SHORT NOTE

AGE AND GROWTH OF THE ANTARCTIC SKATE (AMBLYRAJA GEORGIANA) IN THE ROSS SEA

M.P. Francis⊠ and C. Ó Maolagáin National Institute of Water and Atmospheric Research (NIWA) Ltd Private Bag 14-901, Kilbirnie Wellington, New Zealand Email – m.francis@niwa.co.nz

Abstract

X-rays of vertebral half-centra, and x-rays and transmitted white light examination of caudal thorns, were used to estimate the ages of the Antarctic skate (Amblyraja georgiana) from the Ross Sea. Caudal thorns viewed with transmitted white light provided the clearest growth bands, but reading precision was low, producing uncertain age estimates. Furthermore, annual deposition of thorn bands has not been validated. The maximum estimated age was 14 years, but this should be regarded as a conservative estimate of longevity because of the possibility that thorn growth ceases in large individuals. There was no obvious difference in growth between the sexes, so the von Bertalanffy curve for both sexes provides the best available representation of growth in the species: $L_t = 70.8 \left(1 - e^{-0.308[t+1.10]}\right)$, where L_t is the pelvic length (PL) in centimetres at age t years. Applying this growth curve to the estimated lengths at maturity for males and females (64 and 66–69 cm PL respectively) produced estimated ages at maturity of 6–7 years for males and 8-11 years for females. These estimates are near the middle to upper end of the range of ages at maturity for skates worldwide. The results of this study are preliminary and should be used with caution. Further work is needed to determine whether the thorn ageing technique presented here produces reproducible and reliable age estimates.

Résumé

L'âge de la raie étoilée antarctique (Amblyraja georgiana) de la mer de Ross est estimé par radiographie de coupes longitudinales des corps vertébraux et des épines caudales qui ont également fait l'objet d'un examen à la lumière blanche transmise. Les épines caudales examinées à la lumière blanche donnent les anneaux de croissances les plus clairs, mais la précision de la lecture est faible, ce qui produit des estimations d'âge non fiables. De plus, le dépôt annuel des bandes sur les épines n'est pas validé. L'âge maximal est estimé à 14 ans, mais cette estimation de la longévité doit être considérée comme conservative car il est possible que les épines cessent de croître chez les individus de grande taille. Aucune différence de croissance n'est mise en évidence entre les sexes, ce qui fait de la courbe de von Bertalanffy des deux sexes la meilleure représentation disponible de la croissance de cette espèce : $L_t = 70.8(1 - e^{-0.308[t+1.10]})$, où L_t est la longueur jusqu'à la nageoire pelvienne (PL) en centimètres à l'âge t. L'application de cette courbe de croissance à la longueur estimée à la maturité des mâles et des femelles (PL respective de 64 et 66-69 cm) donne des estimations d'âge à la maturité de 6-7 ans pour les mâles et de 8-11 ans pour les femelles. Ces estimations se situent du milieu à l'extrémité supérieure de l'intervalle d'âges à la maturité des raies dans le monde. Les résultats de cette étude sont préliminaires et doivent être maniés avec prudence. D'autres travaux sont nécessaires pour déterminer si la technique présentée ici de détermination de l'âge par les épines produit des estimations fiables et reproductibles.

Резюме

Для оценки возраста особей антарктического ската (Amblyraja georgiana) из моря Росса использовались рентгенограммы срединного среза тела позвонка, а также рентгенограммы и исследования в проходящем белом свете хвостовых шипов. Просмотр хвостовых шипов в проходящем белом свете дал наиболее четкие кольца роста, но точность считывания была низкой, что привело к недостоверным оценкам возраста. Кроме того, не было подтверждено ежегодное образование колец в шипе. Максимальный возраст по оценке составил 14 лет, что следует рассматривать как осторожную оценку продолжительности жизни, поскольку у крупных особей рост шипов, возможно, прекращается. Заметной разницы в росте между полами не было, поэтому кривая роста Берталанфи для обоих полов дает наилучшее имеющееся описание роста этого вида: $L_t = 70.8 (1 - e^{-0.308[t+1.10]})$, где L_t – длина до брюшных плавников (PL) в см в возрасте t лет. Применение этой кривой роста к оценочной длине по достижении половозрелости для самцов и самок (соответственно 64 и 66-69 см PL) дало оценочный возраст достижения половозрелости 6-7 лет для самцов и 8-11 лет для самок. Эти оценки лежат примерно в середине-верхнем конце диапазона возрастов по достижении половозрелости для скатов во всем мире. Результаты этого исследования являются предварительными и к ним следует относиться с осторожностью. Следует провести дальнейшую работу, чтобы определить, дает ли представленный здесь метод определения возраста по шипам воспроизводимые и достоверные оценки возраста.

