# Age and growth estimates of the thorny skate (*Amblyraja radiata*) in the western Gulf of Maine

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**Abstract**—The northwest Atlantic population of thorny skates (*Amblyraja radiata*) inhabits an area that ranges from Greenland and Hudson Bay, Canada, to South Carolina. Despite such a wide range, very little is known about most aspects of the biology of this species. Recent stock assessment studies in the northeast United States indicate that the biomass of the thorny skate is below the threshold levels mandated by the Sustainable Fisheries Act. In order to gain insight into the life history of this skate, we estimated age and growth for thorny skates, using vertebral band counts from 224 individuals ranging in size from 29 to 105 cm total length (TL). Age bias plots and the coefficient of variation indicated that our aging method represents a nonbiased and precise approach for the age assessment of *A. radiata*. Marginal increments were significantly different between months (Kruskal-Wallis $P<0.001$); a distinct trend of increasing monthly increment growth began in August. Age-at-length data were used to determine the von Bertalanffy growth parameters for this population: $L_\infty$ = 127 cm (TL) and $k$=0.11 for males; $L_\infty$ = 120 cm (TL) and $k$=0.13 for females. The oldest age estimates obtained for the thorny skate were 16 years for both males and females, which corresponded to total lengths of 103 cm and 105 cm, respectively.

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The northeast skate complex consists of seven species endemic to the waters off the New England coast of the United States (New England Fisheries Management Council (NEFMC[1,2]). In the past, these skates were generally discarded because of their low commercial value (NEFMC[1,2]). More recently, the rapidly expanding markets for human consumption of skate wing and for use as lobster bait have made three of these species (winter skate [*Leucoraja ocellata*], little skate [*L. erinacea*], and thorny skate [*Amblyraja radiata*]) commercially more viable (Sosebee, 2000; NEFMC[1,2]). Despite an increasing commercial importance, harvests for skate in the U.S. portion of the western north Atlantic remain unregulated and have the potential to over-exploit the stocks. Moreover, life history information is almost nonexistent for most of these elasmobranch fishes (Frisk, 2000 NEFMC[1,2]).

The available information from the few skates that have been studied categorizes them as equilibrium strategists (K selected) because they reach sexual maturity at a late age, have a low fecundity, and are relatively long-lived (Holden 1977; Winemiller and Rose, 1992; Zeiner and Wolfe, 1993; Francis et al., 2001; Frisk et el., 2001, Sulikowski et al., 2003). These characteristics, coupled with the practice of selective removal of large individuals, make these animals more likely to be over-exploited by commercial fisheries (Brander 1981; Hoenig and Gruber, 1990; Casey and Myers 1998; Dulvey et al., 2000; Frisk et al., 2001).

The thorny skate (*Amblyraja radiata*) is a cosmopolitan species found on both sides of the Atlantic ocean from Greenland and Iceland to the English Channel in the eastern Atlantic (Compagno et al., 1989) and from Greenland and Hudson Bay, Canada, to South Carolina, United States, in the western Atlantic (Robins and Ray, 1986; Collette and Klein, 2002). Along with this broad geographic range, marked differences in size exist for specimens captured in different regions of the Atlantic. For

[1] NEFMC (New England Fishery Management Council. 2001. 2000 stock assessment and fishery evaluation (SAFE) report for the northeast skate complex. NEFMC, 50 Water Street, Mill 2 Newburyport, MA 01950.

[2] NEFMC (New England Fishery Management Council). 2003. Skate fisheries management plan. NEFMC, 50 Water Street, Mill 2 Newburyport, MA. 01950.

example, the thorny skate reaches total lengths of over 100 cm in the Gulf of Maine (Collette and Klein, 2002), whereas specimens captured off the Labrador coast do not reach total lengths >72 cm (Templeman, 1987). Although no directed fisheries for this species exists in the Gulf of Maine, this skate meets the minimum 1¼ pound-cut pectoral-fin size sought after by wing processors (Sosebee, 2000; NEFMC[1,2]). Unfortunately, because landings are not reported by species, the proportion of thorny skates to the total wing market is unknown. Recent assessment studies in the northeast United States (NEFSC[3]) indicate that the biomass of thorny skates is declining, and is below threshold levels mandated by the Sustainable Fisheries Act (SFA; NMFS[4]). Thus, owing to the recent commercial interest in this species and the concomitant decline in population size, obtaining life history information for this species has become more important. In order to provide insight into the biology of this species and to determine the stock status (Simpfendorfer, 1993; Frisk et al., 2001), our objectives were to estimate age and growth rates of *A. radiata* based on banding patterns in vertebral centra from specimens collected in the western Gulf of Maine.

