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Age and growth of the roughtail skate *Bathyraja trachura* (Gilbert 1892) from the eastern North Pacific

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Abstract This study provides the first published age estimates for the roughtail skate, *Bathyraja trachura*. Age and growth characteristics of *B. trachura*, a poorly-known deepwater species, were determined from samples collected along the continental slope of the contiguous western United States. A new maximum size was established at 91.0 cm TL. Age was determined using a traditional structure (vertebral thin sections) with widespread application on multiple skate species and a non-lethal structure (caudal thorns) recently used for age analysis on skate species. Caudal thorns were determined not to be a useful ageing structure for this species based on poor precision and significantly lower age estimates when compared to age estimates from vertebral thin sections. The best model for describing growth of *B. trachura* was the two parameter VBGF, assuming annual vertebral band deposition and using length-at-age data. Although females grew slower and reached a larger maximum size than males, their growth was not statistically different (ARSS; $P = 0.90$); therefore, data were pooled ($L_\infty = 99.38$, $k = 0.09$). Annual band deposition was found to be a reasonable assumption for this species, but has yet to be validated. The maximum age estimated for *B. trachura* was 20 years for males and 17 years for females using vertebral thin sections.

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Introduction

In Californian waters, skates are directly targeted and taken incidentally as bycatch in commercial fisheries (Martin and Zorzi 1993). Landing records often report skate species as ''unidentified skate,'' thus preventing an assessment of the potential effects of fishing on population dynamics (Zorzi et al. 2001). Determining the impact of fishing mortality on exploited skate populations is further hindered by a lack of species-specific life history information (Holden 1972; Martin and Zorzi 1993; Dulvy and Reynolds 2002). This is of concern because some skates have life history characteristics (e.g. slow growth, late age at maturity, low fecundity, and moderate longevity) that make them susceptible to overfishing (Holden 1972; Stevens et al. 2000). If current trends continue, fishing effort on skates is likely to increase, subjecting these vulnerable fishes to possible overexploitation.

Fishing mortality has been associated with the declines of many skate populations worldwide. Walker and Hislop (1998) reported that relative abundance of skate species in north-east Atlantic waters was once dominated by the late-maturing blue skate, *Dipturus batis*. However, because of fishery exploitation, the skate assemblage is now dominated by the early-maturing thorny skate, *Amblyraja radiata*. Fishing mortality has also contributed to population declines in the north-west Atlantic of the winter skate, *Leucoraja ocellata*, barndoor skate, *D. laevis*, blue skate, *D. batis* (Johnson 1979; Brander 1981; Casey and Myers 1998). Knowledge of life history parameters and how they influence population dynamics of individual species is needed to better understand the impact of fishing mortality and to better develop appropriate management strategies.

Fishery biologists incorporate age and growth information into models to analyze the population dynamics of individual species (Campana 2001). Early chondrichthyan age and growth research focused on skates because of their abundance, hardiness and ability to survive in captivity, but was limited to nearshore species (Ishiyama 1951; Holden 1972). Since these early studies fishing pressure in some areas, especially deeper waters, has increased motivating research into the life history of these skates (Casey and Myers 1998; Cailliet and Goldman 2004).

Sharks, skates and rays lack otoliths, therefore other calcified structures such as vertebral centra, neural arches, spines and caudal thorns are used to estimate age (Holden and Meadows 1962; Cailliet et al. 1983; Cailliet and Tanaka 1990; Gallagher and Nolan 1999; Cailliet and Goldman 2004). These structures exhibit a banding pattern of opaque and translucent bands that have been found in many species to form during summer and winter months, respectively. However, this assumption must be validated for each to ensure accurate estimates of age (Campana 2001; Cailliet and Goldman 2004).

Bathyraja trachura is a poorly-known eastern North Pacific (ENP) skate with a range of 213–2550 m (most common below 600 m) and may be vulnerable as bycatch in trawl fisheries (Ishihara and Ishiyama 1985; Ebert 2003). Information about the genus *Bathyraja* (Rajiformes: Arhynchobatidae) in the ENP region is limited to taxonomic guides and a few descriptions of egg cases and advanced embryos (Cox 1963; Ishihara and Ishiyama 1985). *Bathyraja trachura* occurs from the Bering Sea to northern Baja California (Ebert 2003; Love et al. 2005). It is a medium-sized species (89.0 cm maximum total length (TL_{max})) with a dorsal surface that is plum brown or slate gray in color.

The objectives of this study were to provide estimates of age and describe growth characteristics for *B. trachura* in ENP waters. Specifically, we estimated size-at-age for *B. trachura* using age estimates from vertebral thin sections and caudal thorns. We attempted to validate age estimates using centrum edge and marginal increment ratio (MIR). Growth models were generated using length- and weight-at-age data for each sex. Results of this project provide previously unknown but critical life history information for the formulation of an effective management plan for *B. trachura* in the ENP.