Resumen

Se estimó la edad de la raya estrellada antártica (Amblyraja georgiana) que habita en el Mar de Ross mediante radiografías de cortes transversales del centro de las vértebras y de aguijones caudales, y el examen con luz blanca transmitida de estos últimos. El examen de los aguijones caudales con luz blanca transmitida demostró ser el más efectivo para visualizar claramente las bandas de crecimiento, pero la precisión de la lectura fue baja y las estimaciones de la edad fueron dudosas. Además, no se ha convalidado la deposición anual de las bandas en los aguijones. La máxima edad estimada fue 14 años, pero esta estimación de la longevidad debe ser considerada como una subestimación debido a la posibilidad de que cese el crecimiento de los aguijones en los ejemplares de gran tamaño. No se observó una diferencia obvia en el crecimiento de machos y hembras, de manera que la curva de von Bertalanffy para ambos sexos proporciona la mejor representación disponible del crecimiento de las especies: $L_t = 70.8 (1 - e^{-0.308[t+1.10]})$, donde L_t es la longitud de la pelvis (PL) en centímetros a la edad t, en años. La aplicación de esta curva de crecimiento a la talla estimada de madurez de machos y hembras (64 y 66-69 cm PL respectivamente) da como resultado estimaciones de la edad de madurez de 6-7 años para los machos y 8-11 años para las hembras. Estas estimaciones concuerdan con la porción de edades media y máxima del intervalo de edad de madurez calculado para las rayas en otras partes del mundo. Los resultados de este estudio son preliminares y deben utilizarse con prudencia. Se requieren más estudios para evaluar si la técnica de determinación de la edad a partir de aguijones que aquí se presenta rinde estimaciones fiables y reproducibles de la edad.

Keywords: *Amblyraja georgiana*, growth, caudal thorns, sexual maturity, longevity, Ross Sea, CCAMLR

Introduction

Skates are a major by-catch of the toothfish fishery operating in the Ross Sea, although many are now being tagged and released alive. Nevertheless there is concern about the possible impact of the fishery on skate populations. In the North Atlantic Ocean, large, long-lived skate species have proven very vulnerable to fishing pressure, with several becoming regionally extinct (Brander, 1981; Casey and Myers, 1998; Dulvy et al., 2000; Dulvy and Reynolds, 2002). Smaller species have proven more (Walker and Heessen, 1996). The key biological parameter that affects skate vulnerability appears to be age-at-maturity, which is positively correlated with maximum body size (Dulvy and Reynolds, 2002).

Most attempts to age skates have counted growth bands in vertebral centra (e.g. Daiber, 1960; Holden and Vince, 1973; Ryland and Ajayi, 1984; Natanson, 1993; Walmsley-Hart et al., 1999; Francis et al., 2001). More recently, growth bands have

resilient, with some expanding their populations

The main skate species caught in the Ross Sea is the Antarctic skate (Amblyraja georgiana). Previously, the authors investigated the feasibility of ageing A. georgiana by applying a variety of techniques to vertebrae and caudal thorns (Francis and Ó Maolagáin, 2001). The best results were obtained from x-rays of thorns and vertebral halfcentra, but vertebrae produced lower band counts than thorns, possibly because of poor calcification and resolution problems near the margin of the vertebrae. Larger samples of these structures are required to confirm this, and to develop sexspecific growth curves. This study applies these ageing techniques to a larger sample of A. georgiana, fits growth curves to the length-at-age data and estimates age-at-maturity and longevity.

Materials and methods

Whole specimens, or excised vertebral columns with tails and caudal thorns intact, were available from 221 *A. georgiana* collected from the Ross Sea by observers on board commercial longliners during the 2000/01 to 2002/03 seasons. Specimens were labelled by observers with pelvic length (distance between the tip of the snout and the rear edge of the pelvic fins; PL), sex and station. Linear regressions relating PL to total length and disk width were provided by Francis and Smith (2002).