## Materials and methods

### Sampling

Thorny skates were captured by otter trawl in an approximate 900 square mile area centered at 42°50′N and 70°15′W in the Gulf of Maine between June 2001 and May 2002. These locations varied from 30 to 40 km off the coast of New Hampshire. Approximate depths at this location ranged between 100 and 120 m. This area was chosen for two reasons: 1) these waters support the vast majority of commercial fishing in New Hampshire and can be easily accessed during normal fishing operations; and 2) because of rolling closures within the Gulf of Maine, an experimental fishing permit was granted to us by the National Marine Fisheries Service (NMFS) to collect thorny skates in this location during the months of April, May, and June, when these waters are closed to commercial fishing. Although our sampling was conducted in a small portion of the species' range, the sizes of thorny rays collected corresponded to those collected during the NEFSC bottom trawl surveys conducted throughout the Gulf of Maine and Georges Bank (NEFMC[1,]; NEFSC[3]). From this information, it is unlikely that differences in other biological parameters exist.

Skates were maintained alive on board the vessel until arrival at the University of New Hampshire's Coastal Marine Laboratory (CML). There, individual fish were euthanized (0.3g/L bath of MS222). Total length (TL in cm) was measured as a straight line distance from the tip of the rostrum to the end of the tail, and disc width (DW in cm) as a straight line distance between the tips of the widest portion of pectoral fins. Total wet weight (kg) was also recorded.

### Preparation of vertebral samples

Vertebral samples, taken from above the abdominal cavity, were removed from 320 thorny skates (154 females and 166 males), labeled, and stored frozen. After having been thawed, three centra from each specimen were removed from the vertebral column, stripped of excess tissue and air dried. Large centra were cut sagittally with a Dremel™ tool fitted with a mini saw attachment while held with a vice-like device. Smaller centra were sanded with a Dremel™ tool to replicate a sagittal cut. Processed vertebrae were mounted horizontally on glass microscope slides and ground with successively finer-grit (no. 180, no. 400, no. 600) wet-dry sandpaper. Each vertebra was then remounted and the other side ground to produce a thin (300-micrometer) hourglass section.

### Band counts

Vertebral sections were digitally photographed with a Canon Powershot S40 attached to a Leica S8PO dissecting microscope and reflected light. Magnification depended on the size of the section and varied from 4× to 12× (Fig. 1). A growth ring (band count) was defined as one opaque and translucent band pair that traversed the intermedialia and that clearly extended into the corpus calcareum (Casey et al., 1985; Brown and Gruber, 1988; Sulikowski et al., 2003). The birth mark (age zero) was defined as the first distinct mark distal to the focus that coincided with a change in the angle of the corpus calcareum (Casey et al., 1985; Wintner and Cliff, 1996; Sulikowski et al, 2003).

### Precision and bias

Nonconsecutive band counts were made independently by two readers for each specimen used in the study without prior knowledge of the skate's length or of previous counts. A Tukey test was used to test for differences between ages. Age determination bias between readers was assessed through the use of an age-bias plot. This type of graph displays band counts of one reader against a second reader in reference to an equivalence line. Specifically, reader 2 is represented as mean age and 95% confidence intervals corresponding to each of the age classes estimated by reader 1 (Campana et al., 1995). Divergence from the equivalence line, where reader 1 = reader 2, would indicate a systematic difference between readers. Precision estimates of each reader were calculated by using the coefficient of variation (CV) as described by Chang (1982) and Campana et al. (1995).

[3] NEFSC (Northeast Fisheries Science Center). 1999. 30th Northeast regional stock assessment workshop. NEFSC, 166 Water Street, Woods Hole, MA 02543-1026.

[4] NMFS (National Marine Fisheries Service). 2002. Annual report to Congress on the status of U.S. fisheries 2001, 142 p. NMFS, NOAA, Silver Spring, MD 20910.

### Marginal increment analyses

The annual periodicity of band pair formation was investigated using marginal increment analyses (MIA). Because the annuli in older adult specimens were compressed, marginal increments were calculated from randomly selected juvenile specimens (Simpfendorfer, 1993; Sulikowski et al., 2003). For MIA, the distance of the final opaque band and the penultimate opaque band, from the centrum edge, was measured with a compound microscope and optical micrometer. The marginal increment was calculated as the ratio of the distance between the final and penultimate bands (Branstetter and Musick, 1984; Cailliet, 1990; Simpfendorfer, 1993; Simpfendorfer et al., 2000; Sulikowski et al., 2003). Average increments were plotted by month of capture to identify trends in band formation, and a Kruskal-Wallis one-way analysis of variance on ranks was used to test for differences in marginal increment by month (Simpfendorfer et al., 2000; Sulikowski et al., 2003).

