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Abstract—Age and growth estimates for the winter skate (*Leucoraja ocellata*) were estimated from vertebral band counts on 209 fish ranging in size from 145 to 940 mm total length (TL). An index of average percent error (IAPE) of 5.8% suggests that our aging method represents a precise approach to the age assessment of *L. ocellata*. Marginal increments were significantly different between months (Kruskal-Wallis $P < 0.001$) and a distinct trend of increasing monthly increment growth began in July. Estimates of von Bertalanffy growth parameters suggest that females attain a slightly larger asymptotic TL ($L_{\infty} = 1374$ mm) than males ($L_{\infty} = 1218$ mm) and grow more slowly ($k = 0.059$ and 0.074 , respectively). The oldest ages obtained for the winter skate were 19 years for males and 18 years for females, which corresponded to total lengths of 932 mm and 940 mm, respectively. The results indicate that the winter skate exhibits the characteristics that have made other elasmobranch populations highly susceptible to exploitation by commercial fisheries.

Age and growth estimates of the winter skate (*Leucoraja ocellata*) in the western Gulf of Maine

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Little is known about the biology of many elasmobranchs, including important parameters such as validated age, growth, age at maturity, reproductive cycles and annual fecundity (Frisk et al., 2001). Difficulty in obtaining samples, the large size of specimens, their high mobility, and minor commercial value are just a few of the problems that make such studies complicated and in some respects impractical (Cailliet et al., 1983; Cailliet et al., 1986). The recent intensification in commercial fishing of elasmobranchs (Cailliet et al., 1983; Brown and Gruber, 1988; Kusher et al., 1992; Dulvey et al., 2000) has made the collection of their life history information essential to the realistic management of their populations (Cailliet et al., 1983; Ryland and Ajayi, 1984; Dulvey et al., 2000). Historically, batoids have been of minimal commercial value (Otwell and Lanier, 1979; Sosebee, 1998); hence the majority of research on elasmobranchs has focused on commercially valuable sharks (e.g. Holden, 1977; Natanson et al., 1995; Walmsley-Hart et al., 1999). According to the characteristics outlined by Winemiller and Rose (1992) and the comparative analyses of Frisk et al. (2001), skates, like other elasmobranchs, fall into the category of equilibrium strategists and as such reach sexual maturity at a late age, have a low fecundity, and are relatively long-lived. These characteristics, coupled with fisheries that select for the removal of large individuals (especially those over 100 cm total length), make these particular fish highly susceptible to overfishing (Hoenig and Gruber,

1990; Dulvey et al., 2000; Frisk et al., 2001).

Traditionally, skates caught by ground fishing operations were discarded (Martin and Zorzi, 1993; Junquera and Paz, 1998; Sosebee, 1998). New and expanding markets for skate wings have made retention of these fish commercially more lucrative in recent years (Sosebee, 1998; New England Fishery Management Council¹). Skate harvests in the U.S. portion of the western North Atlantic are currently unregulated. Moreover, biological information on skate life histories is almost nonexistent (Frisk, 2000). This combination of factors is believed to have led to a depletion of common skates (*Raja batis*) in the Irish sea (Brander, 1981).

The winter skate (*Leucoraja ocellata*) is a large species (total length over 100 cm) of skate of the family Rajidae (Bigelow and Schroeder, 1953; Robins and Ray, 1986; New England Fishery Management Council¹). It is endemic to the inshore waters of the western Atlantic, from the Newfoundland Banks and the southern Gulf of St. Lawrence in Canada to North Carolina in the United States (Bigelow and Schroeder, 1953). Despite this wide range, little direct biological data is available for this species (Simon and Frank, 1996; Casey and

¹ New England Fishery Management Council. 2001. 2000 Stock assessment and fishery evaluation (SAFE) report for the northeast skate complex, 179 p. New England Fishery Management Council, 50 Water Street, Mill 2 Newburyport, MA 01950.

