Bomb dating and age determination of skates (family Rajidae) off the eastern coast of Canada

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Recent declines in abundance of skates off the eastern coast of Canada have heightened the need for validated age and growth estimates in the region. In all, 502 winter (*Leucoraja ocellata*), little (*Leucoraja erinacea*), thorny (*Amblyraja radiata*), and smooth (*Malacoraja senta*) skate vertebral centra collected seasonally between 1999 and 2004 were sectioned using a mass processing method, then used to reconstruct growth in each species. Bomb radiocarbon ($\Delta^{14}C$) analysis was used to provide evidence of annual band-pair deposition in thorny skates. Estimates of L_∞ from traditional von Bertalanffy growth models (VBGM) ranged from 60.6 cm (little skate) to 89.7 cm (thorny skate), and K estimates from 0.07 (thorny skate) to 0.19 (little skate). A modified two-parameter VBGM ($L_{max} = 94.1$ cm) fitted to winter skate length-at-age data yielded a value of K of 0.15. Maximum observed ages ranged from 12 (little skate) to 19 years in both winter and thorny skates. The year-specific incorporation of $\Delta^{14}C$ milled from thorny and winter skate vertebral sections closely resembled shark-derived reference chronology values from the Northwest Atlantic. Pre-bomb $\Delta^{14}C$ in a thorny skate collected in 1988 and aged at 23 years appeared to validate age interpretations and suggested that thorny skate reach an absolute age of at least 28 years, the oldest validated age reported for any species of batoid.

Keywords: age determination, bomb radiocarbon, eastern Scotian Shelf, mass processing technique, Rajidae, validation, vertebrae.

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Introduction

A recent paper by Dulvy *et al*. (2000) stated that "skates are arguably the most vulnerable of exploited marine fishes", in part because of their relatively large size, slow growth rate, late maturity, low fecundity, large size at birth, and long lifespan, or their "equilibrium" (*k*-selected) life-history strategy (Holden, 1973; Hoenig and Gruber, 1990; Walker and Hislop, 1998). Many species of skate have declined markedly over all or considerable portions of their ranges, the most frequently cited examples being the common skate (*Dipturus batis*) in the Irish Sea (Brander, 1981) and the barndoor skate (*Dipturus laevis*) in the Northwest (NW) Atlantic (Casey and Myers, 1998), both of which were overfished. Recent downward trends in abundance have also been noted in the thorny skate (*Amblyraja radiata*) and the smooth skate (*Malacoraja senta*) in the Gulf of Maine (NEFMC, 2003; Sulikowski *et al*., 2007), and the winter skate (*Leucoraja ocellata*) on the eastern Scotian Shelf (ESS) off Nova Scotia, Canada, which is currently being considered for listing as threatened under Canada's Species at Risk Act (Swain *et al*., 2006).

Age information is crucial to our understanding of the resilience of species to exploitation because it forms the foundation for calculations of growth and mortality rates, age at maturity, and longevity (Campana, 2001). Few studies, however, have validated the temporal nature of growth bands observed in skate and ray (Superorder Batoidea) vertebral centra, and of those carried out, most have used techniques that are difficult to carry out objectively and accurately for all life stages (Beckman and Wilson, 1995; Campana, 2001). Moreover, despite increasing concern for skate populations worldwide (Ebert and Sulikowski, 2007), age has never been rigorously confirmed in any skate species using a direct validation method (Cailliet and Goldman, 2004). The importance of validating the periodicity of band-pair formation over the full age range of any species of elasmobranch was demonstrated in a paper reporting aperiodic deposition in the Pacific angel shark (*Squatina californica*; Natanson and Cailliet, 1990), and more recently highlighted in a paper on porbeagle sharks (*Lamna nasus*), where it was hypothesized that band deposition may stop with the cessation of somatic growth in older sharks (Francis *et al*., 2007).

Four species of exploited NW Atlantic skate (family Rajidae) for which rigorously validated age determinations are lacking are the winter skate, the little skate (*Leucoraja erinacea*), the thorny skate, and the smooth skate. Estimates of age and growth from the Gulf of Maine (Sulikowski *et al*., 2003, 2005) and/or all or portions of the US Northeast coast (Waring, 1984; Frisk and Miller, 2006) have either not been validated (Waring, 1984; Frisk and Miller, 2006) or been validated using marginal increment analysis (MIA; Sulikowski *et al*., 2003, 2005) or captive rearing (Natanson, 1993). Although prevalent in the literature, the reliability and effectiveness of these methods as a means of validating the age interpretations has been questioned, at least in part (Campana, 2001; Cailliet *et al*., 2006). MIA is dependent upon the objective interpretation of vertebral edge characteristics—a task made especially difficult in slow-growing species owing to the progressive narrowing of band pairs at the vertebral margin with age—and captive rearing can yield misleading results given the strong influence of the ambient environment on annulus formation. Moreover, although the confirmation of annulus formation in young fish is often used to infer absolute age, it assumes that annuli form at the same frequency in older fish. More accurate estimates are obtained using direct measures of absolute age, such as bomb radiocarbon dating (Campana, 1997; Andrews *et al.*, 2005; Ardizonne *et al.*, 2006; Kerr *et al.*, 2006).

In the NW Atlantic, skates may be particularly vulnerable to decline because of an increase in both direct and indirect catches of skate in the past few decades in response to declines in traditional finfish stocks. Recent, in some cases marked, downward population trajectories have been noted for all but the little skate in at least some portion of each species' range (Sosebee and Terceiro, 2000; NEFMC, 2005; Swain *et al.*, 2006). Concurrent changes in population structure and distribution have also been documented for several species, causing some to be classified as commercially prohibited (NEFMC, 2005; Swain *et al.*, 2006). In view of the depleted state of skate populations in the NW Atlantic and an overall paucity of life-history data, the goal of this study was to determine age and growth characteristics of the four most common species of skate on the ESS. Specific objectives were to (i) calculate age and growth parameters for each species of NW Atlantic skate, and (ii) compare growth among and within species in an effort to recognize each species' vulnerability. Given that age misinterpretations can lead to potentially serious errors in the management and understanding of fish populations (Beamish and McFarlane, 1983), a third objective of this study was to validate vertebral age interpretations using bomb radiocarbon analysis, an age-validation technique that is particularly well-suited for long-lived fish (Campana, 2001).

Material and methods

Sample collection and preparation

Skates were collected seasonally (i.e. spring, summer, autumn, winter) off the east coast of Canada along the ESS (NAFO Divisions 4VsW) from May 2004 to March 2006 during Canadian Department of Fisheries and Oceans (DFO) groundfish bottom-trawl research vessel (RV) surveys (69 winter skate, 86 little skate, 168 thorny skate, 91 smooth skate), industry–science surveys (59 winter skate, 6 little skate, 100 thorny skate, 22 smooth skate), and from commercial longline fishers (14 thorny skate). For each skate caught, sex and weight (kg) were recorded along with total length (TL), measured from the tip of the rostrum to the end of the tail, and disc width (DW), measured from the tips of the widest portion of the pectoral fins (both to the nearest 0.5 cm). Sex- and length-stratified fish were frozen at sea for later extraction of their vertebrae. During July 2005 and March 2006 RV surveys, egg cases caught with the trawl gear were also frozen at sea and brought back to the laboratory for dissection. All removed embryos were measured (TL and DW), sexed, and weighed (total weight in g). In all, 85 winter skate thoracic vertebral samples collected during RV surveys on the ESS in 1999 and 2000 were used to supplement more-recent samples.

After thawing, a segment of the vertebral column immediately posterior to the scapular origin (mid-dorsal) was removed and refrozen. For embryonic skates, the entire vertebral column was removed under a dissecting microscope. From each fish, 5–7 vertebrae were then separated from frozen vertebral segments using a scalpel, soaked in warm water and/or bleach (6% hypochlorite) for no more than 15 min (Cailliet and Goldman, 2004), rinsed in distilled water, and air-dried for no less than 48 h.

It is difficult to differentiate between little and winter skate <30 cm TL using morphometrics alone (McEachran and Musick, 1973), so to do so, tissue clips were taken from the posterior pelvic fins of fresh or partially thawed skates, and a polymerase chain reaction–restriction fragment length polymorphism (PCR–RFLP) assay was used to differentiate genetically between species as per Alvarado Bremer *et al.* (2005). Skates yielding inconclusive molecular results ($n = 3$ or 10% of winter/little skates <30 cm TL) were eliminated from the study.