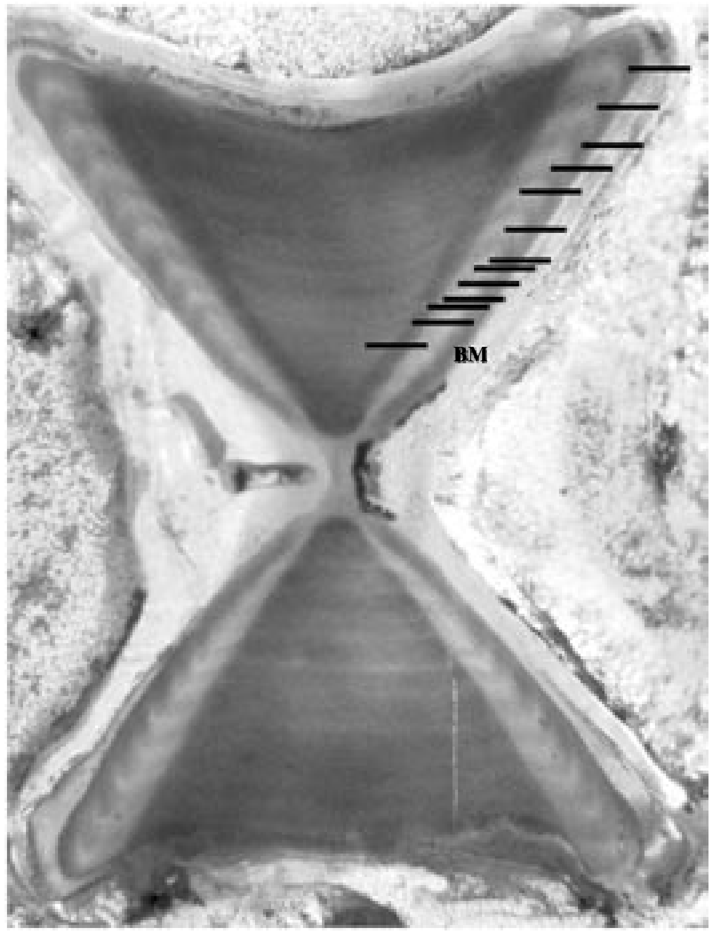


**Figure 1**

Longitudinal cross-section of a vertebral centrum from a 97-cm-TL female *Amblyraja radiata* estimated to be 12 years. BM = birth mark; Black dots represent age in years.

### Growth estimates

A von Bertalanffy growth function (VBGF) was fitted to the data with the following equation (von Bertalanffy, 1938):

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

where $l_t$ = total length at time $t$ (age in years);
$L$ = theoretical asymptotic length;
$k$ = Brody growth constant; and
$t_0$ = theoretical age at zero length.

The VBGF was calculated by using FISHPARM, a computer program for parameter estimation of nonlinear models with Marquardt's (1963) algorithm for least-square estimation of nonlinear parameters (Prager et al., 1987).

## Results

### Morphological measurements

Out of the 320 specimens collected, a total of 224 were used for our study (Table 1). Males ($n$=103) ranged between 29 and 103 cm TL, 18–75 mm DW, and 0.125–10.5 kg body weight (data not shown), whereas females ($n$=121) ranged between 31 and 105 cm TL, 18–74 cm DW, and 0.170–11.4 kg body weight (data not shown). Total length, disk width, and body weight were strongly correlated in males, females, and when data from the sexes were combined (all coefficient of determination [$r^2$] values were greater than 0.87).

### Vertebral analyses

Comparison of counts between two readers indicated no appreciable bias in the counting process (Fig. 2) and the coefficient of variation for all sampled vertebrae was 2.8% This level of precision is considered acceptable (Campana, 2001) and counts generated by both readers were combined (averaged) for the analyses (Skomal and Natanson, 2003).

The relationship between TL and centrum diameter was linear ($r^2$=0.93; $P$<0.05) and there were no significant differences in this relationship (ANCOVA, $P$<0.05) between males and females. Because no significant difference existed between TL and centrum diameter between the sexes, these data were combined (Fig. 3).

A total of 120 skates (10 per month) were used for marginal increment analyses. Marginal increments were significantly different between months (Kruskal-Wallis $P$<0.001); there was a distinct trend of increasing

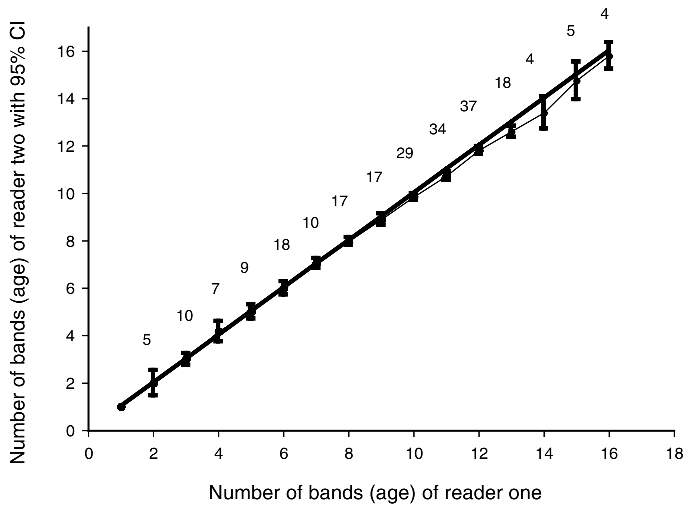


**Figure 2**

Age bias graph for pair-wise comparison of 224 thorny skate (*Amblyraja radiata*) vertebral counts by two independent readers. Each error bar represents the 95% confidence interval for the mean age assigned by reader 2 to all fish assigned a given age by reader 1. The diagonal line represents the one-to-one equivalence line. Sample sizes are given above each corresponding age.