Materials and methods

Specimen collection

Skates were obtained from along the Pacific coast of the contiguous United States between 48.6°and 33.35° North latitude (Fig. 1). Samples were collected in summer and fall 2002–2003 during the Northwest Fisheries Science Center annual groundfish surveys. Additional samples were collected during winter and spring 2004 from commercial fishery landings via the Pacific States Marine Fisheries Commission – West Coast Groundfish Observer Program.

Sex was determined for each specimen, vertebrae and caudal thorns were removed, and biological information was recorded. Total length (TL), disc length (DL), and disc width (DW), were measured to 0.1 cm and total weight (kg) was recorded following Hubbs and Ishiyama (1968). The first eight vertebrae and first six caudal thorns were removed from each specimen and frozen prior to analysis.

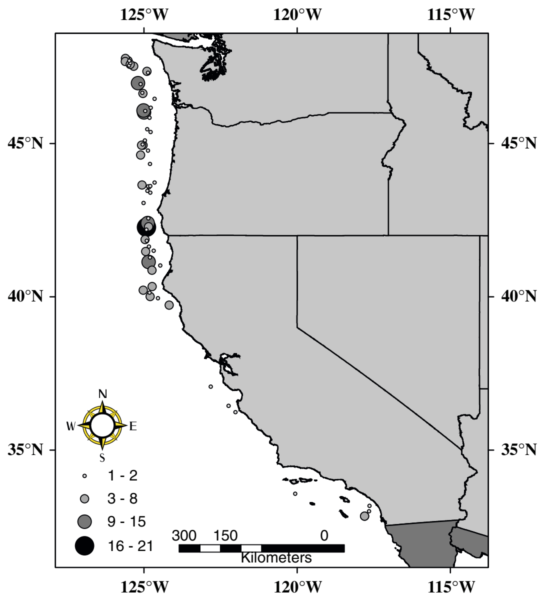

Fig. 1 Map of study area indicating distribution of trawl stations from commercial vessels via the NWFSC and West Coast Groundfish Observers (n = 231). Size of points represents the number of specimen obtained per haul

Preparation and evaluation of ageing structures

Vertebral columns were cleaned of extraneous tissue with a scalpel, neural, and haemal arches were removed and individual centra were separated. To be a useful aging structure, vertebral centra must grow predictably with TL. Mean vertebral centrum diameter was calculated across two perpendicular axis to 0.1 mm. A linear regression was used to determine the relationship between vertebral growth and somatic growth.

Vertebrae were embedded in a polyester casting resin. A 0.3 mm thin section containing the nucleus was removed using a Buehler Isomet low speed saw with paired 10 cm Norton diamond-edged blades. Thin sections were embedded on slides with Cytoseal 60, polished using 1200 grit wet sandpaper, and viewed under a dissecting scope with transmitted light. A pilot study comparing the application of band enhancement techniques following Gruber and Stout (1983) and Gallagher and Nolan (1999) proved that unstained thin sections provided the best band clarity.

All trunk centra from 11 specimens were removed and used to verify consistency of age estimates throughout the vertebral column. Age estimates of the first five vertebrae from the anterior part of the column were compared to age estimates of vertebrae from the last five vertebrae from the posterior part of the column. A paired t-test was used to determine if mean age estimates differed significantly (Zar 1999).

Caudal thorns were manually trimmed of extraneous tissue (Goldman 2004). Whole thorns were submerged in 3% trypsin for 48–72 h to remove remaining tissue (Gallagher and Nolan 1999). A subsample of caudal thorns were partially embedded in a fiberglass resin and sectioned laterally. A banding pattern was not apparent on sectioned thorns therefore, age was determined from whole caudal thorns for remaining samples. Whole thorns were placed on slides at 30°–50° angle and viewed under a dissecting scope with transmitted light.

To determine if caudal thorns would be a useful ageing structure, structural growth, consistency of age estimates, and the potential for thorn replacement were evaluated. Caudal thorn base diameter, measured along anterior-posterior thorn axis, and height was measured from protothorn tip to caudal thorn base using dial calipers to 0.1 mm. Measurements were plotted against TL to determine the relationship between caudal thorn size and body size. A pilot study comparing the application of band enhancement techniques following the methods of Gruber and Stout (1983) and Gallagher and Nolan (1999) concluded that unstained thin sections provided the best band clarity. Age estimates determined during the pilot study were not included in final analysis.