Myers, 1998, Frisk, 2000). Recent assessment studies in the northeast U.S. (Northeast Fisheries Science Center²), suggest that the biomass of the winter skate may be below threshold levels mandated by the Sustainable Fisheries Act (SFA). To add insight into the life history of this species and the status of the stock (Simpfendorfer, 1993; Frisk et al., 2001), we estimated age and growth rates of *L. ocellata* by interpreting annular counts and marginal increments on vertebral centra from specimens collected in the western Gulf of Maine.

Materials and methods

Sampling

A total of 304 winter skates were captured by otter trawl between November 1999 and May 2001 at locations that ranged from 1.6 to 32 km off the coast of New Hampshire. Approximate depths at these locations ranged between 9 and 107 m. Skates were maintained alive on board the vessel until transport to the University of New Hampshire's Coastal Marine Laboratory (CML). There, individual fish were euthanized (0.05g/L bath of MS222). We measured total length (TL in mm) as a straight line distance from the tip of the rostrum to the end of the tail, and disc width (DW in mm) as a straight line distance between the tips of the widest portion of pectoral fins. Total wet weight (kg) was also recorded. In order to differentiate between the small, immature specimens of little skates (*Leucoraja erinacea*, a congener species also found in the Gulf of Maine) and winter skates, rows of teeth in the upper jaw were counted. Skates whose number of teeth ranged between 72 and 110 per row were identified as *L. ocellata* and skates whose number of teeth ranged between 38 and 64 per row were identified as *L. erinacea* (Bigelow and Schroeder, 1953). To reduce any uncertainty in species identification, skates having between 38 and 71 teeth per row were not used in this study.

Preparation of vertebral samples

Vertebral samples, taken from above the abdominal cavity, were removed from 132 females and 98 males, labeled, and stored frozen. After defrosting, three centra from each specimen were freed from the vertebral column, stripped of excess tissue and air dried. Large centra were cut sagittally, while held within a vise, with a DremelTM tool fitted with a mini-saw attachment. Smaller centra were sanded with a DremelTM tool to replicate a sagittal cut. Processed vertebrae were mounted horizontally on glass microscope slides and ground with successively finer grits (#180, #400, #600), of wet-dry sandpaper. Each vertebra was then remounted and the other side ground to produce a thin (300 micrometer) "hourglass" section.

Counts of annuli

Vertebral sections were viewed through a compound microscope (25–40×) with reflected light (Fig. 1). A growth ring (annulus) was defined as an 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). 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).

Three nonconsecutive counts of annuli were made for the three vertebral sections from each specimen without prior knowledge of the length of the skate or previous counts. If the variability between readings was more than two years, that particular specimen was eliminated from further analyses. Count reproducibility was estimated by using the index of average percent error (IAPE) described by Beamish and Fournier (1981):

$$IAPE = 1/N \sum \left(1/R \sum \left(|X_{ij} - X_j| / X_j \right) \right) \times 100,$$

where N = the number of skates aged;
 R = the number of readings;
 X_{ij} = the i th age determination of the j th fish; and
 X_j = the average calculated for the j th fish.

An upper limit for the IAPE was arbitrarily set at 15% for each vertebra. Vertebrae with statistically acceptable IAPE indexes were used for estimation of asymptotic growth rates (Brown and Gruber, 1988; Cailliet and Tanaka, 1990). The average of the mean counts for all three centra defined the age estimate for each specimen (Casey et al., 1985; Wintner and Cliff, 1996).