**Table 1**

Average total length (TL) and disc width (DW) at age for male and female thorny skates (*A. radiata*). Sizes are presented as mean ±1 SEM; sample sizes are given in parentheses.

| Age (years) | Male TL (cm) | Female TL (cm) | Sexes combined | Male DW (cm) | Female DW (cm) | Sexes combined |
|---|---|---|---|---|---|---|
| 2 | 33 (5) ±1 | | 33 (5) ±1 | 23±1 | | 2±1 |
| 3 | 37 (3) ±1 | 37 (7) ±1 | 37 (10) ±1 | 26 ±1 | 27 ±0 | 27 ±1 |
| 4 | 43 (5) ±1 | 42 (2) ±2 | 42 (7) ±1 | 29 ±0 | 29 ±1 | 29 ±1 |
| 5 | 48 (2) ±2 | 49 ( 7) ±2 | 48 (9) ±1 | 33 ±0 | 35 ±0 | 34 ±1 |
| 6 | 64 (1) ±1 | 54 (17) ±1 | 54 (18) ±1 | 44 ±0 | 39 ±2 | 39 ±2 |
| 7 | 69 (5) ±1 | 62 (5) ± 3 | 64 (10) ±1 | 50 ±1 | 44 ±2 | 47 ±1 |
| 8 | 71 (6) ±1 | 73 (11) ±2 | 72 (17) ±2 | 52 ±1 | 53 ±2 | 53 ±1 |
| 9 | 78 (9) ±1 | 78 (8) ±2 | 78 (17) ±1 | 57 ±2 | 57 ± 1 | 57 ±1 |
| 10 | 86 (14) ±1 | 82 (15) ±1 | 84 (29) ±1 | 63 ±2 | 60 ±1 | 61 ±1 |
| 11 | 88 (17) ±1 | 89 (17) ±1 | 89 (34) ±1 | 65 ±1 | 65 ±1 | 65 ±1 |
| 12 | 93 (18) ±1 | 92 (19) ±0 | 92 (37) ±1 | 68 ±1 | 66 ±1 | 67 ±1 |
| 13 | 99 (10) ±1 | 95 (8) ±1 | 97 (18) ±1 | 73 ±1 | 68 ±1 | 70 ±1 |
| 14 | 97 (3) ±3 | 98 (1) ±0 | 96 (4) ±2 | 70 ±2 | 70 ±0 | 70 ±1 |
| 15 | 102 (2) ±1 | 101 (3) ±0 | 101 (5) ±1 | 70 ±1 | 74 ±2 | 74 ±1 |
| 16 | 101 (3) ±2 | 105 (1) ±0 | 102 (4) ±2 | 75 ±1 | 70 ±1 | 75 ±1 |

monthly increment growth that peaked in July, followed by a large decline in August (Fig. 4). Based on this information, the increment analyses support the likelihood that a single opaque band may be formed annually on vertebral centra during August or September. The marginal analysis was only conclusive for juvenile-size animals (skates ≤80 cm TL). As thorny skates matured, their growth slowed dramatically and the band counts in older specimens became compressed, making it difficult to discern monthly changes in margin width.

### Age and growth estimates

The von Bertalanffy growth curves (VBGC) fitted to total length-at-age data (Fig. 5) provided a reasonable fit with a low standard error for males, females, and both sexes combined (Table 2). Furthermore, the VBGC parameters for males, females, and the sexes combined were similar, and because no differences in age-at-size existed between males and females ($P$>0.05 ANOVA), those data were combined (Fig. 5).

## Discussion

Precision estimates, the relationship between TL and centrum diameter, and marginal increment analysis support the use of vertebral centra for age analyses of thorny skates captured in the Gulf of Maine (Conrath et al., 2002; Sulikowski et al., 2003). Furthermore, the 2.8% coefficient of variation indicates that our aging method represents a precise approach for the age assessment of *A. radiata* (Campana, 2001). Minimal width of the marginal increment for thorny skates captured in August and September (Fig. 4) supports the hypothesis of annual band formation in this species. Moreover, these results compare favorably to cycles in marginal increments (Sulikowski et al., 2003) and to annual vertebral band patterns in other skate species (Holden and Vince, 1973; Waring, 1984; Natanson, 1993; Zeiner and Wolfe, 1993; Walmsley-Hart et al., 1999; Francis et al., 2001). However, because the band counts of the largest and oldest animals in the population were compressed (too small for us to discern marginal increments from their widths), the marginal increment analysis included only juvenile skates that were ≤80 cm total length and the annular nature of the growth bands was verified for only those length groups. Nevertheless, we assumed that as the skates grew larger and older, the annual nature of growth ring deposition continued throughout their lifetime (Conrath et al, 2002).