All caudal thorns were removed from the tail of 11 specimens and used to evaluate consistency of age estimates along the tail. Age estimates from the first five anterior most caudal thorns were compared to age estimates from the last five posterior most caudal thorns. A paired t-test was used to determine if mean age estimates differed (Zar 1999). To determine the potential for thorn replacement, caudal thorns were counted on each specimen and plotted against TL. A linear regression was used to determine the relationship between thorn count and somatic growth.

Age determination and validation

The birthmark in each vertebral centrum was identified as the change in angle of the corpus calcareum and was located on thin sections through all size classes (Fig. 2). Banding patterns were not enhanced using these staining methods, therefore thin sections were processed unstained.

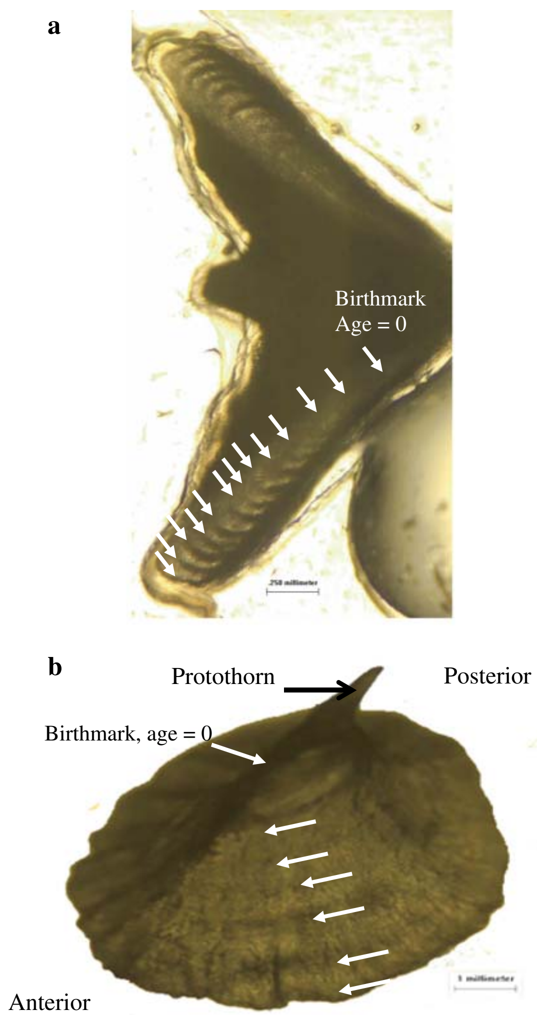

Fig. 2 Description of banding pattern for vertebral thin sections from a 59.8 cm TL female (**a**) and caudal thorns from a 46.5 cm TL male (**b**). On vertebral thin section the change in angle of the corpus calcerum signifies the birthmark (age = 0). On caudal thorns, the birthmark is a prominent ridge which encompasses the thorn below the protothorn. Subsequent white arrows identify opaque bands. (vertebral thin section age = 12, magnification 3.2×; caudal thorn age = 6, magnification = 1.25×)

Each opaque and translucent band pair was considered to represent one year of growth.

A sample of 100 caudal thorns was selected for analysis using stratified random sampling representing all size classes. Four samples were damaged, leaving a total of 96 caudal thorns (51 females, 45 males) for age analysis. The birthmark, identified on caudal thorns through all size classes, was identified as a distinct ridge at the base of the protothorn (Fig. 2). The protothorn forms the tip of the caudal thorn and lacks growth bands. Each opaque and translucent band pair was considered to represent one year of growth

Age estimates were determined using three rounds of independent age estimates by one reader without advanced knowledge of length, season of capture, or sex of the sample. If agreement was not achieved among these three estimates, a fourth read was completed. If agreement was not achieved by the fourth read, samples were removed from analysis. A clarity grade was assigned to each sample based on criteria adapted from Officer et al. (1996). Samples receiving a poor clarity grade were removed from analysis.

Age estimates were evaluated for reader precision and structural bias. Precision among age estimates was assessed using average percent error (APE) (Beamish and Fournier 1981), coefficient of variation (CV) and the index of precision (D) (Chang 1982). Percent agreement (PA) was calculated to determine precision of age estimated between rounds and was evaluated for exact agreement, agreement within one year, and within two years of age (Cailliet and Goldman 2004). Age-bias plots were used to determine the potential bias of age estimates within and between each independent read and between structures (Campana et al. 1995).

Final age estimates were compared between vertebrae and caudal thorns from the same animal. Precision and bias were calculated as previously described to evaluate variation of age estimates between structures. A paired *t*-test was used to determine if there was a significant difference between mean age estimates (Zar 1999).