Vertebrae measuring 4.0–7.0 mm in diameter were mass-embedded and sectioned to a thickness of 0.5–0.7 mm using techniques modified from those commonly used in the production ageing of teleosts (Strong *et al.*, 1985), which significantly reduced processing time. Preliminary preparation and imaging of vertebrae indicated that anterior thoracic vertebrae are superior to more posterior thoracic and caudal vertebrae for age analyses owing to their larger centra and more readily distinguishable growth bands, and that sectioned vertebrae are preferable to whole centra in all four species. As part of the mass production process, haemal arches were removed and whole centra were fixed face-up along their longitudinal axes on polyester resin plates using 5-min epoxy before the application of resin topcoats. A high-speed modified surface grinder with diamond blades was used to simultaneously section 50–75 vertebrae plate^{-1}, allowing hundreds of vertebrae to be processed daily. Vertebrae measuring ≥ 7.0 mm in diameter were sectioned using a low-speed Isomet saw with three Buehler^{TM} 4-in diamond blades separated by spacers. Each centrum was cut at its widest diameter along the mid-sagittal axis, resulting in two "bowtie" sections 0.5–0.7 mm thick. Vertebrae too small for mass production (i.e. measuring 1.0–4.0 mm in diameter) were embedded individually in Araldite epoxy and hardener, and sectioned using the same techniques employed for the largest vertebrae of each species. Before imaging, vertebral sections were sanded and polished to enhance band visibility. For vertebrae ≤ 1.0 mm in diameter (i.e. from embryonic and young-of-the-year skates), whole vertebral centra were mounted longitudinally on microscope slides using a thermal setting resin (Crystal Bond^{TM}), and lightly sanded with successively finer 3M^{TM} aluminum oxide lapping film to produce half centra with exposed bowtie faces for imaging.

Subsamples of vertebrae from each species were immersed in ethanol (95% ETOH) for durations ranging from 75 h to 5 months (McFarlane and King, 2006) and/or stained with alizarin red-S (Lessa *et al.*, 1999) in an effort to enhance band visibility; however, neither technique improved the clarity of bands in vertebral sections of each species, resulting in the use of untreated sections in all subsequent analyses.

Assignment of age

Digital images (minimum resolution of 1280 × 1024) of ethanol-immersed sections were taken under reflected light against a black background using a Nikon SMZ1000 dissecting microscope with a Diagnostic Instruments SPOT CCD digital camera and Image Pro Plus image analysis software. Adobe Photoshop CS2 was used to enhance the contrast between adjacent growth bands and to increase overall sharpness and clarity. In all species, band pairs assumed to be annual consisted of a wide opaque band (which appeared white under reflected light) and a thin translucent band (which appeared black). Age estimates were generated by counting visible translucent bands in the corpus calcareum with the clearest, most discernible pattern (Figure 1). The spacing and clarity of bands, inflections near the outside and inside edges of the corpus calcareum, and band continuity across the intermedialia (for bands close to the focus, or the midpoint of the isthmus) were used to distinguish true bands from checks. Section quality was rated on a scale of "1" (very good) to "4" (poor), with quality being dependent on criteria such as band clarity along the corpus calcareum and closeness of the sagittal cut to the focus (or the centre of the vertebrae). For all species, length-at-age data were compared visually between lower quality vertebrae (i.e. quality ratings "3" and "4") and higher quality vertebrae (i.e. quality ratings "1" and "2") to examine potential length (or age) bias among ratings. No appreciable bias was apparent and, as such, only images with quality ratings ≤ 2 (i.e. "very good" or "good") were included in subsequent analyses to minimize unnecessary variability. Of all vertebral sections examined, 74% (87 males, 70 females) of winter skate vertebrae (Figure 1a), 97% (41 males, 48 females) of little skate vertebrae (Figure 1b), 61% (81 males, 90 females) of thorny skate vertebrae (Figure 1c), and 75% (47 males, 38 females) of smooth skate vertebrae (Figure 1d) were assigned a quality rating of ≤ 2 and used in subsequent growth modelling. Maximum and minimum lengths of fish whose vertebrae were assigned quality ratings ≤ 2 were similar to those collected overall. Measurements of vertebral radius (VR, mm) were made from the midpoint of the full bowtie to the distal margin of the corpus calcareum with the clearest band pairs, using Image Pro Plus 5.1 (Figure 1).

In some thorny and smooth skate sections assigned overall quality ratings of ≤ 2, it was difficult to discern translucent bands close to the focus (Figure 1e and f). In those skates, "missing" band counts were estimated using measurements of the straight-line distance from the focus to the first distinguishable band (measured along the same diagonal as VR measurements) and species-specific regressions between total band count (#) and VR (mm) generated from vertebral sections deemed to have "complete" counts. Total counts were obtained by summing visible and estimated band counts. Growth curves were then fitted to all length-at-age data including sections deemed unreadable near the focus. Maximum likelihood ratio tests (Kimura, 1980; Cerrato, 1990) were used to examine whether the inclusion of sections with calculated "inner" bands significantly affected species-specific growth parameters.

The location of the birth band (BB) in each species was confirmed by comparing suspected birth band radius (BR)

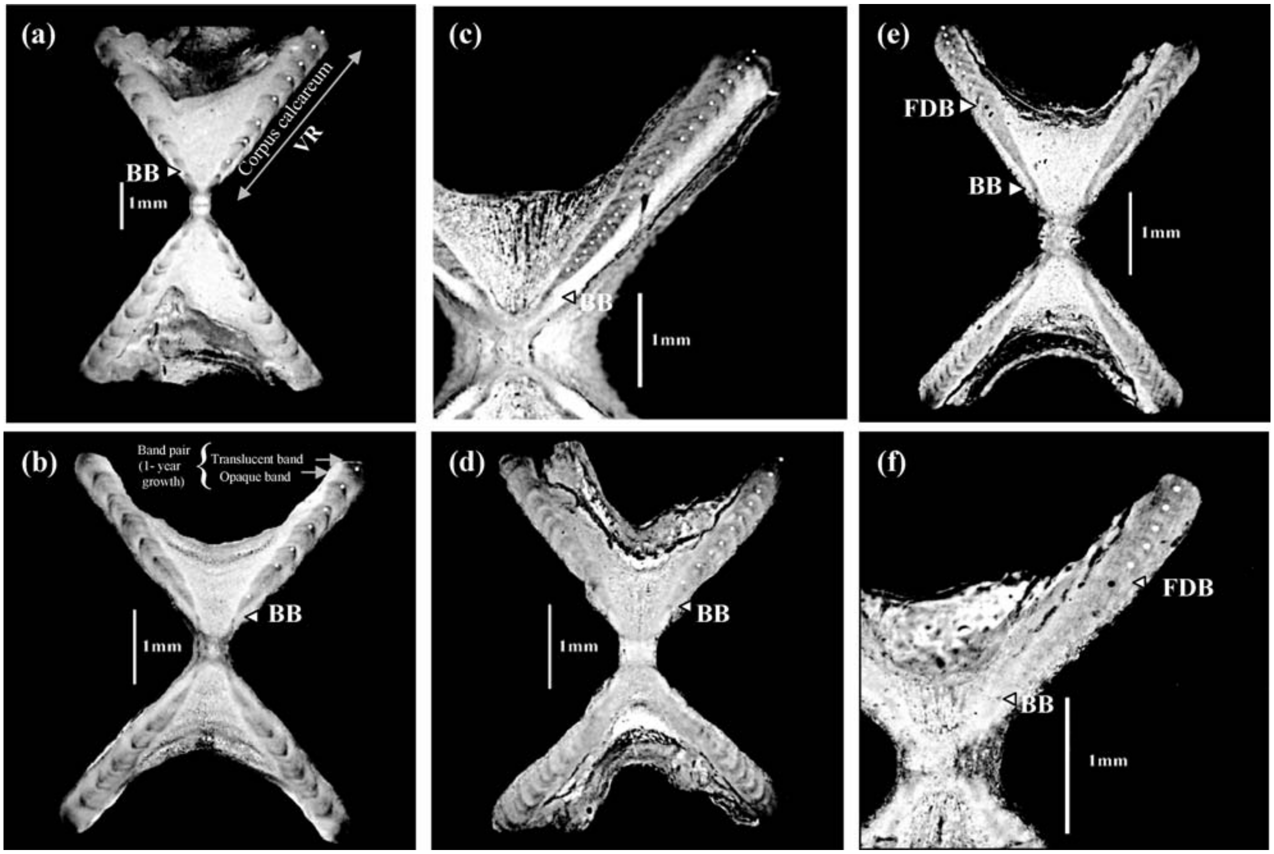

Figure 1. Digitally enhanced photograph of sectioned and polished centra from (a) a winter skate (female, TL = 80 cm) estimated to be 8 years old, (b) a little skate (male, TL = 54.5 cm) estimated to be 7 years old, (c) a thorny skate (THARC, a thorny skate from the Atlantic reference Centre; male, TL = 64.5 cm) estimated to be 23 years old, (d) a smooth skate (female, TL = 51 cm) estimated to be 10 years old, (e) a thorny skate (male, TL = 74 cm) estimated to be 14 years old (nine visible bands + five calculated inner bands), and (f) a smooth skate (male, TL = 51.5 cm) estimated to be 12 years old (six visible bands + six calculated bands). Visible translucent bands are denoted by white dots. The position of the BB is denoted, as is the first distinguishable band (FDB) (black dot), on centra whose counts were deemed "incomplete".

measurements with VR measurements of available late-term embryos (well-formed, pigmented skate with no external yolk sacs) and/or early young-of-the-year fish (i.e. with internal yolk sacs). Regressions between VR and TL for each species, along with published hatch lengths, were also used to verify the location of the BB along the corpus calcareum of each section (Campana, 2001).

Vertebral sections were aged 3–5 times by a primary reader. A second reader independently aged a random subsample of winter and thorny skates. Pairwise age bias plots were used to test for systematic biases in inter-reader age estimates. The coefficient of variation (*CV*) was used to assess precision (Campana, 2001; Cailliet and Goldman, 2004).