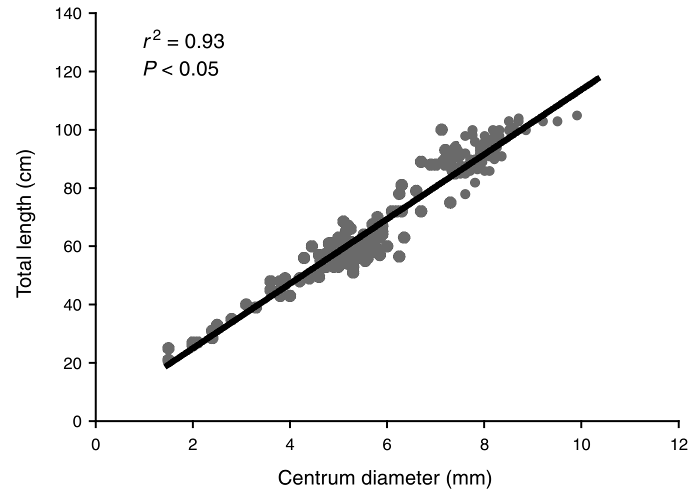


**Figure 3**

The relationship of total length (cm) to centrum diameter (mm) for combined sexes of thorny skate (*Amblyraja radiata*).

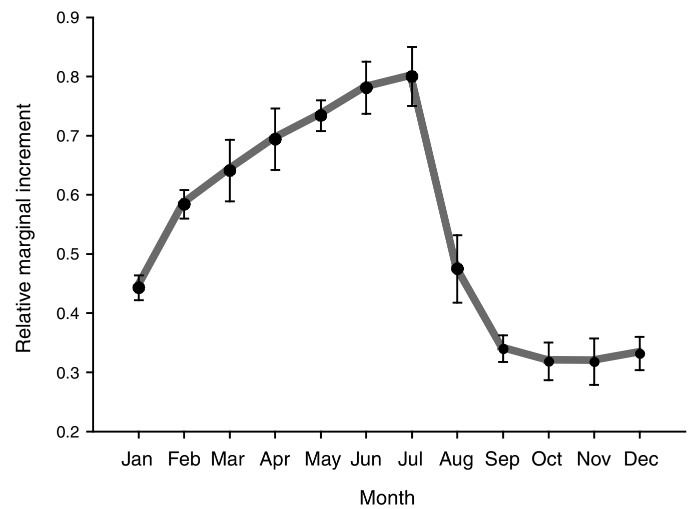


**Figure 4**

Mean monthly marginal increments of opaque bands for *Amblyraja radiata* from the Gulf of Maine. Marginal increments were calculated each month from 10 specimens whose centra contained less than 10 annuli. Error bars represent 1 ±SEM.

During 42 sampling trips from June 2001 through May 2002 (approximately three trips per month), individuals <30 cm TL were rarely captured. The lack of specimens in this size class and smaller size classes was most likely due to the mesh size of the commercial trawl nets. Trawl nets used by commercial fishermen in the Gulf of Maine are restricted to a 6½-inch diamond mesh-size opening, which facilitates the release of most fish below 30 cm TL.

Our estimates of $L_\infty$ exceed the largest specimens in our field collections for both females and males. Growth parameters estimated from the Gompertz and logistics equations also produced over-estimations of $L_\infty$ for the thorny skates in our study. Because the von Bertalanffy growth curve (VBGC) is most widely used and accepted in elasmobranch age and growth studies, we chose to use this function to fit our data. Over estimation of $L_\infty$ with the VBGC has been documented in most skate species studied to date (Table 3). Campana (2001) suggested that the smallest and largest specimens are the most influential in the estimation of growth. Moreover, both Walmsley-Hart et al. (1999) and Sulikowski et al. (2003) suggested that rareness of large individuals was most likely responsible for their over estimation of $L_\infty$. Similarly, in a study of the blue shark (*Prionace glauca*) in the northwest Atlantic, Skomal and Natanson (2003) suggested that earlier studies on the same species contained artificially inflated $L_\infty$ estimates and lower growth rates because of the lack of maximum-size fish. The rareness of large specimens in our study may have been due to these larger individuals being able to avoid the fishing gear or may indicate that mortality, natural or fishing induced, prevents them from attaining these lengths. Exploratory manipulation of our data indicated that inclusion of maximum observed sizes (i.e., thorny skates over 103 cm TL) produced divergent results with regard to von Bertalanffy parameters. For example, the addition of maximum-size fish, using 20 years as the maximum age (Templeman, 1984) and 105 cm as the maximum total length (from the present study), reduced the combined sex $L_\infty$ from 124 cm TL to 116 cm TL. However, the same effect was not documented when adding hatching size (age zero) fish (note: because no documented size for thorny skates exists within the Gulf of Maine, the authors used known hatching sizes for a similar congener species, the winter skate [*Leucoraja ocellata*]). Be that as it may, the reasonable fit of the thorny skate data (Table 2) to the VBGC (Fig. 5) for *A. radiata*, along with a comparison with other batoid studies (Table 3), indicates that this is an appropriate model for this skate species.