Validation of vertebral band deposition was attempted using edge analysis and marginal increment ratio (MIR) (Hyndes et al. 1992; Campana 2001). Edge analysis is an optical classification of a thin sections' outermost band as opaque or translucent. Alternately MIR is a measured ratio representing the relative completion of the newest deposited band compared to the previously completed band pair and was calculated as: MIR = MW/PBW, where MW is margin width and PBW is previous band width (Conrath et al. 2002). The resulting ratios were plotted against month of collection to determine the periodicity of band deposition (Cailliet and Goldman 2004). Equality of variances was determined using Cochran's test, following which an ANOVA was used to test for seasonality of band deposition (Zar 1999).

Growth

The von Bertalanffy (VBGF) and Gompertz growth functions were fitted to length- and weight-at-age data for both sexes (Cailliet et al. 2006). The parameter estimates for each function were estimated using SigmaPlot version 8.0 (SPSS Inc., 2002). To determine if growth differed between sexes, analysis of the residual sums of squares (ARSS) was calculated (Haddon 2001).

The VBGF was fitted to length-at-age data and was calculated as: $l_t = L_\infty(1 - e^{-k(t-t_o)})$ where l_t is the predicted length at age t, L_∞ is the maximum length predicted by the equation, k is the growth coefficient, t_o is the theoretical age at which length is zero (Beverton and Holt 1957). Fabens (1965) incorporated known size at birth to better reflect biological reality. A two parameter VBGF with a fixed length at birth (L_o) was calculated as: $l_t = L_\infty - (L_\infty - L_o)\, e^{(-kt)}$ where l_t is the predicted length at age t, L_∞ is the maximum length predicted by the equation, k is the growth coefficient and L_o is set to the known length at birth (19.0 cm). A von Bertalanffy growth function fitted to weight-at-age data following Fabens (1965) and Ricker (1979) was also applied: $W_t = W_\infty(1 - e^{-k(t-t_o)})^3$ where W_∞ is the theoretical asymptotic weight, and values for k, t, t_0 are the same as previously described.

The Gompertz function (Ricker 1979) was fitted to weight and length-at-age data: $W_t = W_\infty e^{(-ke^{-gt})}$ where W_t is age, t is estimated age, g is the instantaneous growth coefficient, k is a dimensionless parameter and the other parameters are as previously described. To evaluate goodness-of-fit, the standard estimate of the error (SEE) and plots of standardized residuals were evaluated (Cailliet et al. 1992). Model selection was based on statistical fit (r^2), convenience, and biological relevance.

Results

Sample collection

Vertebral centra of 231 specimens (102 females, 129 males) and caudal thorns from 100 specimens (54 females, 46 males) were used for age estimation. The smallest female was 14.5 cm TL and male was 16.0 cm TL. The largest female was 86.5 cm TL and male was 91.0 cm TL (Fig. 3).

Preparation and evaluation of ageing structures

Vertebrae were determined to be a useful ageing structure based on the positive linear relationship between their size and TL (Fig. 4). There was no significant difference in this relationship between sexes ($F_{0.05,1,206} = 1.665$, $P = 0.198$); therefore, values were pooled for analysis. A positive linear relationship was identified between TL and centrum diameter ($n = 231$, y = 0.071x–0.2402, $r^2 = 0.92$, $P < 0.001$).

Whole vertebral columns were removed from 11 specimens to determine if age was consistent throughout the structure. However, clear age estimates were only available in anterior and posterior vertebrae from nine specimens. There was no significant difference between age estimates from anterior and posterior vertebral thin sections ($n = 9$, $t_{(0.05(2),8)} = 0.748$, $P = 0.47$). All age estimates were based on anterior vertebral centra.

The utility of caudal thorns as ageing structures was not demonstrated (Fig. 5). Caudal thorn size increased with body size, there was no evidence of thorn replacement, and ages were consistent along the tail. A logarithmic curve represented the best fit between thorn height and total length