Growth curve estimates

For each species, growth curves were fitted to length-at-age data for each sex separately and for sexes combined using non-linear least-squares estimation (R-Project 2.3.1). The traditional three-parameter von Bertalanffy growth function (VBGF; von Bertalanffy, 1938) is expressed as

$$L_t = L_\infty[1 - e^{-K(t-t_0)}], \tag{1}$$

where L_t is length at age t, L_∞ the maximum theoretical TL, K a growth constant that describes how rapidly the horizontal asymptote is approached, and t_0 the theoretical age at length zero. A modified, two-parameter VBGF (2VBGF; Fabens, 1965) was fitted to the combined winter skate data, where L_∞ was replaced with a maximum length, $L_{\max}$, of 94.1 cm TL or 95% of the maximum reported length for winter skate on the ESS in the past 10 years of DFO RV surveys. Length at birth (L_0) was then calculated from the von Bertalanffy growth curve parameters using the equation $L_0 = L_\infty$ (or $L_{\max}$)$(1 - e^{Kt_0})$ to provide an additional biological measure by which models could be assessed.

Also fitted to the length-at-age data for each species were: (i) a modified form of the Gompertz growth function, expressed as

$$L_t = L_0[e^{G(1-e^{-kt})}], \tag{2}$$

where L_0 is theoretical length at birth, G the instantaneous rate of growth at time t, and k the rate of decrease of G, and (ii) a logistic growth equation expressed as

$$L_t = \frac{L_\alpha}{1 + [(L_\alpha - L_0)/L_0]e^{-rt}}, \tag{3}$$

where L_a is the asymptotic TL, r the logistic growth coefficient, and L_0 the theoretical TL at birth. Asymptotic TL (L_∞) was estimated from the parameters obtained by fitting the Gompertz model, using the equation $L_\infty = L_0\, e^G$. Akaike's Information Criterion (AIC) (Buckland *et al.*, 1997), significance level ($p < 0.05$), the coefficient of determination (r^2), and the closeness of estimated model parameters (i.e. L_0 and L_∞) to known and/or published hatch length and maximum TL values were used to evaluate the resultant growth models. As a basis for presenting and ranking growth models, a measure of each model relative to the best model (ΔAIC) was calculated as

$$\Delta\mathrm{AIC} = \mathrm{AIC}_i - \min \mathrm{AIC}, \tag{4}$$

where AIC_i is the AIC value of model i, minAIC the AIC value of the best model (or the model with the lowest AIC_i), and ΔAIC values >10 can be omitted from consideration (Burnham and Anderson, 2002). Once the best model was determined for each species, maximum likelihood ratio tests (Kimura, 1980; Cerrato, 1990) were used to evaluate statistical differences between sex-specific growth curves. For winter skate, the size range over which the sex-specific growth curves were fitted and compared was limited to TLs less than the maximum observed female size (84 cm TL), because of poor representation of the largest size classes in the female sample relative to that of males.

Longevity

Initial values of lifespan ($t_{\max}$) for each species on the ESS were obtained from the oldest vertebral age estimates in this study. Theoretical longevities [$T_{\max(\mathrm{th})}$] of each species were determined using Taylor's (1958) definition of lifespan of teleost fish as the time required to reach 95% of the mean theoretical maximum length (L_∞):

$$T_{\max(\mathrm{th})} = t_0 - \frac{\ln(1 - 0.95)}{K}, \tag{5}$$

where t_0 and K are the parameters of the von Bertalanffy growth curve, and Fabens' (1965) equation is based on the same assertion:

$$T_{\max(\mathrm{th})} = \frac{5(\ln 2)}{K}, \tag{6}$$

where K is the growth coefficient from the VBGF.

Although observed longevity values from fished populations are likely to underestimate true maximum ages (Natanson *et al.*, 2002), theoretical longevities sometimes appear to exceed actual maxima. Actual longevities probably lie somewhere between the two extremes.

Age validation

Bomb radiocarbon analyses were used to assess the accuracy of vertebral band-pair counts as annual age indicators. Some 3–4 sections (0.7–1.0 mm thick) of cervical vertebrae from seven winter skates collected in 2005 and six winter skates collected in 1999 and 2000 on the ESS, and one thorny skate [thorny skate from the Atlantic Reference Centre (THARC)] collected in 1988 off the slope of the Scotian Shelf (Figure 1c) were selected for extraction of specific band pairs based on dates of collection, assigned annulus ages and quality ratings of the sections (i.e. "1" and "2" only). Multiple pieces (7–20 pieces, 0.2–1.5 mg each) corresponding to the same growth bands, but from different corpus calcarea, were extracted from each of the sections using a computer-controlled micromilling machine (Merchantek Micromill). Samples were milled to exclude the outer edge of the vertebrae and to ensure no adherent tissue or resin contamination. All isolated, solid pieces were then pooled for a total of 5–15 mg specimen^{-1}. For six of the vertebrae collected in 2005, samples corresponding to the last three fully formed growth bands were extracted and pooled. For the vertebrae collected in 1999 and 2000 (and for one vertebra collected in 2005), the first five fully formed growth bands were removed and pooled for analysis. From THARC, the last five and first five fully formed growth bands were extracted, as were the five bands deposited immediately distal to the first five bands (i.e. growth bands 6–10; Figure 1c). The presumed date of sample formation was calculated as the year of skate collection minus the number of band pairs counted between the midpoint of the sample and the distal edge of the section. The potential uncertainty for each assigned year of sample formation was calculated by multiplying the overall *CV* by the difference between year of collection and presumed year of band-pair formation, as per Ardizonne *et al.* (2006). After sonification in Super Q water and drying, the sample was weighed to the nearest 0.1 mg in preparation for ^{14}C assay with accelerator mass spectrometry (AMS). AMS assays also provided δ^{13}C (‰) values used to correct for isotopic fractionation effects. Radiocarbon values were subsequently reported as Δ^{14}C, which is the per mil (‰) deviation of the sample from the radiocarbon concentration of 19th century wood, corrected for sample decay before 1950 according to methods outlined by Stuvier and Polach (1977). The mean standard deviation (s.d.) of the individual radiocarbon assays was ~5‰.

Atmospheric testing of atomic bombs in the 1950s and 1960s resulted in an abrupt, worldwide increase in radiocarbon (Δ^{14}C), detectable in marine dissolved inorganic carbon (DIC) and in all biogenic marine carbonates growing in surface waters during the 1960s (Druffel, 1989; Campana, 1997). This increase in radiocarbon was incorporated synchronously into a wide variety of marine organisms growing at that time (i.e. corals, bivalves, fish), providing interchangeable Δ^{14}C carbonate chronologies based on known-age material (i.e. reference chronologies) against which samples with unknown dates of formation could be compared (Campana, 2001). To determine the dates of formation of the milled skate samples, skate-derived radiocarbon values were compared with radiocarbon values from a carbonate reference chronology from the NW Atlantic (1949–2001). However, other studies have found that the bomb radiocarbon chronologies recorded in shark vertebrae lag those of carbonates by up to 3 years owing to the metabolic origin of the carbon in the vertebrae (Campana *et al.*, 2002; Ardizonne *et al.*, 2006). For this reason, a reference chronology developed from NW Atlantic porbeagle (*L. nasus*), 1955–2000, and shortfin mako (*Isurus oxyrinchus*) vertebrae (Campana *et al.*, 2002) was also compared with the Δ^{14}C of skate samples.

The optimal years of sample formation for Δ^{14}C-based ageing fall between 1958 and 1965, the period of most rapid ^{14}C increase and, therefore, the most sensitive period for dating (Campana *et al.*, 2002; Andrews *et al.*, 2005; Kerr *et al.*, 2005; Piner *et al.*, 2005). However, finding archived skate vertebral tissue with band pairs which would have formed in marine surface waters in the 1960s was extremely difficult. All skates used in this study were collected relatively recently and had presumed ages of no more than 19 years. Of the 167 winter, little, thorny, and smooth skates examined at the ARC, only one fish (THARC) was sufficiently old (band-pair count of 23 years) and collected during the 1980s that it might have been born in the 1960s. The remaining skate samples were formed more recently, so were presumed to fall within the post-bomb decay portions of the reference chronologies (i.e. post-1970).

Discrepancies between the observed and expected Δ^{14}C level found in THARC suggested age-underestimation from vertebral band counts. To estimate the minimum magnitude of any underageing, the estimated date of formation (1967, based on band-pair counts) of the sample taken from the first five fully formed bands of THARC was adjusted until the corresponding Δ^{14}C value was aligned with the porbeagle reference chronology (1961/1962). The magnitude of the adjustment required to align the chronologies was thus equal to the age underestimation.

Results

In all, 213 winter skates (120 males, 93 females), 92 little skates (43 males, 49 females), 282 thorny skates (139 males, 143 females), and 113 smooth skates (62 males, 51 females) were examined (Figure 2). The sampled length ranges for each species reflected expected ranges based on previously published values, except for winter skate, of which young skate and mature females were undersampled (Table 1). Based on PCR–RFLP analyses, little skate dominated catches of winter/little skate $<$30 cm TL (18 out of 26, or ~69%). The smallest winter skate caught was 21.0 cm TL.