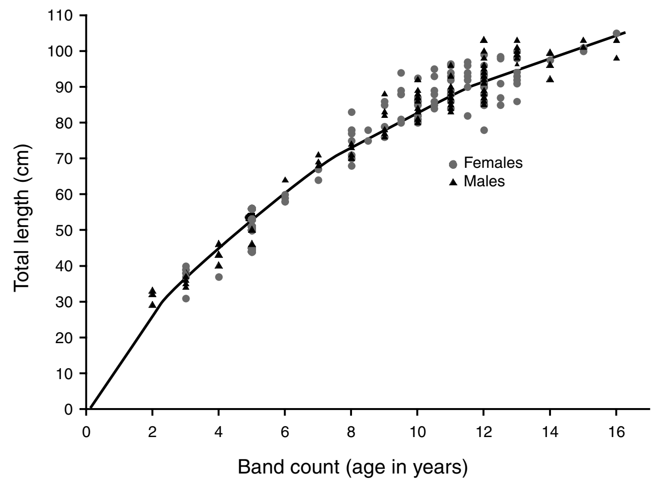


**Figure 5**

Von Bertalanffy growth curve generated from combined vertebral data for female and male thorny skates (*Amblyraja radiata*) from the western Gulf of Maine. Individual VBGC parameters are given in Table 2.

Growth rates were similar for both sexes of thorny skate ($k$=0.13 for females and $k$=0.11 for males) and commensurate with other skate species of a similar size. The oldest age obtained for male and female thorny skates was 16 years (Table 1). These data are in agreement with the assumption that larger batoids, such as *A. radiata, R. pullopunctata* (Walmsley-Hart et al., 1999), and *L. ocellata* (Sulikowski et al., 2003) are longer lived and slower growing than smaller species. For instance, *R. erinacea,* which reaches a total length of 52 cm, has been aged to 8 years and found to have a corresponding $k$ value of 0.352 (Johnson, 1979; Waring, 1984).

**Table 2**

Calculated von Bertalanffy parameters for male, female, and combined sexes of *A. radiata*.

| Parameter | Male | Female | Combined sexes |
|---|---|---|---|
| $L_\infty$ (cm TL) | 127.00 | 120.00 | 124.00 |
| $K$ (/year) | 0.11 | 0.13 | 0.12 |
| $t_0$ (year) | −0.37 | −0.4 | −0.35 |
| $r^2$ | 0.96 | 0.92 | 0.94 |
| SE | 0.01 | 0.01 | 0.001 |
| $n$ | 103.00 | 121.00 | 224.00 |

The reduction in biomass of the thorny skate below threshold levels mandated by the SFA necessitates the development of management measures to rebuild these stocks in accordance with the Magnuson-Stevens Fishery Conservation and Management Act. However, the development and implementation of a successful fisheries management plan for the species require in-depth analyses of appropriate biological information. Moreover, accurate stock assessment data for skates is difficult to collect in the northeast U.S. because individual species are rarely differentiated in landings information (NEFMC[1,2]). As a result, fluctuations in stock size will continue to be difficult to detect and successful implementation of fisheries management plans will remain problematic. This article is the first in a series aimed at providing life history data for the management of thorny skates indigenous to the Gulf of Maine. The basic age and growth parameters for the thorny skate provided in the present study support the hypothesis that *A. radiata*, like other elasmobranchs, require conservative management because of their slow growth rate and susceptibility to over-exploitation (Brander, 1981; Kusher et al., 1992; Zeiner and Wolf, 1993; Frisk et al., 2001; Sulikowski et al., 2003).

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**Table 3**

Comparison of von Bertalanffy derived $L_\infty$ to the observed total lengths ($L$) for a number of skate species. $L_\infty$ (mm) = disk width.