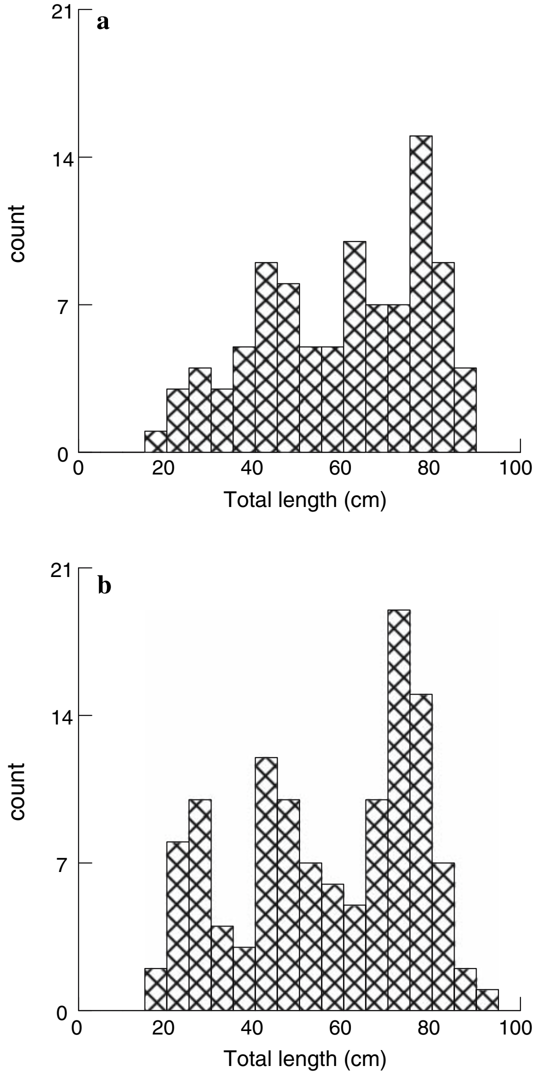

Fig. 3 Size frequency histogram of specimens used in age analysis; males (**a**;n = 110, a) and females (**b**;n = 86, b)

(n = 100, y = 0.6737Ln(x) + 0.3329, r^2 = 0.24) and between thorn base length and total length (n = 100, y = (2.4073 × Ln(x))–5.652, r^2 = 0.60) (Fig. 5a). Meristic counts of caudal thorns (from 248 additional specimens not aged in this study) indicated that caudal thorn count and TL were not significantly related (y = –0.0266x + 26.91, r^2 = 0.04, P < 0.001) (Fig. 5b). The presence of healed scars suggests that thorn replacement does not occur in this species. Additionally, there was no significant difference between age estimates from anterior and posterior caudal thorns ($t_{(0.05(2),7)}$ = 1.62, P = 0.149); age was estimated from anterior caudal thorns.

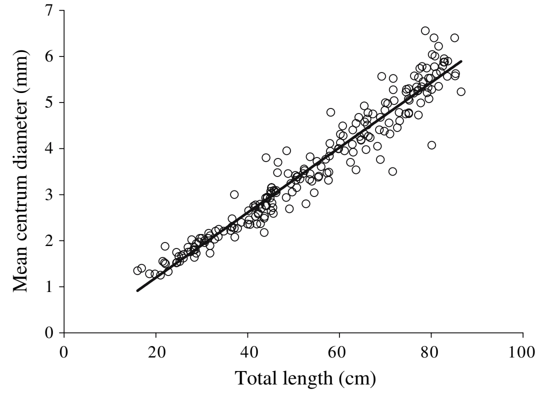

Fig. 4 Relationship between mean vertebral centrum diameter and total length for sexes combined (n = 231, y = 0.071x – 0.2402, r^2 = 0.92)

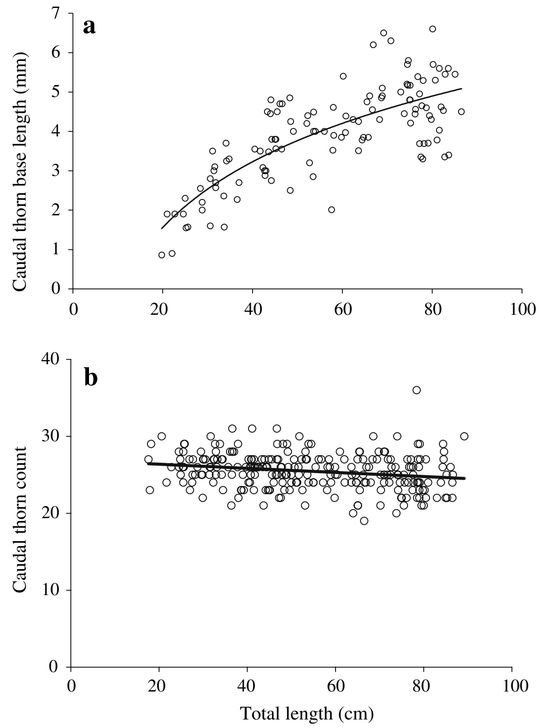

Fig. 5 Best fit relationships between caudal thorn base length and body size (**a**; y = 2.4073Ln(x) - 5.652, r^2 = 0.60, n = 100) and number of caudal thorns and body size (**b**; y = –0.0266x + 26.91, r^2 = 0.04, n = 248) are depicted for *Bathyraja trachura*

