement for improved readability (Licandeo et al. 2006; McFarlane and King 2006; Ainsley 2009; Winton 2011). The histological sectioning technique requires specialized equipment and chemicals (see Natanson et al. 2007) and is more expensive and labor intensive than the gross sectioning technique. The histological technique has been shown, however, to greatly enhance the banding pattern of several skate species, which in turn can improve accuracy and precision of age estimates (Natanson et al. 2007; Ainsley 2009; Maurer 2009; Winton 2011).

The appropriate band enhancement technique depends on the species in question and gross sectioning

should be considered for efficacy before attempting the histological technique. For this study, the histological technique undoubtedly enhances the banding pattern of *R. stellulata*, increasing band clarity over the gross sectioning technique, but the reduced sample size and slightly more biased results precludes a definitive recommendation of this technique for this species. Some skate age estimates using band counts from gross sections have been shown to be underestimates of age when validated using bomb radiocarbon analysis (McPhie and Campana 2009), therefore the older age estimates using the histological technique should not be dismissed, especially since they reflect more conservative life history characters including an older maximum age and a smaller growth coefficient estimate.

**Fig. 7** Two parameter von Bertalanffy growth curve fit to **a**) gross sections ( $n=189$ ) and **b**) histological sections ( $n=68$ ) of *R. stellulata*. Sexes were combined for all functions

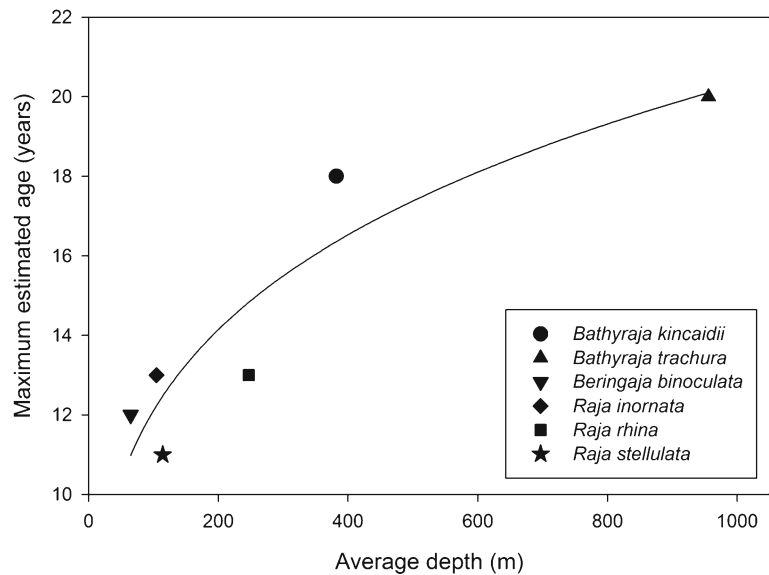


Band pair deposition was expected to be annual and similar between age structure preparation techniques. Results from the indirect validation support all models (annual, biannual, and no cycle) for both preparation techniques. These inconclusive trends may stem from uneven sample sizes among months, especially with the histological sections. Several other skate species have been shown to deposit one band pair per year using captive rearing and MIR, solidifying that for skates, the assumption of annual band pair deposition is justified (Natanson 1993; Sulikowski et al. 2003, 2005; Matta and Gunderson 2007; Natanson et al.

2007; Sagarese and Frisk 2010). An annual band pair deposition is plausible for *R. stellulata* gross sections based on both CEA and MIR.

Researchers have studied the use of caudal thorns as a non-lethal method to age skates, but caudal thorns are not an appropriate ageing structure for most eastern North Pacific skate species in which this structure has been examined [*Bathyrhaja interrupta* (Ainsley 2009); *B. kincaidii* (Perez et al. 2011); *B. lindbergi* and *B. maculate* (Maurer 2009); *B. minispinosa* (Ainsley et al. 2011); *B. taranetzi* (Ebert et al. 2009); *B. trachura* (Davis et al. 2007; Winton 2011)] and several Atlantic

**Fig. 8** Power relationship of the maximum estimated age of central California skates with mean depth (adj  $r^2=0.812$ ). Standard error of mean depth (not shown) was less than 15 m for each species



species completely lack banding [*Raja brachyura*, *R. montagui*, and *Leucoraja naevus* (Gallagher 2000; Gallagher et al. 2005)]. Findings from this study are consistent with the Atlantic rajids listed above. Gallagher (2000) suggested that the absence of ridge and trough banding may be due to the smoother transition between seasonal bands experienced by faster growing temperate skate species as compared with deeper, slower growing species. This may be the case, but more research into band deposition in caudal thorns is necessary to explain presence or absence of a banding pattern.