| Scientific name | Sex | $L_\infty$ (mm) | $L$ observed (mm) | Max. age (yr) | Source |
|---|---|---|---|---|---|
| *Raja microocellata* | ♀ ♂ | 1370 (TL) | 875[1] | 9 | Ryland and Ajayi, 1984 |
| *Raja montagui* | ♀ ♂ | 978 (TL) | 710[1] | 7 | Ryland and Ajayi, 1984 |
| *Raja clavata* | ♀ | 1047 (TL) | 1392 | 7 | Ryland and Ajayi, 1984 |
| *Raja erinacea* | ♀ ♂ | 527 (TL) | 520 | 8 | Waring, 1984 |
| *Raja rhina* | ♂ | 967 (TL) | 1322 | 13 | Zeiner and Wolf, 1993 |
| *Raja rhina* | ♀ | 1067 (TL) | 1047 | 12 | Zeiner and Wolf, 1993 |
| *Raja wallacei* | ♂ | 405 (DW) | 512 | 15 | Walmsley-Hart et al., 1999 |
| *Raja wallacei* | ♀ | 435 (DW) | 571 | 15 | Walmsley-Hart et al., 1999 |
| *Raja pullopunctata* | ♂ | 771 (DW) | 696 | 18 | Walmsley-Hart et al., 1999 |
| *Raja pullopunctata* | ♀ | 1327 (DW) | 747 | 14 | Walmsley-Hart et al., 1999 |
| *Raja pullopunctata* | ♀ | 1327 (DW) | 747 | 14 | Walmsley-Hart et al., 1999 |
| *Dipturus nasutus* | ♀ ♂ | 700 (TL) | 913 | 9 | Francis et al., 2001 |
| *Dipturus innominatus* | ♀ ♂ | 1330 (TL) | 1505 | 24 | Francis et al., 2001 |
| *Leucoraja ocellata* | ♀ ♂ | 1314 (TL) | 936[1] | 19 | Sulikowski et al., 2003 |
| *Amblyraja radiata* | ♀ ♂ | 1240 (TL) | 1020[1] | 16 | Present study |

[1] Average of male and female observed TL.

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## Literature cited


Brander, K.
1981. Disappearance of common skate *Raia batis* from Irish Sea. Nature 290 (5801):48–49.

Branstetter, S., and J. A. Musick.
1984. Age and growth estimates for the sand tiger in the northwestern Atlantic ocean. Trans. Am. Fish. Soc. 123:242–254.

Brown, C. B., and S. H. Gruber.
1988. Age assessment of the lemon shark, *Negaprion brevirostris*, using tetracycline validated vertebral centra. Copeia 3:747–753.

Casey, J. G., H. L. Pratt, and C. E. Stillwell.
1985. Age and growth of the sandbar shark (*Carcharhinus plumbeus* ) from the western North Atlantic. Can. J. Fish. Aquat. Sci. 42(5):963–975.

Casey, J. M., and R. A. Myers.
1998. Near extinction of a large widely distributed fish. Science 28:690–692.

Cailliet, G. M.
1990. Elasmobranch age determination and verification: an updated review. *In* Elasmobranchs as living resources: advances in the biology, ecology, systematics and the status of the fisheries (L. Pratt Jr, S. H. Gruber, and T. Tanuichi (eds.), p. 157–165. NOAA Tech. Report NMFS 90.

Campana, S. E.
2001. Accuracy, precision and quality control in age determination including a review of the use and abuse of age validation methods. J. Fish. Biol. 59:197–242.

Campana, S. E., M. C. Annand, and J. I. Mcmillan.
1995. Graphical and statistical methods for determining the consistency of age determinations. Trans. Am. Fish. Soc. 124:131–138.

Chang, W. Y. B.
1982. A statistical method for evaluating the reproducibility of age determination. Can. J. Fish. Aquat. Sci. 39:1208–1210.

Collette, B., and G. Klein-MacPhee, eds.
2002. Bigelow and Schroeder's fishes of the Gulf of Maine, 3rd ed., p. 62–66. Smithsonian Institution Press, Washington, D. C.

Compagno, L. J. V., D. A. Ebert, and M. J. Smale.
1989. Guide to the sharks and rays of southern Africa, 158 p. New Holland (Publ.) Ltd., London.

Conrath, C. L., J. Gelsleichter, and J. A. Musick.
2002. Age and growth of the smooth dogfish, *Mustelus canis*, in the northwest Atlantic. Fish. Bull. 100:674–682.

Dulvey, N. K., J. D. MetCalfe, J. Glanville, M. G. Pawson, and J. D. Reynolds.
2000. Fishery stability, local extinctions, and shifts in community structure in skates. Cons. Biol. 14 (1): 283–293.

Francis, M., C. O. Maolagain, and D. Stevens.
2001. Age, growth, and sexual maturity of two New Zealand endemic skates, *Dipturus nasutus* and *D. innominatus*. N. Z. J. Mar. Freshw. Res. 35:831–842.

Frisk, M. G.
2000. Estimation and analysis of biological parameters in elasmobranch fishes and the population dynamics of the little skate *Raja erinacea*, thorny skate *R. radiata* and Barndoor skate *R. laevis*. M.S. thesis, 112 p. Center for Environmental Science, Univ. Maryland, Cambridge, MD.

Frisk, M. G., T. J. Miller, and M. J. Fogarty.
2001. Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. Can. J. Fish. Aquat. Sci. 58(5 ):969–981.