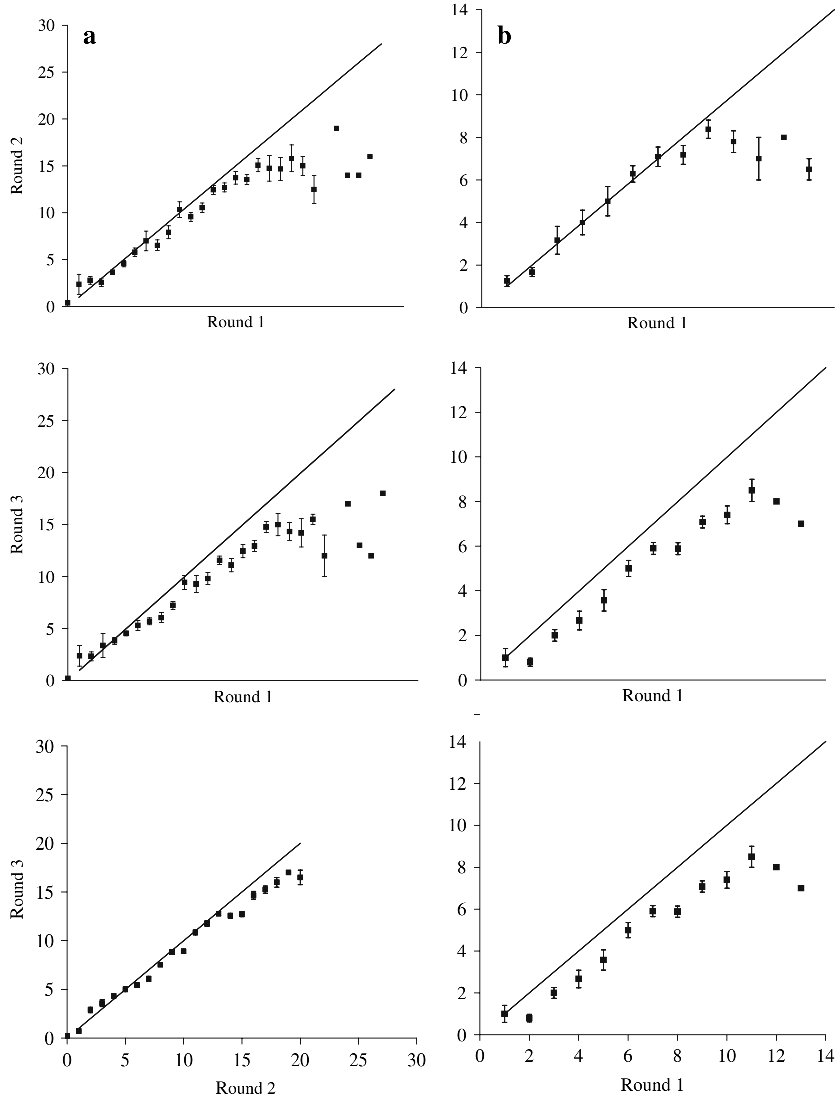

Fig. 6 Age bias plots of age estimates between independent rounds of (**a**) vertebral age estimates (n = 197) and (**b**) caudal thorn (n = 96) band counts. The 45° line represents 1:1 agreement of age estimates between rounds

Age determination and validation

Final age estimates were determined from 197 vertebral samples which provided the best band clarity. Analysis of vertebral band clarity grades indicated that visibility of bands was variable and inconsistent between samples. Approximately 9.6% were determined to be of poor clarity (grade 5) and were not included in analysis.

Calculations of bias and precision indicated the first round of vertebral band counts was biased toward older age estimates. Average percent error and coefficient of variation were acceptable between the three independent rounds of band counts (APE: 13.6%, CV: 18.6%, D: 9.3). Percent agreement within ±2 years was 76.1% and 67.5% respectively, for first vs. second and first vs. third rounds of band counts. Greater agreement was found between the second and third round of band counts (86.8%). Age-bias plots indicated that the first round of band counts were biased toward older age estimates (Fig. 6a).

Caudal thorn samples that received poor clarity grades (2.0%) were removed from analysis and final age was determined for 96 samples. Analysis of clarity grades indicated that visibility of bands were variable and inconsistent between samples. Approximately 2.2% were determined to be of poor clarity (grade 5) and were not included in analysis.

Precision and bias estimates indicated that the first round of band counts had the greatest variation. Average percent error and coefficient of variation values for caudal thorns were highest when all rounds of band counts were combined (APE: 17.7%, CV: 24.6%, D: 12.3). Percent agreement calculations also indicated that the second and third round of band counts were most similar, 82.2% within two band counts. Age bias plots indicated that the first round of band counts produced greater bias when compared to later rounds, indicating that reader ability improved over time (Fig. 6b).