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

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

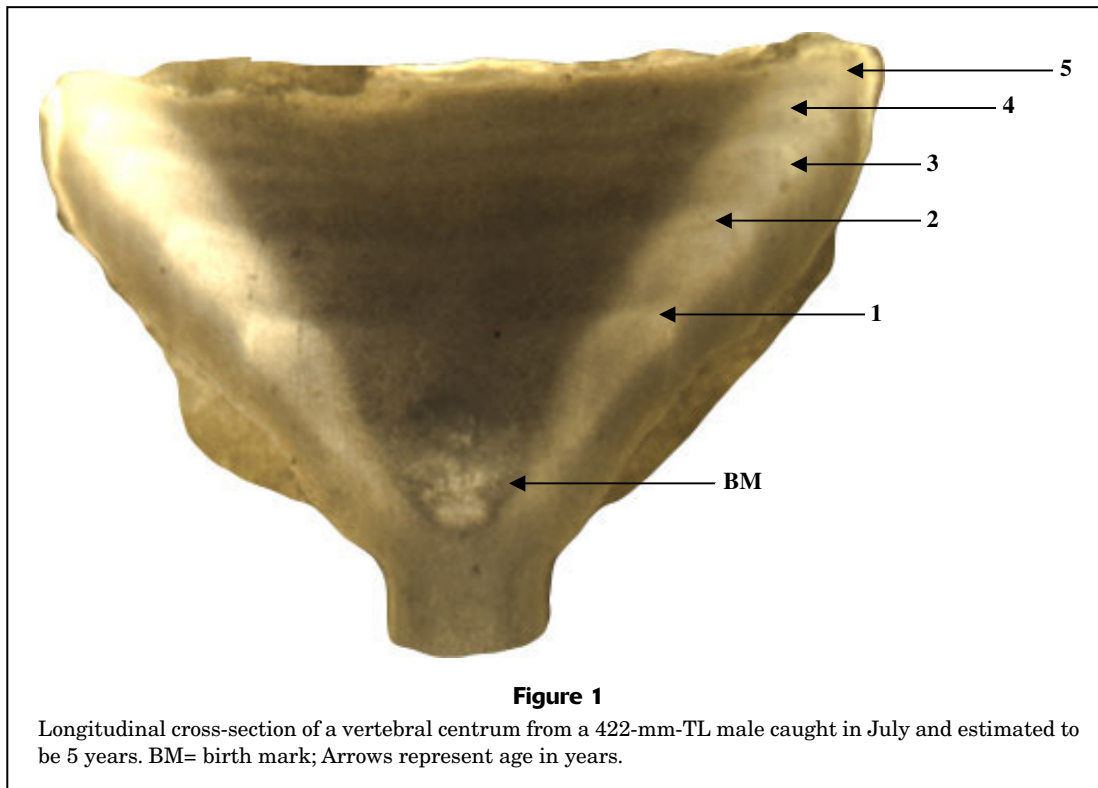
where L_t = total length at time t (age in years);
 L_∞ = theoretical asymptotic length;
 K = Brody growth constant; and
 t_0 = theoretical age at zero length.

Growth in length data were analyzed 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).

Marginal increment analyses

The annual periodicity of band pair formation was investigated by using marginal increment analyses (MIA). Because the annuli in older specimens were closer together, marginal increments were calculated from five specimens per month whose centra contained either four or five annuli. For MIA determination, the distance of the final opaque band and the penultimate opaque band from the centrum edge were measured with an ocular micrometer.

² Northeast Fisheries Science Center. 1999. 30th northeast regional stock assessment workshop, 477 p. Northeast Fisheries Science Center, 166 Water Street Woods Hole, MA 02543-1026.



The marginal increment was calculated as the ratio of the distance between the last and penultimate bands (Branstetter and Musick, 1994; Cailliet, 1990; Simpfendorfer, 1993; Simpfendorfer, 2000). Mean average increments by month of capture were plotted to identify trends in band formation by using a Kruskal-Wallis one-way analysis of variance on ranks. (Simpfendorfer, 1993; 2000).

Results

Morphological measurements

A total of 230 specimens were used for this study. Males ($n=98$) ranged between 147–932 mm TL, 82–601 mm DW, and 0.015–6.2 kg. Females ($n=132$) ranged between 145–940 mm TL, 82–635 mm DW, and 0.015–7.5 kg. A linear relationship existed between the total length, disk width, and mass relationships for male, female, and the sexes combined (all r^2 values were greater than 0.85). Two skates (one male: TL=147 mm, DW=82 mm, weight=0.015 kg; and one female TL=145 mm, DW=82 mm, weight=0.015 kg) hatched from egg cases during May 2001 in the CML after gestating 18 months. One wild male specimen (age-0, TL=175 mm, DW=100 mm, weight=0.027 kg) was also captured and incorporated into the results of this study.