Appearance of vertebral bands

VR (mm) increased linearly with TL (cm) in winter skate (Figure 3a, $VR = 0.057\ TL - 0.044$, $r^2 = 0.90$, $n = 203$), little skate (Figure 3b, $VR = 0.061\ TL - 0.204$, $r^2 = 0.94$, $n = 88$), and thorny skate (Figure 3c, $VR = 0.054\ TL + 0.118$, $r^2 = 0.94$, $n = 271$), although the fit slightly exceeded the observed values in small thorny skates. In smooth skate, a quadratic curve best described the relationship between VR and TL (Figure 3d, $VR = 0.090 + 0.030\ TL + 0.0004\ TL^2$, $r^2 = 0.94$, $n = 107$). There were no significant differences in VR and TL relationships between males and females (ANCOVA, $p > 0.05$) for any of the four species.

In most winter and little skate sections, a BB was distinguishable as a distinct band or an angle change in the corpus calcareum at a distance of 0.7 and 0.5 mm from the focus, respectively (Figure 1a and b). BB locations of 0.59–0.68 mm for winter skate and 0.53–0.64 mm for little skate obtained using published hatch lengths (winter skate $TL_{hatch} = 11.2–12.7$ cm, Collette and Klein-MacPhee, 2002; little skate $TL_{hatch} = 9.0–10.8$ cm, Waring, 1984) and fitted VR–TL regressions from this study corroborated the identification of birthmark increments in the centra of older, larger fish. Moreover, the mean VR in two free-swimming little skate $<$12 cm TL was 0.50 mm, suggesting that little skate neonates form a dark band $<$0.50 mm from the focus upon emergence from the egg capsule.

In most thorny and smooth skates, the BB was not readily discernible. The location of the BB in thorny skates was determined from two embryonic (mean $TL = 12.1$ cm) and two newly hatched, free-swimming fish (mean $TL = 12.1$ cm) that had mean VR measurements of 0.55 and 0.60 mm, respectively. For smooth skates, the location of the BB was approximated using two methods: (i) reported hatch lengths for little skate ($TL_{hatch} = 9.0–10.8$ cm, Waring, 1984)—which reaches a maximum size similar to smooth skate (54 vs. 58 cm TL, Collette and Klein-MacPhee, 2002)—were inserted into the quadratic regression relationship between VR and TL determined using older smooth skates; and (ii) the VR of the smallest free-swimming smooth skate captured—with a TL (9.5 cm) within the reported hatch length range for little skate—was determined. The first method yielded approximate BB locations at distances of 0.39–0.46 cm from the focus, whereas the latter method suggested a BR of $<$0.44 mm (Figure 1c and d).

A noticeable number of thorny ($n = 39$, 23%) and smooth ($n = 19$, 22%) skate vertebrae appeared to be missing a small number of growth bands near the focus (Figure 1e and f). This appeared to be a characteristic of the species rather than preparation artefacts.

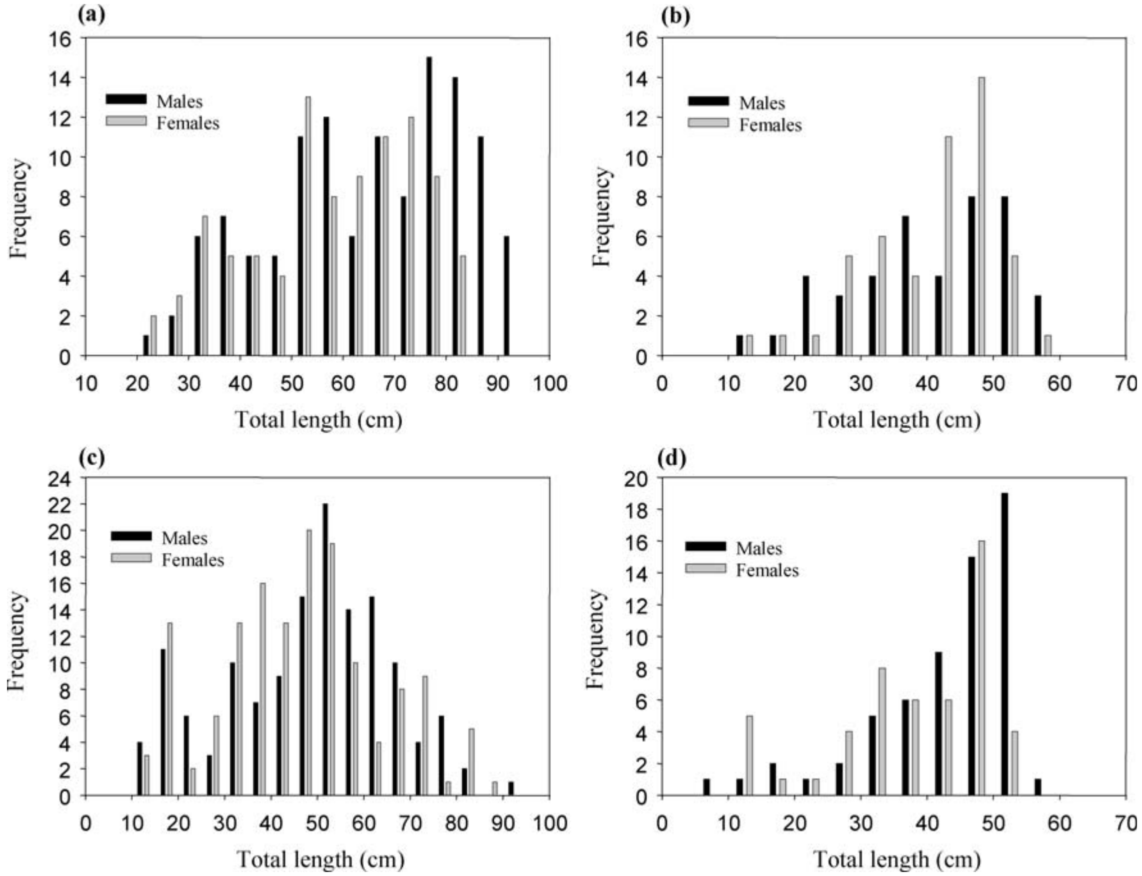

Figure 2. Length frequency distribution of (a) winter skate, (b) little skate, (c) thorny skate, and (d) smooth skate used in this study.

To avoid age underestimation in those skate, S-curves were fitted to total band count (BC) vs. VR (mm) data from examples of each species whose counts were deemed “complete” (thorny skate, $BC = e^{3.365-3.289/VR}$, $r^2 = 0.89$, $p < 0.01$, $n = 118$, Figure 4a; smooth skate, $BC = e^{3.437-2.709/VR}$, $r^2 = 0.89$, $p < 0.01$, $n = 57$, Figure 4b) and the equations used to estimate the

Table 1. TL at age (years) for winter skate, little skate, thorny skate, and smooth skate (sexes combined).

	Winter skate			Little skate			Thorny skate			Smooth skate		
Age	**Mean TL**	**s.d.**	***n***	**Mean TL**	**s.d.**	***n***	**Mean TL**	**s.d.**	***n***	**Mean TL**	**s.d.**	***n***
0	–	–	–	11	0.0	2	14	1.5	13	11	1.2	7
1	23	2.2	4	21	2.4	5	19	1.4	12	18	0.0	2
2	36	4.5	14	25	4.0	5	22	1.8	3	21	4.6	2
3	41	9.9	12	31	2.1	10	33	7.8	2	29	–	1
4	53	7.3	17	36	5.5	12	33	3.9	7	30	3.5	4
5	59	8.5	17	43	4.5	8	42	10.7	9	33	4.0	8
6	64	6.8	11	45	5.1	18	40	5.7	8	35	4.1	7
7	71	10.0	7	48	5.9	14	46	6.8	11	36	4.1	3
8	65	8.6	10	50	3.9	7	46	5.9	5	47	–	1
9	70	9.3	13	49	3.2	4	49	7.8	12	46	3.6	12
10	79	6.4	11	52	3.9	2	52	10.9	15	48	3.4	7
11	77	6.0	10	53	–	1	52	9.2	11	46	3.3	10
12	79	9.5	10	53	–	1	62	11.2	16	50	2.3	10
13	80	5.8	5				60	10.9	14	48	2.2	4
14	82	4.6	7				63	11.6	12	50	1.3	5
15	89	2.1	4				60	12.7	9	54	2.8	2
16	84	2.5	2				76	15.6	4			
17	88	–	1				64	9.2	5			
18	90	–	1				68	9.5	2			
19	86	–	1				83	–	1			

Mean ± s.d. and sample size (number of fish in sample) are given for each species.