Vertebral thin sections were determined to be a better structure than caudal thorns for age estimation of *B. trachura*. Age estimates between the structures were consistent until age 7 and then became quite variable (Fig. 7). Age estimates compared between structures produced unacceptable precision values and bias (APE: 29.9%, CV: 40.4%, D: 28.5). There was a significant difference between ages estimated from vertebral thin sections and those estimated from caudal thorns ($t_{0.05(2)17} = 3.003$, $P = 0.007$). Age estimates of vertebral thin sections were more precise, and were used for validation and growth analyses. The maximum ages determined by estimates from vertebral thin sections were 17 years (females) and 20 years (males).

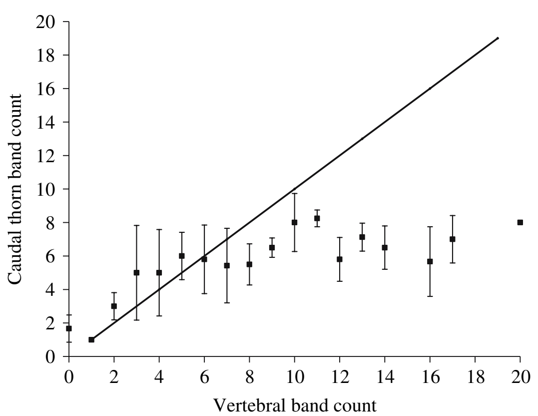

Fig. 7 Age bias plot of caudal thorn and vertebral age estimates (n = 74). The 45° line represents 1:1 agreement of age estimates between structures

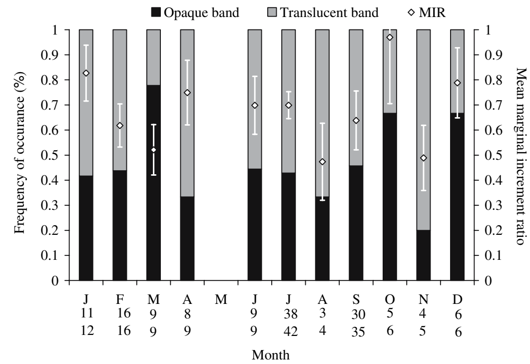

Fig. 8 The frequency of occurrence (FO; n = 153) of opaque and translucent bands and mean Marginal Increment Ratio (MIR; n = 139) are plotted by month. Black bars indicate frequency of opaque bands, grey bars depict frequency of translucent bands, and white diamonds represent mean MIR values. Numerical values reported below month indicate sample size of MIR (top) and FO (bottom)

Band deposition could not be validated using the methods applied in this study. About 35% of thin sections were removed from edge analysis because of poor clarity of the thin section. Edge analysis did not show a significant difference between the occurrence of opaque and translucent bands among months ($\chi^2_{0.05,3} = 1.06$, $P < 0.75$; Fig. 8). Likewise, seasonality of band formation could not be validated using MIR. About 65% of thin sections were of optimal clarity and used for MIR analysis. There was no significant difference between MIR values among months ($F_{0.05,10,128} = 0.75$, $P = 0.67$; Fig. 8). Although validation was not achieved using edge and MIR analysis, growth models were derived assuming annual deposition of one opaque and translucent band.

Growth

The model providing the most biologically reasonable fit for the data was the two parameter VBGF (Fig. 9). Females reached a larger maximum size ($L_\infty = 101.53$) with a slightly lower growth coefficient ($k = 0.08$) than males ($L_\infty = 100.17$, $k = 0.09$). However, there was no significant difference between female and male growth ($F_{0.05,1,307} = 0.196$, $P = 0.90$). Therefore, data were combined and the resulting growth parameters for

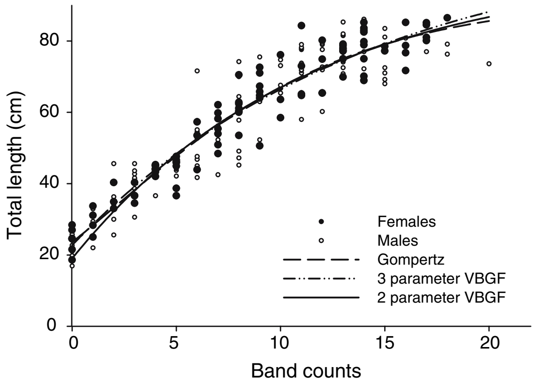

Fig. 9 Growth functions fitted to length-at-age data for combined sexes. Note VBGF = von Bertalanffy growth function

the pooled two parameter VBGF were L_∞ = 101.25 cm and k = 0.09.

Discussion

Our study expanded the known size range of *B. trachura* to include a new TL_{max}, one adult male was measured at 91.0 cm TL. Prior to this study the maximum size was 89.0 cm TL (Ishihara and Ishiyama 1985; Craig 1993). Samples were obtained from commercial fisheries and fishery-independent surveys, but neither source used trawling gear that could sample the entire depth range of this species; it is possible that larger specimen exist.