Vertebral analyses

No difficulty was encountered in estimating the age of *L. ocellata*. False bands (bands that do not completely encircle

the centra) were easily distinguished from complete bands. Of the 230 processed vertebrae, 209 (91%) were readable. These 209 vertebrae (males=88; females=121) had annular count estimates that agreed within two years, resulting in an IAPE of 5.8%. Mean total length and disk width at age for male, female, and sexes combined are given in Table 1. The relationship between TL and centrum diameter was linear ($r^2=0.92$; $P<0.05$; Fig. 2) and there were no significant differences (ANCOVA, $P<0.05$) between males and females. Because no significant difference existed for TL and centrum diameter between the sexes, the data were combined (Fig. 2).

Marginal increments were averaged from five specimens for each month, except June when skates belonging to the 4 and 5 year age classes were unavailable. Marginal increments were significantly different between months (Kruskal-Wallis $P<0.001$) and a distinct trend of increasing monthly increment growth began in July (Fig. 3). Maximum marginal increment measurement occurred in May. Minimum marginal increment measurement occurred in July. Two recently hatched males (one from the laboratory (147 mm TL) and one from field collections (175 mm TL)) had opaque zones on the distal edge of their vertebral centra. Reviewing this information, we suspect that a single opaque band may be formed annually on the vertebral centra during June–July in the winter skate.

Age and growth estimates

We assumed that opaque-translucent band pairs were formed annually, and we fitted von Bertalanffy growth

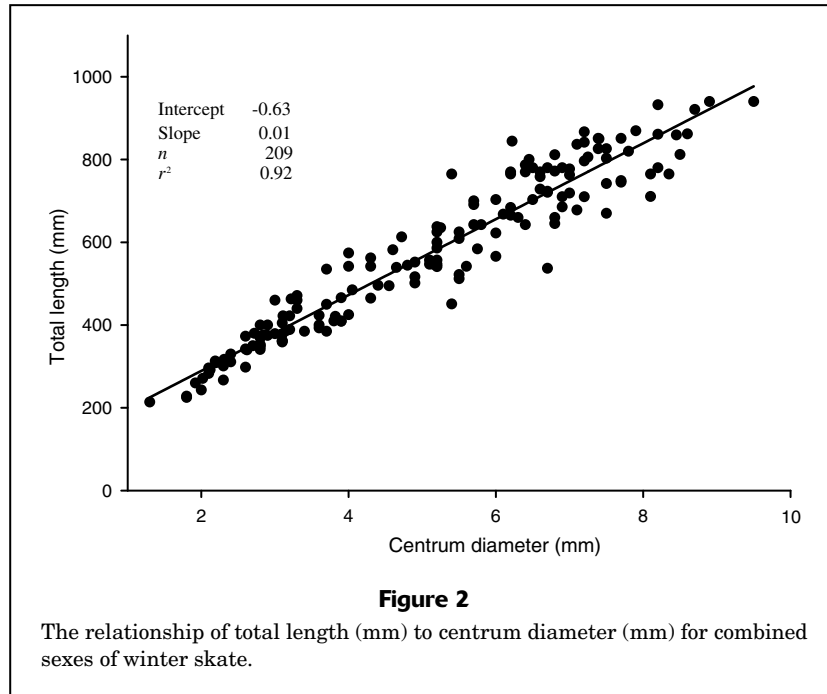


Table 1

Average total length, TL, and disc width, DW, at age for winter skates (*L. ocellata*) by sex and combined sexes. Mean \pm 1 SEM; sample sizes (no. of fish in sample) are given in parentheses.