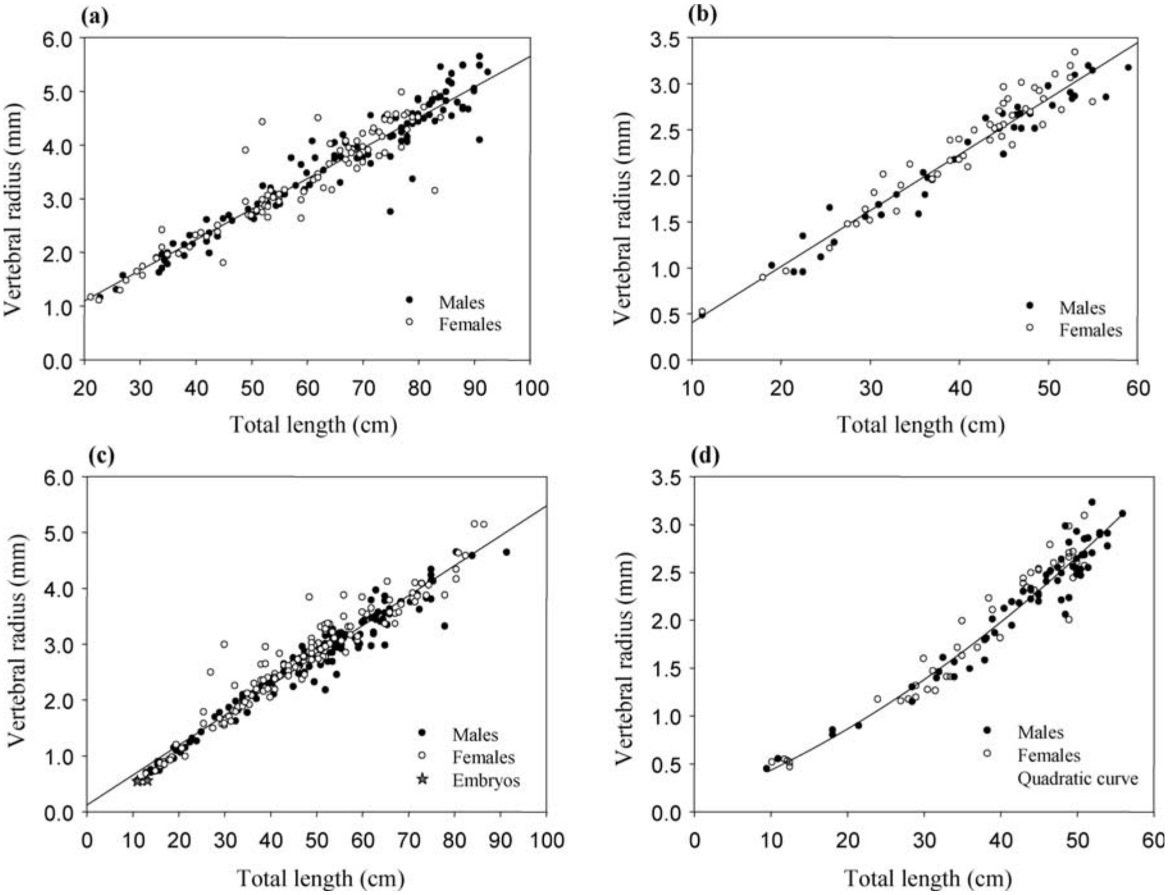

Figure 3. Scatterplots of TL and VR for male and female (a) winter skate, (b) little skate, (c) thorny skate, and (d) smooth skate. Embryonic thorny skates are marked as grey stars. Linear regressions are fitted to all data except those for smooth skate, where a quadratic curve best described the data.

number of missing bands in the incomplete growth sequences. The average numbers of missing bands estimated were 3 (s.d. = 1.1) for thorny skate and 4 (s.d. = 2.0) for smooth skate. Maximum likelihood ratio tests indicated no significant differences ($p > 0.05$) between growth curves fitted to all sections (including those with calculated "inner" band counts), and those sections deemed fully readable, for both thorny and smooth skates.

Intraager *CV* estimates for the final two readings for each species were 4.7% for winter skate, 3.8% for little skate, 3.3% for thorny skate, and 6.2% for smooth skate. Interager *CV* estimates for winter and thorny skates were 2.5 and 2.7%, respectively. Age-bias plots indicated no systematic bias between successive readings generated by the principal reader or between those generated by different readers, so the counts generated by the principal reader were used for the analyses.

Growth curves

The traditional VBGF provided the best fit to winter and thorny skates length-at-age data based on absolute values of AIC (AIC_i). For smooth and little skates, the models that provided the best fit to combined length-at-age data were the Gompertz growth model and the logistic growth equation, respectively. Nevertheless, differences in absolute AIC values between all candidate models and the one that resulted in the minimum AIC value (ΔAIC) were extremely small (≤ 10; Burnham and Anderson, 2002). Of all the growth functions fitted to the species-specific length-at-age data, the VBGF (or 2VBGF, for winter skate) consistently provided the most biologically reasonable growth parameter estimates based on known and/or published hatch lengths and maximum TLs (Tables 2 and 3). L_∞ estimates obtained using the traditional three-parameter VBGF only slightly exceeded (little and smooth) or closely approached (thorny) the observed maximum TLs in this study, as well as previously reported maximum lengths for little (54.0 cm TL) and smooth (57.7 cm TL) skates (Collette and Klein-MacPhee, 2002). The combined L_∞ parameter for thorny skate—although less than the maximum observed TL in this study (91.5 cm TL)—is consistent with biannual DFO groundfish RV survey data from 1997 to 2006, with only four thorny skates ≥ 90 cm TL having been caught on the ESS in the last 10 years. The combined estimate of L_0 for little skate is consistent with published lengths at birth for the species (9.0–10.8 cm TL, Waring, 1984), whereas for thorny and smooth skates, based on TLs of embryonic and recently hatched thorny skate and on the TL of the smallest free-swimming smooth skate (9.5 cm TL) in this study, L_0 estimates from the VBGFs were slight overestimates (Table 2).

When the traditional VBGF was fitted to the combined winter skate age–length data, L_∞ (88.4 cm TL) was slightly underestimated relative to the maximum observed length in this study (92.5 cm TL) and previously reported maximum sizes for this

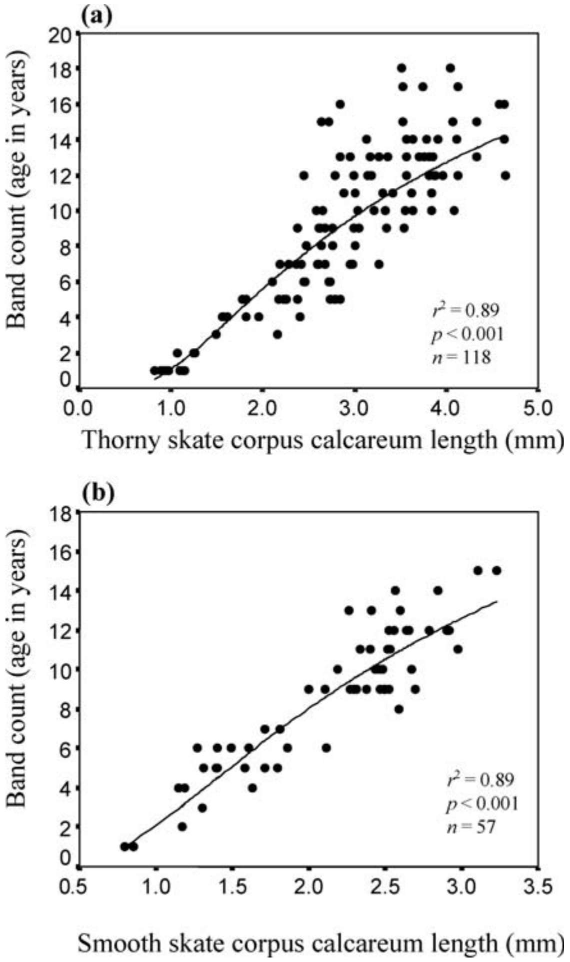

Figure 4. Scatterplot of band count and corpus calcareum length for high quality (a) thorny skate and (b) smooth skate vertebral sections which were deemed readable from the focus to the edge. Fitted S-curve regressions are shown, which were used to calculate band count from the focus to the first distinguishable band (FDB) on vertebrae deemed unreadable near the focus.

species off the coast of Nova Scotia (114+ cm TL; Simon and Frank, 1996). The modified two-parameter VBGF (Fabens, 1965) fitted to the length-at-age data had the same r^2 as the traditional VBGF and a ΔAIC value of only 0.57 (Table 2), indicating a good fit to the available data. However, the L_0 value for winter skate calculated using the 2VBGF was slightly higher than the published birth length range for the species (11.2–12.7 cm TL, Collette and Klein-MacPhee, 2002; Table 2), implying that, along with the VBGF, this model was also not a completely accurate predictor of growth of winter skate.

For all species, likelihood ratio tests comparing VBGFs between males and females indicated that differences in length-at-age data were not significant ($p > 0.05$; Kimura, 1980; Figure 5).

Longevity

Observed longevities ($t_{\max}$) ranged from 12 (little skate) to 19 years of age (winter and thorny skates; Table 1). Smooth skate reached a $t_{\max}$ of 15 years. Differences in $t_{\max}$ between sexes of each species were minimal ($\leq$5 years), with the largest difference being between male ($t_{\max}$=19 years) and female ($t_{\max}$=14 years) winter skates. Theoretical longevity estimates [$T_{\max(\text{th})}$] varied widely depending on the species and the method used. Fabens' (1965) equation yielded the highest estimates of longevity for all species (winter, 24 years; little, 19 years; thorny, 47 years; smooth, 29 years), whereas Taylor's (1958) method resulted in estimates closer to $t_{\max}$ (winter, 19 years; little, 15 years; thorny, 39 years; smooth, 23 years).