Caudal thorns were not determined to be a valid structure for age estimation of *B. trachura.* Caudal thorns of *B. trachura* did not grow linearly with body size, suggesting that their growth slowed with increased size and age estimation of larger individuals would be difficult (Francis and Maolagáin 2005). Caudal thorn height was difficult to relate to TL because of protothorn erosion in larger specimens. Because thorns originate from dermal dentical scales and, unlike vertebrae, do not support mass; thorn growth may not be inherently linked to somatic growth (Gallagher et al. 2005). Caudal thorns were originally considered as a possible ageing structure for this study because of the consistency of age estimates throughout the structure. Subsequent evaluation of precision proved that age estimates from thorns were not precise. Maximum ages determined by caudal thorns were less than half the maximum age determined by vertebral thin sections.

Gallagher and Nolan (1999) first used caudal thorns as an ageing structure for four species of *Bathyraja* from the Falkland Islands: *B. brachyurops*, *B. griseocauda*, *B. scaphiops*, and *B. albomaculata*. Caudal thorns were found to be suitable ageing structures that provided precise age estimates and ease of band interpretation. Since their publication caudal thorns often have proven to be a difficult structure to age, producing poor precision (Francis and Maolagáin 2005) and may be complicated by the slowing of thorn growth with increased somatic growth (Perez 2005). Perez (2005) found evidence of thorn replacement in *B. kincaidii*, indicating that not every thorn depicted actual age for this species.

Seasonality of band pair deposition in vertebral thin sections could not be validated using MIR and edge analysis. Diminished clarity of the banding pattern was caused by poor calcification of the vertebral edge, distortion of edge quality caused by overpolishing or inability to acquire a clear photographic image of the region. This lack of clarity limited the number of samples included in MIR analysis, potentially restricting detection of band periodicity.

Although vertebral band deposition was not validated, standard age determination methods were applied. Vertebral thin sections have been used for ageing more than 67 elasmobranch species (Cailliet and Goldman 2004; Perez 2005; Licandeo et al. 2006; McFarlane and King 2006). Among the studies, annual band deposition was validated for 54 species including seven skate species (Cailliet and Goldman 2004). These findings support the assumptions used to determine age for *B. trachura.* However, caution is necessary when using unvalidated age estimates for management purposes because of the inherent possibility for over or underestimation of age (Campana 2001; Cailliet and Goldman 2004).

In this study, multiple growth functions were used to model growth and the criteria used for growth model selection were statistical fit, convenience, and biological relevance (Cailliet et al 2006, Table 1). Growth functions fitted to weight-at-age data provided lowest variance about the mean, however W_∞ was underestimated by both

Table 1 Growth functions and estimated parameters for *Bathyraja trachura*. Length and weight-at-age data are represented for sexes combined. Note: SEE = standard error of the estimate, VBGF = von Bertalanffy growth function, t_o = size at birth, k and g = growth coefficients, L_o (W_o) = size(weight) at birth, L_∞ (W_∞) = maximum size(weight)

Parameter	Length-at-age			Weight-at-age	
	3 Parameter VBGF	2 Parameter VBGF	Gompertz	VBGF	Gompertz
L_∞ (W_∞)	112.11	101.25	92.62	(3.23)	(3.22)
$L_o(W_o)$	22.85	19.0	23.59	–	(0.02)
k	0.06	0.09	1.37	0.19	5.07
t_o	–3.45	–	2.20	0.70	7.70
g	–	–	–	0.19	0.21
SEE	5.36	5.55	5.26	0.49	0.54
r^2	0.93	0.92	0.92	0.79	0.74

functions (W_{max} = 5.0 kg). The two-parameter VBGF, fitted to length-at-age data, estimated a reasonable L_∞ and was the only length model that did not overestimate L_o; making it the most biologically reasonable choice. Since the three-parameter VBGF is the most commonly applied model for elasmobranch species (Cailliet and Goldman 2004), these values were used for comparison with the published literature.

The predicted growth parameters for *B. trachura* are not consistent with the assumption that larger batoids live longer and grow slower than smaller batoids. *Bathyraja trachura* is a medium sized species (91 cm) with a growth coefficient (k = 0.06) that is smaller than some smaller relatives such as *R. erinacea* (k = 0.35; Waring 1984) but not some others like *Raja clavata* (k = 0.05; Brander and Palmer 1985). Maximum age of *B. trachura* was determined to be 20 years, which is older than smaller species but not younger than all larger species such as *Amblyraja radiata* (16 years; Sulikowski et al. 2005).

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