Age	Male TL	Female TL	Sexes combined	Male DW	Female DW	Sexes combined
0	161 (2) \pm 14	145 (1)	156 (3) \pm 10	93 \pm 7	81	89 \pm 7
1	228 (1)	—	228 (1)	139	—	139
2	264 (5) \pm 14	268 (4) \pm 21	266 (9) \pm 11	153 \pm 5	158 \pm 8	155 \pm 5
3	340 (4) \pm 20	317 (9) \pm 9	324 (13) \pm 9	198 \pm 6	188 \pm 6	191 \pm 6
4	379 (12) \pm 8	392 (25) \pm 8	388 (37) \pm 6	223 \pm 8	233 \pm 5	230 \pm 4
5	435 (4) \pm 19	429 (16) \pm 13	430 (20) \pm 6	264 \pm 11	259 \pm 13	260 \pm 6
6	536 (5) \pm 13	501 (7) \pm 16	516 (12) \pm 12	338 \pm 8	310 \pm 15	322 \pm 11
7	609 (1)	551 (12) \pm 6	556 (13) \pm 7	392	342 \pm 6	346 \pm 6
8	651 (1)	565 (11) \pm 13	570 (12) \pm 13	401	352 \pm 10	356 \pm 10
9	658 (9) \pm 24	632 (9) \pm 20	645 (18) \pm 15	420 \pm 18	403 \pm 16	411 \pm 11
10	690 (12) \pm 20	704 (8) \pm 18	696 (20) \pm 14	441 \pm 22	447 \pm 17	444 \pm 11
11	735 (10) \pm 17	761 (5) \pm 22	744 (15) \pm 14	479 \pm 24	498 \pm 20	485 \pm 14
12	743 (5) \pm 24	763 (5) \pm 19	753 (10) \pm 15	488 \pm 12	501 \pm 15	494 \pm 8
13	830 (3) \pm 7	772 (3) \pm 16	801 (6) \pm 15	495 \pm 6	506 \pm 8	500 \pm 5
14	838 (4) \pm 10	803 (3) \pm 23	821 (7) \pm 13	530 \pm 9	527 \pm 24	529 \pm 10
15	841 (4) \pm 12	—	841 (4) \pm 12	541 \pm 19	—	541 \pm 13
16	860 (4) \pm 4	842 (1) \pm 0	857 (5) \pm 5	565 \pm 16	542	560 \pm 10
17	921 (1)	—	921 (1)	579	—	579
18	—	940 (2) \pm 0	940 (2) \pm 0	—	623 \pm 13	623 \pm 13
19	932 (1)	—	932 (1)	601	—	601

curves (VBGC) to total length-at-age data (Fig. 4). The VBGC provided a good fit with a low standard error for males, females, and both sexes combined (Table 2). The t_0 values (-1.4 to -1.6) compared favorably with gestation rates for

the two skates hatched in captivity (1.5 years) (Table 2). The von Bertalanffy growth parameters for males, females, and the sexes combined were similar but k values were higher for males and sexes combined, than for females.