The 2 VBGF was the most appropriate growth function for both techniques since it incorporates  $L_0$ , which is known for *R. stellulata*, and provides realistic growth parameter estimates with small sample sizes ( $n < 200$ ; Thorson and Simpfendorfer 2009). The 2 VBGF is recommended for use with chondrichthyan age and growth over the 3 VBGF due to the inclusion of  $L_0$ , which is biologically meaningful, rather than  $t_0$  (Cailliet et al. 2006). Additionally, the 2 VBGF has been chosen to describe the growth of several skate species including *B. trachura* (Davis et al. 2007), *L. ocellata* (McPhie and Campana 2009), and *Malacoraja senta* (Natanson et al. 2007). The Gompertz function also provided similar growth parameter estimates, especially for gross sections, but *R. stellulata* does not increase in volume disproportionate to length, therefore it did not provide better parameter estimates than the 2 VBGF.

The life history characteristics of *R. stellulata* fall within the spectrum of variability observed among skates. At least seven species of rajid skates throughout

the northern hemisphere attain similar maximum ages (11–15) as *R. stellulata*, *Leucoraja erinacea* (Frisk and Miller 2006; McPhie and Campana 2009), *M. senta* (Natanson et al. 2007; McPhie and Campana 2009), *Okamejei acutispina* (Joung et al. 2011), *B. binoculata* and *R. rhina* (Zeiner and Wolf 1993), *R. inornata* (W. Smith and D. Ebert unpubl. data), and *R. undulata* (Coehlo and Erzini 2002). Each of these species is part of a regional skate assemblage that exhibits a wide range of life history characteristics.

A comparison among skate species found in the California Current ecosystem highlights the inter-species variability of this skate assemblage. The other rajids of the assemblage, *B. binoculata*, *R. inornata*, and *R. rhina* exhibit similar maximum ages (12, 13, and 13; Zeiner and Wolf 1993; W. Smith and D. Ebert unpubl. data), however two sympatric bathyrarid skates, *B. kincaidii* and *B. trachura* attain slightly older maximum ages of 18 and 20 years, respectively (Davis et al. 2007; Perez et al. 2011). The range of maximum sizes used in these studies is larger for the rajids (76–161 cm) than for the bathyrarids (64–94 cm), so differences are not driven by size. Two other obvious differences between the rajids and bathyrarids in the California Current ecosystem are taxonomy and habitat.

The central California skate assemblage (*B. kincaidii*, *B. trachura*, *B. binoculata*, *R. inornata*, *R. rhina* and *R. stellulata*) exhibits an inter-species trend of increasing lifespan with increasing depth (Fig. 8). There are distinct taxonomic and environmental differences between the rajids and the bathyrarids; they belong to different

families (Rajidae and Arynchobatidae) and are found in habitats with different depths and temperatures (Ebert 2003; Tolimieri and Levin 2006). Bathyradjids tend to inhabit continental slopes while most eastern North Pacific rajids tend to inhabit continental shelves (Ebert 2003). The same inter-species trend of increased lifespan with increased habitat depth was observed in the Alaskan skate assemblage among bathyradjid species (Winton 2011). The trend is likely driven by the effects of depth on the skate's metabolism. Decreased metabolic rates have been observed for some benthic deep-sea fishes when compared to their shallow water counterparts (Cailliet et al. 2001; Drazen and Seibel 2007). Deep-dwelling chondrichthyans were also associated with higher vulnerability to extinction from fishing due to their increased longevity and decreased growth rates (Garcia et al. 2008).

Several hypotheses have been used to describe this decreased metabolism. Beverton and Holt (1959) determined that the growth rate of poikilothermic fishes decreased with decreasing temperature, which decreases with increasing depth. More recently, Childress et al. (1990) suggested the “visual-interaction hypothesis”, which is based on the idea that metabolic declines are related to the demand for energy for predator–prey interactions. These interactions rely on vision and light, which are low to absent at increasing depths, so fewer predator–prey interactions may suggest less selective pressure for rapid locomotion, which is metabolically taxing, to chase prey or evade predators (Childress 1995; Seibel and Drazen 2007). This hypothesis applies only to visually oriented species, which includes skates. Therefore, slower growth and increased lifespan would be expected at deeper depths to balance decreased metabolic rates. This trend may be helpful in assessing life history characteristics of species that have little data available for them and are susceptible to fishing pressure.

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