Age validation

Bomb radiocarbon analysis yielded relatively constant δ^{13}C levels consistent with those previously observed for other species of elasmobranch (mean = −15.48‰, n = 15; Table 4), indicating dietary (metabolic) uptake of carbon (Fry, 1988; Kalish, 1993; Campana, 1997). In contrast, Δ^{14}C ranged widely from −80.2 (s.d. = 5) in a sample presumed to have formed in 1967 to 53.7 (s.d. = 5) in a sample presumed to have formed in 1987 (Table 4). All winter skate assay values were consistent with the age estimates based on vertebral band-pair counts (Figure 6). However, as all assay values were well above zero (indicating a year of formation after about 1970), it would have been difficult to detect age under- or overestimation of up to 13 years. Age underestimation exceeding 13 years would have been easily detected, because band pairs formed before about 1970 would have been significantly and substantially depleted in radiocarbon. As would be expected based on tissue type, post-bomb Δ^{14}C values from winter skate vertebrae (ranging from 31.5 to 53.7) plotted against estimated year of sample formation were more similar to those of porbeagle and shortfin mako than to those of the otolith-derived chronology, because of the demonstrated metabolic origin of carbon in both shark and skate vertebrae (Figure 6). Post-bomb Δ^{14}C values from growth bands 6–10 of THARC (−2.7) and from the last five fully formed bands of THARC (6.4) paralleled the reference radiocarbon chronology, but at a lower level, presumably reflecting residence of older skates in deeper, radiocarbon-depleted waters (Figure 6).

Of greater significance was the Δ^{14}C value obtained from the first five fully formed growth bands of THARC (−80.2) which was almost certainly pre-bomb (i.e. characteristic of material formed before 1958), making it extremely useful as a dated marker (Figure 6). Band-pair counts resulted in an age of 23 years and a presumed date of band formation of 1967; however, based on all available Atlantic marine reference chronologies for water depths of up to ~300 m, Δ^{14}C values around −80 are only compatible with material (whether calcium carbonate or cartilaginous) formed on or before the late 1950s (otolith chronology) or early 1960s (porbeagle chronology). This discrepancy between the observed and expected Δ^{14}C levels suggested that vertebral band counts underestimated age by ~5 years in this skate, resulting in a minimum absolute age of 28 years (Figure 6). The post-bomb assay values in the intermediate growth bands (annuli 6–10) were consistent with this interpretation, because age underestimation of more than ~5 years would have produced markedly lower radiocarbon values. In contrast, if age based on band counts had been overestimated (i.e. growth bands formed biannually), the Δ^{14}C value from the first five fully formed bands of THARC would have been ~70‰ higher than the corresponding date-specific reference chronology values.

Discussion

Vertebral growth band deposition has been validated as annual in many species of shark and is now widely regarded as the norm

Table 2. Parameter estimates, variance explained (r^2), sample size (n), and overall measures of fit (AIC_i and ΔAIC) for von Bertalanffy growth curves fitted to winter, little, thorny, and smooth skate length-at-age data.

	von Bertalanffy growth curve parameters								
Species and sex	L_∞	k	t_0	r^2	n	AIC_i	ΔAIC	L_0	L_{max}
Winter skate									
Males	90.6	0.18	−0.7	0.82	87	613.52	0.00	10.3	92.5
Females	79.6	0.24	−0.5	0.82	70	474.23	0.00	8.7	84.0
Combined	88.4	0.18	−0.8	0.82	157	1089.27	0.00	11.8	92.5
Little skate									
Males	63.0	0.17	−1.2	0.80	41	261.68	1.67	11.5	59.0
Females	58.5	0.20	−0.9	0.87	48	264.12	1.91	9.7	55.0
Combined	60.6	0.19	−1.0	0.83	89	527.26	3.23	10.8	59.0
Thorny skate									
Males	81.2	0.09	−2.1	0.76	81	594.43	0.00	13.9	91.5
Females	102.0	0.06	−2.7	0.74	90	658.80	0.00	14.7	86.5
Combined	89.6	0.07	−2.4	0.75	171	1246.21	0.00	14.2	91.5
Smooth skate									
Males	57.1	0.15	−1.4	0.93	47	244.74	0.00	10.7	56.0
Females	64.7	0.10	−2.0	0.93	38	208.06	0.59	11.7	51.0
Combined	60.7	0.12	−1.7	0.93	85	452.54	0.76	11.3	56.0
	Fabens (1965) von Bertalanffy growth curve parameters								
	L_{max}	k	t_0	r^2	n	AIC_i	ΔAIC	L_0	L_{max}
Winter skate									
Combined	94.1	0.15	−1.3	0.82	157	1089.84	0.57	16.2	92.5

Calculated length at birth (L_0) and maximum observed length (L_{max}) are given for each sex separately and for sexes combined.

(Cailliet and Goldman, 2004). However, at least one species of elasmobranch (*S. californica*) lays down bands inconsistently (Natanson and Cailliet, 1990), and another (*L. nasus*) ceases laying bands altogether at great age (Francis *et al.*, 2007), highlighting the need to test the assumption of predictable, annually deposited growth bands on a species-specific basis. In this study, bomb radiocarbon assays from skate vertebral sections appeared to validate the age interpretations of NW Atlantic skate estimated from vertebral band counts. Pre-bomb radiocarbon material (−80.2) in the oldest thorny skate aged in this study (THARC) set a minimum age of 28 years for the species (based on comparison with the porbeagle reference chronology), which was only slightly older than the age interpretation (23 years) based on vertebral band-pair counts. However, there are two alternative

Table 3. Parameter estimates and overall measures of fit (AIC_i and ΔAIC) from Gompertz and logistic growth functions fitted to species-specific length-at-age data from males, females, and both sexes combined.

	Gompertz model						Logistic model				
Season and sex	L_∞	k	G	L_0	AIC_i	ΔAIC	L_∞	r	L_0	AIC_i	ΔAIC
Winter											
Males	87.5	0.26	1.5	19.2	614.52	1.00	85.9	0.33	23.4	616.08	2.56
Females	76.7	0.35	1.6	15.8	474.57	0.34	75.0	0.47	18.9	475.51	1.28
Both	84.8	0.27	1.5	19.2	1 092.49	3.22	82.9	0.35	22.9	1 096.81	7.54
Little											
Males	57.3	0.30	1.5	13.3	260.59	0.58	54.9	0.43	14.6	260.01	0.00
Females	53.5	0.35	1.5	11.4	262.39	0.18	51.3	0.50	12.8	262.21	0.00
Both	55.3	0.32	1.5	12.6	524.87	0.84	53.0	0.46	13.9	524.03	0.00
Thorny											
Males	70.6	0.18	1.6	14.9	594.44	0.01	66.7	0.27	15.9	595.22	0.79
Females	80.9	0.13	1.6	16.6	660.92	2.12	74.8	0.20	18.2	663.11	4.31
Both	74.8	0.16	1.6	15.7	1 248.63	2.42	70.0	0.24	17.0	1 251.97	5.76
Smooth											
Males	53.3	0.25	1.5	11.9	244.93	0.19	51.6	0.35	13.0	246.37	1.63
Females	54.4	0.21	1.5	12.1	207.47	0.00	50.8	0.32	12.6	207.83	0.36
Both	54.3	0.22	1.5	12.0	451.78	0.00	51.7	0.33	12.8	453.59	1.81

For the Gompertz function, asymptotic length (L_∞) was calculated from estimated parameters using the equation $L_\infty = L_0 e^G$ (Mollet *et al.*, 2002).