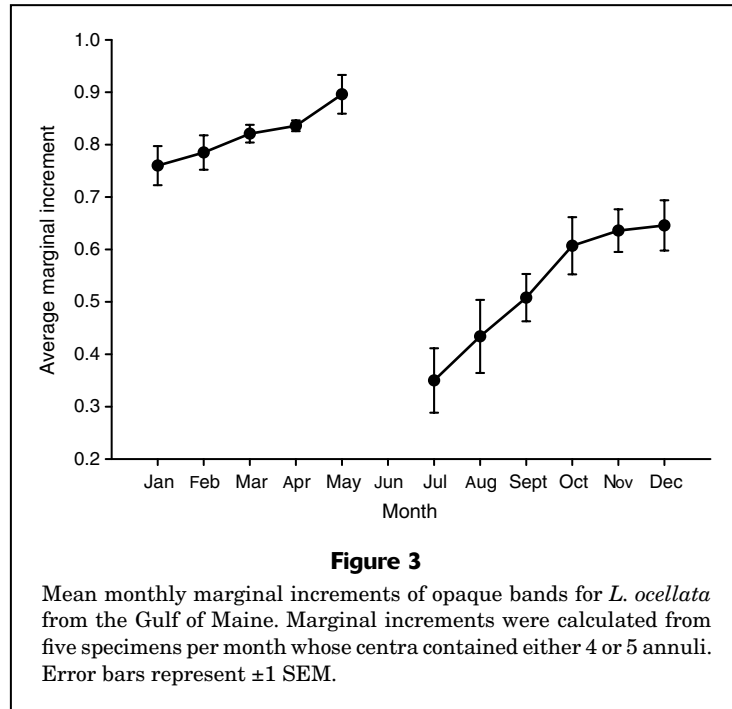


Figure 3

Mean monthly marginal increments of opaque bands for *L. ocellata* from the Gulf of Maine. Marginal increments were calculated from five specimens per month whose centra contained either 4 or 5 annuli. Error bars represent ± 1 SEM.

Discussion

The relationship between TL and centrum diameter was linear and significant, indicating that the centra grew proportionally to skate length for all size classes, and thus this structure was useful for age analyses (Kusher et al., 1992). The 5.8% IAPE index suggests that our aging method represents a precise approach to the age assessment of *L. ocellata*. Minimal width of the marginal increment for winter skates captured in May supports the hypothesis of annual band formation in this species. Moreover, these results compare favorably to growth cycles in marginal increments for other skates found in temperate waters whose vertebral bands are formed annually (Holden and Vince, 1973; Waring, 1984; Natanson, 1993).

Von Bertalanffy parameters, as determined by our study, suggest that females attain a slightly larger asymptotic TL_{∞} (1374 mm) than males (1218 mm) and grow more slowly ($k=0.059$ and 0.074 , respectively). This trend follows a common pattern in batoids. Holden (1977), Waring (1984), Ryland and Ajayi (1984), Brander (1981), and Walmsley-Hart et al. (1999) found similar tendencies in several species of skates, and Martin and Cailliet (1988) found comparable results in the bat ray (*Myliobatis californica*).

Our estimates of L_{∞} exceeded those of the largest specimens in our field collections (940 mm for females and 932 mm for males). Nevertheless, data from extensive trawl surveys in the western Gulf of Maine and the Mid-Atlantic offshore region spring and autumn bottom trawl surveys from 1967 to 2000 (Northeast Fisheries Science Center²) indicated that mean TL did not exceed 1000 mm. Thus, we suspect that our von Bertalanffy equation produces an accurate estimation of L_{∞} for winter skate. Walmsley-Hart