Hoenig, J., and S. H. Gruber.
1990. Life history patterns in the elasmobranchs: implications for fisheries management. *In* Elasmobranchs as living resources: advances in the biology, ecology, systematics and the status of the fisheries (H. L. Pratt Jr, S. H. Gruber, and T. Tanuichi, eds.), p. 1–16. NOAA Tech. Report, NMFS 90.
Holden, M. J.
1977. Elasmobranchs. *In* Fish population dynamics (J. A. Gulland, ed.), p. 187–214. J. Wiley and Sons, London, England.
Holden, M. J., and M. R. Vince.
1973. Age validation studies on the centra of *Raja clavata* using tetracycline. J. Cons. Int. Explor. Mer 35:13–17.
Johnson, G. F.
1979. The biology of the little skate, *Raja erinacea*, in Block Island Sound, Rhode Island. Unpubl. M.A. thesis, 119 p. Univ. Rhode Island. Kingston, RI.
Kusher, D. I., S. E. Smith, and G. M. Cailliet
1992. Validated age and growth of the leopard shark, *Triakis semifasciata*, with comments on reproduction. Environ. Biol. Fish. 35:187–203.
Magnuson Fishery Conservation and Management Act.
1994. 16 U.S.C.1801-1882 (1994), amended by Sustainable Fisheries Act, Pub. L. No. 104-297, 110 Stat. 3559 (1996).
Marquardt, D. W.
1963. An algorithm for the least squares estimation of nonlinear parameters. J. Soc. Ind. Appl. Math. 2: 431–441.
Natanson, L. J.
1993. Effect of temperature on band deposition in the little skate, *Raja erinacea*. Copeia 1993:199–206.
Prager, M. H., S. B. Saila, and C. W. Recksiek.
1987. Fishparm: a microcomputer program for parameter estimation of nonlinear models in fishery science. Old Dominion University, Norfolk Virginia, Tech. Rep. (87–10):1–37.
Robins, C. R., and G. C. Ray.
1986. A field guide to Atlantic coast fishes of North America, 354 p. Houghton Mifflin Co., Boston, MA.
Ryland, J. S., and T. O Ajayi.
1984. Growth and population dynamics of three *Raja* species (Batoidei) in Carmarthen Bay, British Isles. J. Cons. Int. Explor. Mer 41:111–120.
Simpfendorfer, C.A.
1993. Age and growth of the Australian sharpnose shark, *Rhizoprionodon taylori*, from north Queensland, Australia. Environ. Biol. Fish. 36:(3):233–241.
2000. Age and growth of the whiskery shark, *Furgaleus macki*, from south-western Australia. Environ. Biol. Fish. 58:335–343.
Skomal, G. B, and L. J. Natanson.
2003. Age and growth of the blue shark (*Prionace glauca*) in the North Atlantic Ocean. Fish. Bull. 101:627–639.
Sosebee, K.
2000. Skates. Status of fishery resources off the northeastern United States. NOAA Tech. Mem. NMFS-NE. 115:114–115.
Sulikowski, J. A., M. D. Morin, S. H. Suk, and W. H. Howell.
2003. Age and growth of the winter skate, *Leucoraja ocellata*, in the Gulf of Maine. Fish. Bull. 101:405–413.
Templeman, W.
1984. Migrations of thorny skate, *Raja radiata*, tagged in the Newfoundland area. J. Northw. Atl. Fish. Sci. 5(1):55–63.
1987. Differences in sexual maturity and related characteristics between populations of thorny skate *Raja-radiata* in the northwest atlantic. J. Northw. Atl. Fish. Sci. 44 (1):155–168.
Von Bertalanffy, L.
1938. A quantitative theory of organic growth (inquiries of growth laws II). Human Biology 10:181–183.
Walmsley-Hart, S. A., W. H. H. Sauer, and C. D. Buxton.
1999. The biology of the skates *Raja wallacei* and *R. pullopunctata* (Batoidea:Rajidae) on the Agulhas Bank, South Africa. S. Afr. J. Mar. Sci. 21:165–179.
Waring, G. T.
1984. Age, growth and mortality of the little skate off the northeast coast of the United States. Trans. Am. Fish. Soc. 113:314–321.
Winemiller, K. O., and K. A. Rose.
1992. Patterns of life history diversification in North American fishes: implication for population regulation. Can. J. Fish. Aquat. Sci. 49:2196–2218.
Wintner, S. P., and G. Cliff.
1996. Age and growth determination of the blacktip shark, *Carcharhinus limbatus*, from the east coast of South Africa. Fish. Bull. 94 (1):135–144.
Zeiner, S. J., and P. G. Wolf.
1993. Growth characteristics and estimates of age at maturity of two species of skates (*Raja binoculata* and *Raja rhina*) from Monterey Bay, California. *In* Conservation biology of elasmobranches (S. Branstetter, ed.), p. 87–90. NOAA Tech. Report NMFS 115.