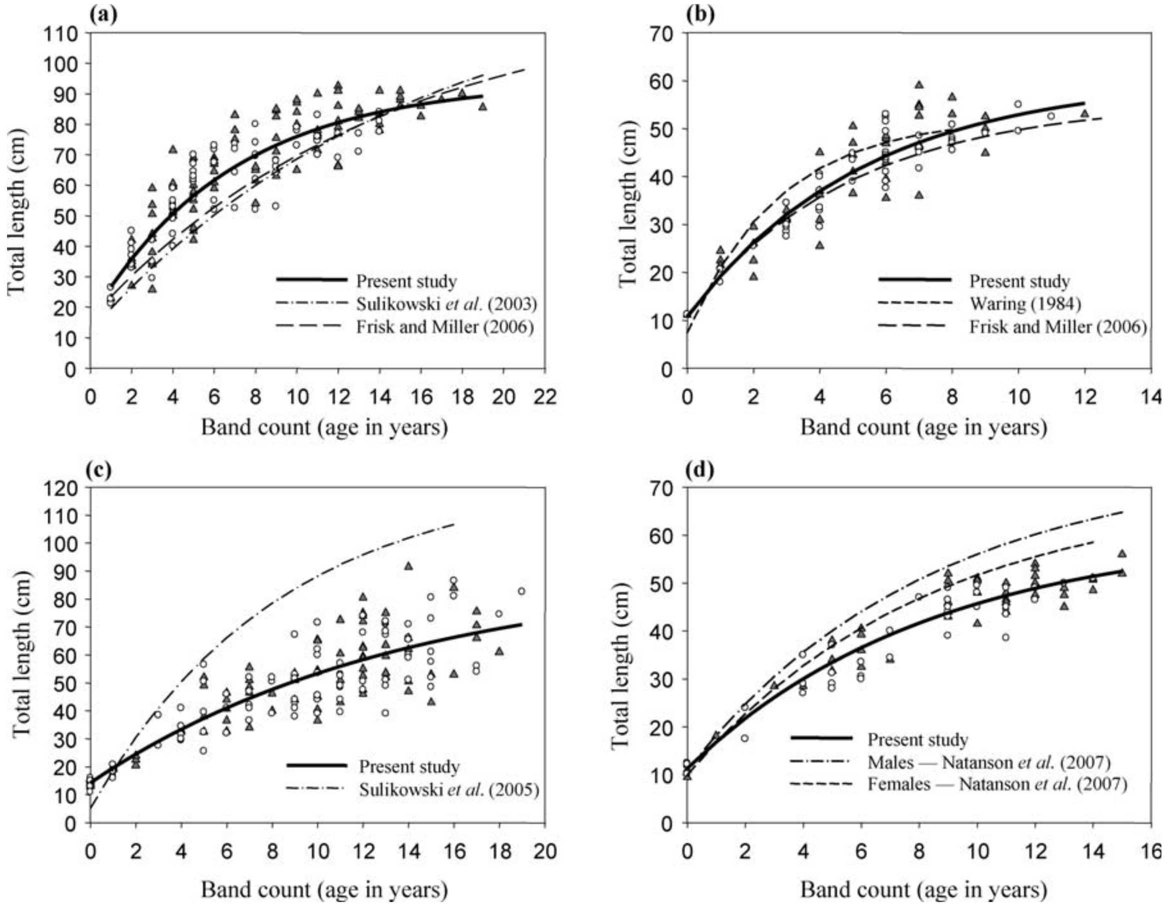

Figure 5. Scatterplot of TL at age for male (grey triangle) and female (white circle) (a) winter skate, (b) little skate, (c) thorny skate, and (d) smooth skate. Length-at-age plots for little, thorny, and smooth skate are fitted with a traditional three-parameter von Bertalanffy growth curve, whereas that for winter skate is fitted with a modified von Bertalanffy growth curve (Fabens, 1965). Growth models from previously published studies from other geographic regions are overlaid.

Table 4. Summary of $\Delta^{14}C$ and $\delta^{13}C$ assay results for band pairs isolated from skate vertebrae chosen for bomb radiocarbon analysis.

Species	Sample	TL (cm)	Year of collection	Total age based on band-pair counts (years)	Assigned year of band-pair formation	Uncertainty around assigned year of band-pair formation[a,b]	$\delta^{13}C$ (‰)	$\Delta^{14}C$
Winter	47 (90)	90.0	1999	18	1983	0.8	−15.3	51.6
Winter	13 (90)	86.0	1999	15	1986	0.6	−15.5	53.6
Winter	15 (52)	89.0	2000	15	1987	0.6	−15.6	53.7
Winter	7 (48)	91.0	2000	15	1987	0.6	−15.1	53.0
Winter	16 (9)	85.5	2005	19	1988	0.8	−15.5	51.9
Winter	89 (85)	85.0	1999	13	1988	0.5	−14.4	48.0
Winter	1 (36)	77.0	2000	12	1990	0.5	−15.6	46.5
Winter	16 (11)	72.0	2005	6	2003	0.1	−15.9	31.5
Winter	8 (9)	69.5	2005	8	2003	0.1	−16.0	45.9
Winter	53 (80)	80.0	2005	8	2003	0.1	−15.7	47.2
Winter	19 (9)	59.0	2005	6	2003	0.1	−15.5	42.0
Winter	19 (11)	68.0	2005	9	2003	0.1	−16.1	34.3
Winter	10 (9)	69.0	2005	6	2003	0.1	−16.2	53.0
Thorny	THARC	64.5	1988	23	1967	0.7	−15.9	−80.2
Thorny	THARC	64.5	1988	23	1972	0.5	−14.9	−2.7
Thorny	THARC	64.5	1988	23	1985	0.1	−14.0	6.4

[a] *CV* = 4.7% for winter skate and 3.3% for thorny skate.

[b] Individual age uncertainties calculated by multiplying the difference between year of collection and presumed year of band-pair formation by overall *CV* as per Ardizonne *et al.* (2006).

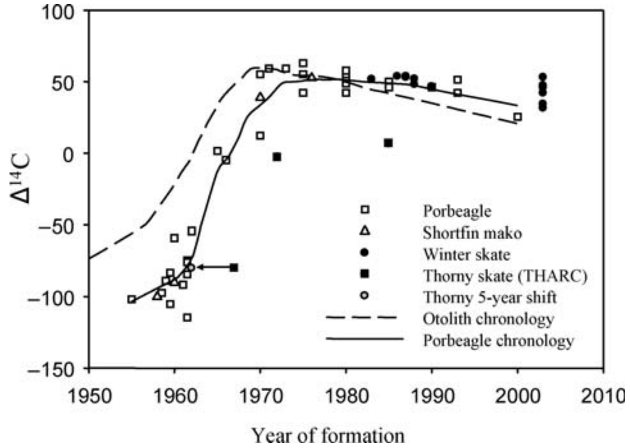

Figure 6. Δ^{14}C in individual growth bands of winter skate and a thorny skate (THARC) vs. year of formation inferred from counts of growth bands. The post-bomb Δ^{14}C values of skate were similar to those of an otolith-derived reference chronology from the NW Atlantic (dashed line, Loess curve); however, values were closer to those of a vertebrae-derived reference chronology from NW Atlantic porbeagles (solid line, Loess curve) and shortfin mako, owing to dietary (metabolic) uptake of Δ^{14}C by elasmobranchs. The discrepancy between the pre-bomb Δ^{14}C level from the THARC collected in 1988 and those of the porbeagle reference chronology suggests that band counts underestimated actual age by at least 5 years in this animal, resulting in a minimum absolute age of 28 years when the thorny skate pre-bomb Δ^{14}C value was shifted to fall upon the porbeagle chronology (arrow).

explanations for these results, each of which will be considered in turn: (i) phase-shifting attributable to trophic delay and (ii) attenuation of the bomb signal as a consequence of deep-water residence or food sources.

The phase shift in THARC radiocarbon values relative to NW Atlantic shark-derived values is readily explained by slight under-counting of growth band pairs, but is not readily attributable to a phase lag in skates or to attenuation from deep food sources. Several studies have suggested that upper-trophic-level predators may experience a delay in the appearance of bomb radiocarbon in their vertebrae because of the incorporation of radiocarbon from larger, older prey, or prey inhabiting deep, radiocarbon-depleted waters (Campana *et al*., 2002; Ardizonne *et al*., 2006; Kerr *et al*., 2006). For example, Kerr *et al*. (2006) reported unexpectedly low Δ^{14}C values in white shark vertebrae, presumably reflecting dietary shifts to deeper, more radiocarbon-depleted habitats. As skates occupy a low trophic level, any trophic delay would be expected to fall between that of carbonates (which show no lag, and exactly represent the ^{14}C content of the DIC) and high-trophic-level sharks. However, the observed lag was greater than that observed in porbeagle, a high-trophic-level predator. In addition, young skates generally reside in waters shallower than those exhibiting delayed bomb Δ^{14}C signals, i.e. $<$200-m deep (Williams *et al*., 1987), and only large, very old skate tend to reside in very deep, radiocarbon-depleted waters (i.e. up to 1540 m for thorny skate; Collette and Klein-MacPhee, 2002). Therefore, although deep-water attenuation likely explains the reduced radiocarbon values observed in the growth bands formed during the adult life-history stage of THARC, it cannot explain the lower-than-expected radiocarbon value found in the first-formed bands of that fish, when it would have been present in shallow coastal waters. Indeed, the post-bomb Δ^{14}C of winter skate was consistent with post-bomb radiocarbon results from NW Atlantic porbeagle sharks, with only minor discrepancies between skate- and shark-derived Δ^{14}C levels. Therefore, the most likely explanation for the slight discrepancy between the pre-bomb Δ^{14}C from THARC and that of the porbeagle reference chronology is that the band-pair counts underestimated actual age by $\sim$5 years.

The similarities between Δ^{14}C levels among elasmobranch species and the dissimilarities in magnitude (but not the shape of the chronology) between vertebrae- and carbonate-derived chronologies can be explained by the different sources of carbon in each case, with the sources of cartilaginous, non-calcified tissue being diet rather than DIC (Fry, 1988). Both Campana *et al*. (2002) and Ardizonne *et al*. (2006) found that radiocarbon chronologies from sharks (porbeagle and shortfin mako, respectively) were phase-shifted by up to 3 years towards more recent dates relative to a reference carbonate Δ^{14}C chronology characteristic of bivalves, corals, and fish otoliths in the NW Atlantic. They concluded that Δ^{14}C levels in shark vertebrae reflect the Δ^{14}C signature of prey and, therefore, correspond to dates older than the surrounding water because of trophic-level delay, a phenomenon also observed in the white shark (*Carcharodon carcharias*) by Kerr *et al*. (2006). The remaining phase-shift in each case was attributed to the depth range occupied by the sharks and their prey, with depths $>$200 m exhibiting delayed bomb Δ^{14}C signals relative to surface waters (Williams *et al*., 1987).

It is well known that growth bands in fish become increasingly narrow as somatic growth slows after maturity, making it difficult to distinguish marginal growth in long-lived individuals (Natanson *et al*., 2002). This characteristic of slow-growing fish is the most likely explanation of the age underestimation in THARC. In addition, perhaps bands close to the focus were missed in this particular skate, given an inability to discern the BB and growth bands closest to the focus (to a maximum of age 8) in some of the thorny and smooth skate vertebral sections. Figure 4 supports this hypothesis, with many band counts falling below the curve in both thorny and smooth skate, especially at corpus calcareum lengths of 2–3.5 mm. However, the *CV*s for all species were consistently $<$7%, suggesting high precision of age estimates relative to other elasmobranch ageing studies where vertebrae were used as ageing structures (Campana, 2001).