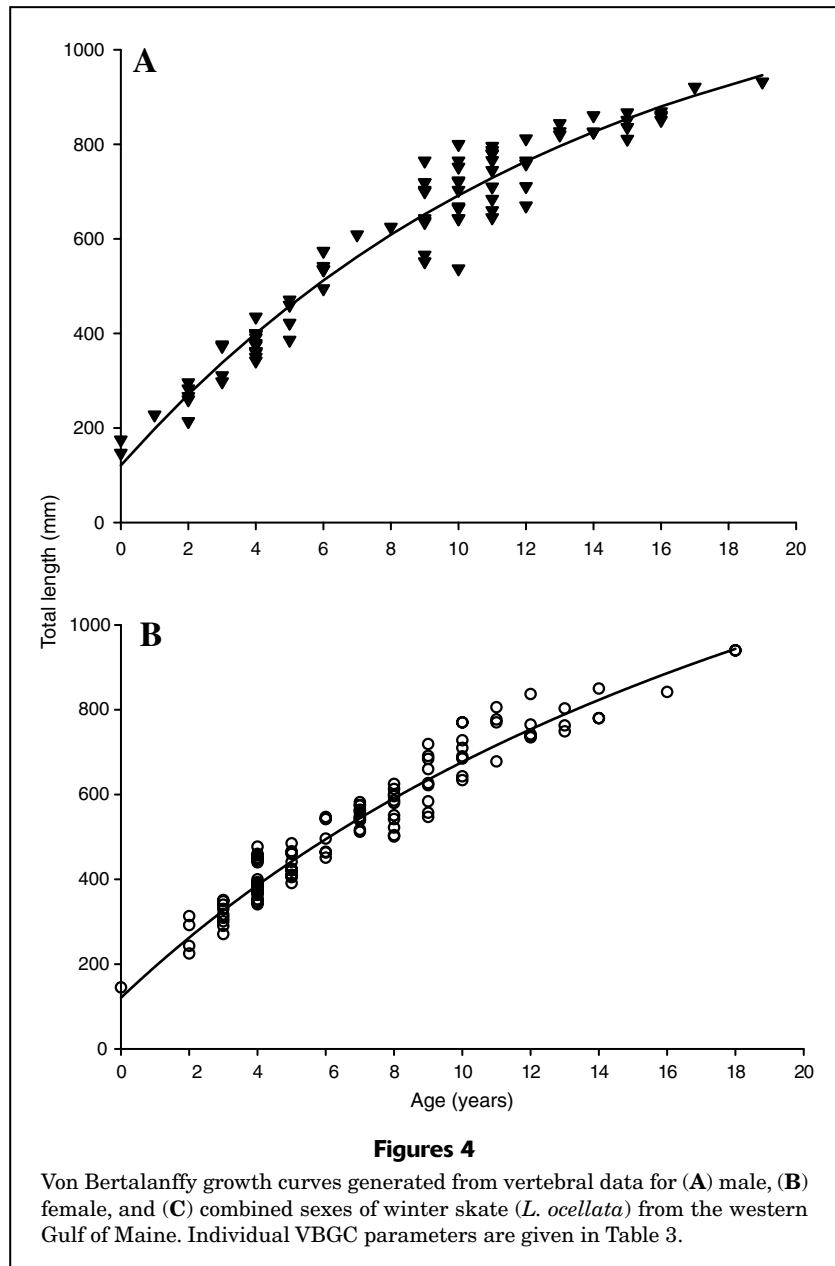
Table 2

Calculated von Bertalanffy parameters for male, female, and combined sexes of *L. ocellata*. r^2 is the coefficient of determination.

Parameter	Male	Female	Combined sexes
L_{∞} (mm TL)	1218	1374	1314
k (year ⁻¹)	0.074	0.059	0.064
t_0 (year)	-1.418	-1.609	-1.531
r^2	0.946	0.939	0.946
SE	0.01	0.01	0.001
n	88	121	209

et al. (1999) overestimated L_{∞} for *R. pullopunctata* and suggested that small sample size and rareness of large individuals were most likely responsible. Because fishing gear was not biased towards a specific marketable skate size and because all size classes of *L. ocellata* were represented, it is quite possible that the rareness of large individuals led to the augmented L_{∞} in combined and individual sexes in our study. Possibly, a larger sample size of winter skates would produce significant and divergent results with regard to von Bertalanffy parameters. However, the close fit of the data to the VBGc for *L. ocellata* indicates the VBGc is an appropriate model for this species.

Preliminary estimates of age and growth parameters are available for winter skate in Canadian waters (eastern Scotian Shelf) from Simon and Frank (1996), who reported the results of a study conducted at St. Mary's University by R. Nearing. Combined sexes of winter skates ($n=242$) with TL



ranging from 120 to 1060 mm and ages from 0 to 16 years provided von Bertalanffy parameters of $L_{\infty} = 114.1$ cm, $k = 0.14405$, and $t_0 = 0.00315$. However, these data should be viewed with caution because no IAPE values nor validation of the annual nature exist for these estimates, and it is likely that the older specimens had been under-aged by four or more years (Simon³).

K values (an estimation of how quickly an animal grows to L_{∞}) were similar for both sexes of winter skate. These growth rates are commensurate with other skate species of

similar size, but slower than skate species of smaller size (Table 3). The oldest ages obtained for the winter skate were 19 and 18 years for males and females, respectively. These data are in agreement with the assumption that larger batoids, such as *L. ocellata* and *R. pullopunctata* (Walmsley-Hart et al., 1999) are longer lived and grow more slowly than smaller species, such as *R. erinacea*, which has been aged to 8 years with a k value of 0.352 (Johnson, 1979; Waring, 1984).

Accurate stock assessment data for skates is difficult to collect in the northeast United States because species are rarely differentiated in landings information (New England Fishery Management Council¹). Because of this lack of differentiation of species in landings, fluctuations in stock size

³ Simon, J. 2001. Personal commun. Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

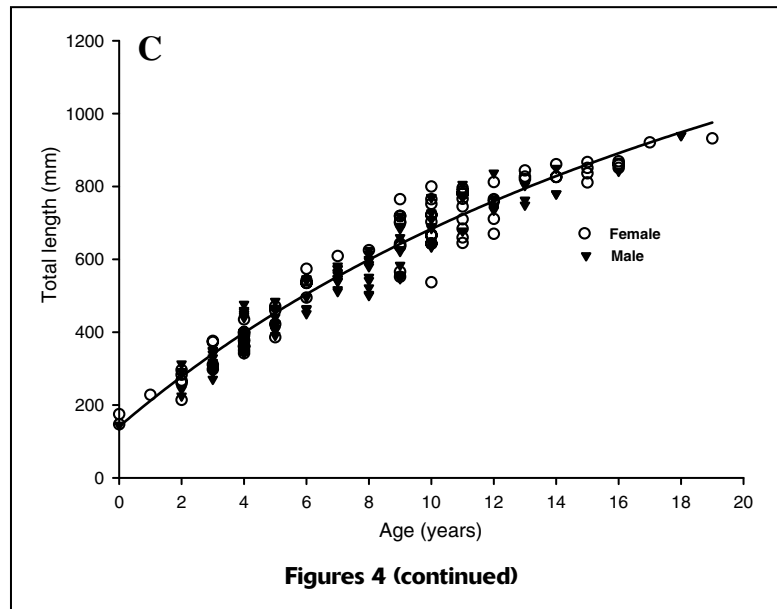


Table 3
Comparison of von Bertalanffy growth parameters for several skate species.

Scientific name	Sex	L_{∞} (mm)	k	t_0 (years)	Max age (yr)	Source
<i>Raja rhina</i>	♀♂	1047 (TL)	0.17	-0.16	13	Zeiner and Wolf, 1993
<i>Raja microocellata</i>	♀♂	1370 (TL)	0.086	-3.009	9	Ryland and Ajayi, 1984
<i>Raja montagui</i>	♀♂	978 (TL)	0.152	-1.719	7	Ryland and Ajayi, 1984
<i>Raja erinacea</i>	♀♂	527 (TL)	0.352	-0.449	8	Waring, 1984
<i>Raja wallacei</i>	♀♂	422 (DW)	0.26	-0.17	15	Walmsley-Hart et al., 1999
<i>Raja clavata</i>	♀♂	1050 (TL)	0.215	0.045	10	Brander and Palmer 1985
<i>Raja pullopunctata</i>	♂	771 (DW)	0.05	-2.20	18	Walmsley-Hart et al., 1999
<i>Raja pullopunctata</i>	♀	1327 (DW)	0.08	-1.95	14	Walmsley-Hart et al., 1999
<i>Leucoraja ocellata</i>	♀♂	1314 (TL)	0.064	-1.531	19	This study

will be difficult to detect and successful implementation of fisheries management plans will remain problematic. Our study provides some basic age and growth parameters for the winter skate and it supports the hypothesis that *L. ocellata*, like other elasmobranchs, require conservative management because they grow slowly and are susceptible to overexploitation (Brander, 1981; Kusher et al., 1992; Zeiner and Wolf, 1993; Frisk et al., 2001).

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