Underageing could also have occurred through cessation of vertebral growth in old skate. This theory was recently proposed to explain disagreements between Δ^{14}C levels in porbeagle sharks collected off New Zealand and those caught in the NW Atlantic (Francis *et al*., 2007), and it might help explain a delay in the bomb radiocarbon signal in school shark (*Galeorhinus galeus*) from the western South Pacific (Kalish and Johnston, 2001). However, plots of body length against VR for three of the species examined in this study were isometric and linear over the entire length range, indicating that centra grow proportionally to skate length in all size classes, and suggesting that uncoupling of somatic growth and axial (anterior–posterior) vertebral growth did not take place. In addition, the relationship between VR and TL in smooth skate was slightly curvilinear, providing some evidence that radial vertebral growth continues and that annual increments continue to be deposited even after somatic growth slows.

Given that trophic delay and deep-water attenuation of the radiocarbon signal do not explain the radiocarbon results for THARC, the conclusion that thorny skate produce annual growth increments in their vertebrae, and that they live to at least 28 years, is well supported by the data. The radiocarbon-based age validation of thorny skates is also supported by a long-term tagging study by Templeman (1984), which demonstrated that thorny skate live to at least 20 years of age. In contrast, other more recent studies have obtained substantially younger maximum ages of 15–16 years (Sulikowski *et al*., 2005; Gallagher *et al*., 2006). Other studies on skates and rays have inferred maximum ages close to or more than 28 years (*D. batis*, 50 years, Dubuit, 1972; *Dipturus innominatus*, 24 years, Francis *et al*., 2001; *Dasyatis americana* 26–28 years, Henningsen, 2002), but age interpretations were either not validated or validated using less rigorous methods. Therefore, this is the oldest validated age reported for any species of batoid and therefore has significant implications for the management of skate species in the NW Atlantic and worldwide.

The radiocarbon-based confirmation of annulus formation in thorny skate does not necessarily indicate that the age interpretations for winter, little, and smooth skates in this study are valid. Nevertheless, the same ageing protocol was used for all four species. If in fact the same principles apply to the other skate species, perhaps band counts may underestimate absolute age in old examples of other NW Atlantic skate species too. Given the potentially severe management implications of improper age assessments (Beamish and McFarlane, 1983), future studies may want to address the possibility that band-pair deposition ceases in old skate. In the interim, the findings of this study highlight the need for further age validation studies on skates encompassing the full age range of each species.

Sex-combined VBGF parameters for all species differed in magnitude from those reported in previous studies from other geographic regions. For two of the four species (thorny and smooth skate) we examined on the ESS, the growth rate was slower, the maximum observed ages were greater, and the *K*-values were less than have been reported for the same species in the Gulf of Maine (Sulikowski *et al*., 2005; Natanson *et al*., 2007; Figure 5). Differences in growth rate were less marked for little skate on the ESS than those from the US Northeast coast (Frisk and Miller, 2006), although Waring (1984) reported younger maximum ages, lower maximum sizes (L_∞), and correspondingly faster growth rates and higher *K*-values (Figure 5) from New England–Georges Bank waters. For these three species, these findings are consistent with many studies on elasmobranch age and growth that have noted slower growth rate, large maximum size, and long lifespan in cold-water populations (Branstetter *et al*., 1987; Carlson and Parsons, 1997; Yamaguchi *et al*., 1998; Driggers *et al*., 2004; Frisk and Miller, 2006). The annual estimated marginal mean bottom-water temperature on the ESS is considerably less than in the Gulf of Maine (Mountain and Jessen, 1987; Gregory, 2004), so is consistent with a slower growth rate. Preferential exploitation of the larger, faster-growing skates on the ESS relative to other areas might also account for some of the observed differences in growth. However, fishing-induced mortality by species and length group has not yet been compared among areas, precluding a test of the gear-selectivity hypothesis. Moreover, adaptive evolution is likely to be slow relative to the period of intense commercial exploitation, which, for skates on the ESS, was at most 56 years (1950–2006) or 4–7 generations (generation time of NW Atlantic skate = 8–14 years, RPM and SEC, pers. obs.), making genetic change an unlikely contributor to growth differences among regions.

In contrast to the other three species, age and growth studies on winter skate from the US Northeast coast (Frisk and Miller, 2006) and the Gulf of Maine (Sulikowski *et al*., 2003) reported slower growth, higher L_∞ values, and correspondingly lower *K*-values than observed here (Figure 5), as well as equal or older maximum observed ages, results contrary to what one might expect based on latitudinal temperature effects. Given patterns observed in other species of elasmobranch, it is unlikely that winter skate exhibit countergradient variation in growth (Conover, 1990; Conover and Present, 1990), although this hypothesis was recently proposed to explain faster growth in bonnethead sharks (*Sphyrna tiburo*) in NW Florida than in more southerly locations (Lombardi-Carlson *et al*., 2003). Another possible explanation for interregional differences in winter skate growth rates is that heavy fishing on the ESS may have relaxed intraspecific competition, increased *per capita* food availability, and promoted faster growth in this species than in others (i.e. a compensatory response; Walker and Hislop, 1998). However, this is also an unlikely explanation given that, along with winter skate, both thorny and smooth skate on the ESS have experienced substantial declines in abundance (COSEWIC, 2004; DFO, 2006; Swain *et al*., 2006), with no indication of compensatory growth.

As there is no single hypothesis that appears to explain the apparent differences in growth rate among regions for all four species, differences in life-history parameters among regions are likely the result of a combination of (i) temperature-influenced differences in the rates of physiological processes such as metabolism and growth, and (ii) inconsistencies in the preparation and interpretation of vertebral centra among studies. Within-species dissimilarities in age and growth across studies are often due to artefacts of different preparation and interpretation methods (Cailliet *et al*., 1990; Tanaka *et al*., 1990; Lombardi-Carlson *et al*., 2003; Cailliet and Goldman, 2004). For skate in general, poor visibility of bands near the focus (especially in thorny skate) may well have been interpreted differently among studies, leading to different estimated growth parameters. The use of standardized techniques and/or calibration studies can eliminate this source of error, but it has not yet been attempted.

In most studies of elasmobranch age and growth to date, only the von Bertalanffy growth model has been considered despite growing evidence that alternative, more suitable, descriptors of these characteristics may exist (Knight, 1968; Roff, 1980; Cailliet *et al*., 2006). This study is the first to examine alternative growth models for NW Atlantic skate. All models used to characterize growth and longevity in each species of NW Atlantic skate provided reasonable fits to the observed length-at-age data. However, the three-parameter VBGF (and a modified 2VBGF, for winter skate) produced the most biologically realistic age and growth parameters based on published and/or observed hatch lengths and maximum TLs. Slight discrepancies between observed lengths and those estimated using each of the tested growth models (including those that provided the best fits to species-specific length-at-age data) suggest that more suitable models may exist to describe growth in each species. In this study, relatively small sample sizes of small and large fish may have hindered accurate parameterization of winter skate growth using both the VBGF and the modified VBGF (Francis and Francis, 1992).

Results of this study demonstrate that, except for winter skate, NW Atlantic skate are slower-growing and longer-lived than previously thought. Elasmobranchs as a group are characterized by their slow growth rates, but previously derived growth coefficients

(K) cover a broad range of values (Cailliet and Goldman, 2004). Keeping in mind that comparisons and interpretations of growth coefficients are limited by differing methodologies between researchers (Cailliet and Goldman, 2004), growth rates among elasmobranchs are generally considered slow if K-values are ≤ 0.1 year^{-1} (Branstetter, 1990). Of the NW Atlantic skate species examined in this study, thorny skate can be considered a relatively slow-growing elasmobranch, with a growth coefficient ($K = 0.07$) approximating those obtained for several other species of large oviparous batoids (*D. batis*, $K = 0.057$, Dubuit, 1972; *D. pullopunctata*, $K = 0.05$, Walmsley-Hart *et al.*, 1999; *D. dipterura*, $K = 0.05$–0.10, Smith *et al.*, 2007). Overall, the K-value obtained for thorny skate was more similar to those displayed by several large, long-lived shark species, such as 0.058–0.065 for white shark (Cailliet *et al.*, 1985; Wintner and Cliff, 1999), 0.059 for the sandbar shark (Sminkey and Musick, 1995), and 0.066 for the porbeagle (Natanson *et al.*, 2002). In contrast, most skate species studied to date have exhibited growth coefficients more than 0.1 year^{-1}, as was the case with winter, little, and smooth skates in this study.

In a review of the life-history characteristics of long-lived marine species, Musick (1999) concluded that species with K coefficients of ≤ 0.10 year^{-1} are extremely susceptible to decline as a consequence of overexploitation. Among NW Atlantic skate, thorny skate may be particularly susceptible to exploitation because of its combined characteristics of large size, slow growth rate, and newly demonstrated longevity. Winter, little, and smooth skates, although exhibiting higher K-values than thorny skate, are also potentially susceptible to decline under commercial fishing pressure, given their relatively slow growth rates and long lifespans compared with teleosts and other elasmobranchs.

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