In the laboratory, vertebrae from above the posterior body cavity were removed, thawed and trimmed of muscle and connective tissue. Individual centra were then separated and immersed in 42 g.l⁻¹ sodium hypochlorite until all of the muscle and connective tissue had been removed (about one hour). Excessive soaking tended to dissolve the centra and made the articulating surfaces brittle and crumbly. After overnight soaking in freshwater, vertebrae were air-dried for one week. Vertebrae were bisected in the transverse plane and x-rays were taken of half-centra with a Phillips 45 kV X-ray machine at 5 mA.

Caudal thorns were usually removed from the base of the tail near the pelvic fins or from the pelvic region itself. However, thorns from this region were sometimes eroded, or otherwise damaged, and so samples were occasionally taken from elsewhere on the tail. Thorns were x-rayed dorso-ventrally (i.e. from vertically above for a thorn in its natural orientation). A subsample of 150 thorns was soaked in a solution of ca. 3% trypsin at 35–37°C, and the adhering skin and cartilaginous plug inside each thorn were removed with forceps.

The narrow opaque growth bands were counted by one reader from thorn x-rays (twice) and from thorns viewed with transmitted white light (twice). All readings were made without knowledge of the size, sex or date of capture of the skate, although thorn or centrum size provided some indication of skate size. Band readability was scored subjectively on a scale from 1 (excellent) to 5 (unreadable).

It was sometimes difficult to decide where to begin counting thorn bands. The apex of each thorn (which consists of the earliest deposited material) sometimes had what appeared to be split bands. Furthermore, caudal thorns are probably present in embryonic skates inside the egg case, so the region of earliest thorn growth should not be included in the band count. The smallest individual aged from thorns was 31 cm PL. Thorns from a 17.8¹ cm PL neonate *A. georgiana* found in an Antarctic toothfish (*Dissostichus mawsoni*) stomach and preserved at the Museum of New Zealand (NMNZ P37792) were also examined.

Spatial variation in caudal and body thorn size was determined for a whole 63.3 cm PL female *A. georgiana*. Thorns were removed from various locations on the tail and mid-body, cleaned as described above, and the length (greatest dimension) of the base of each thorn was measured to the nearest 0.1 mm under a dissecting microscope.

Band counts were assessed for within-reader ageing bias using age-bias plots, as recommended by Campana et al. (1995). The index of average percentage error (IAPE) and mean coefficient of variation (CV) for each skate were calculated to assess precision among sets of age determinations (Campana et al., 1995). Campana (2001) reported an empirical regression relationship linking the two quantities: CV = -0.15 + 1.41 IAPE. In fact, the two quantities are linked analytically by the constant $\sqrt{2}$, so CV = 1.4142 IAPE.

Von Bertalanffy growth curves were fitted to the data using non-linear least squares regression:

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

¹ Corrected for shrinkage in preservative (actual measurement of preserved specimen was 17.0 cm PL).



Figure 1: Relationship between thorn length and pelvic length, with fitted linear regressions, for a subsample of the *Amblyraja georgiana* aged in this study. Also shown for comparison are the range of thorn lengths found in a 63.3 cm PL female and a neonate 17.8 cm PL skate.

where L_t is the expected length at age t years, L_{∞} is the asymptotic maximum length, K is the von Bertalanffy growth constant, and t_0 is the theoretical age at zero length.

Results

Vertebral half-centra

X-rays of many vertebral half-centra contained growth bands, but they were indistinct, indicating poor contrast in calcification. The number of bands visible in centra was usually fewer than those found in caudal thorns from the same specimens. This confirms the preliminary observations from the authors' previous study (Francis and Ó Maolagáin, 2001), and suggests that vertebrae are not suitable for ageing *A. georgiana*.

Caudal thorns

Caudal thorns were largest in the pelvic region, i.e. the rear of the body disk and the anterior part of the tail. Thorn length increased with skate length and there was no difference in this relationship between males and females (Figure 1). Comparison of thorn size-at-length with the known range of thorn sizes in a 63.3 cm PL female suggested that occasionally thorns aged in this study were among the smallest or largest present on a skate,

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but usually they fell in the middle of the size range (Figure 1); this is consistent with the strategy of selecting thorns from the anterior tail region where possible.

Caudal thorns sampled from a 17.8 cm PL skate taken from a toothfish stomach were smaller than would have been expected based on data from larger skates (Figure 1). The two largest thorns taken from the pelvic region had base lengths of 4.3 and 4.6 mm compared with an expected length of about 8 mm. Possible explanations for this discrepancy include thorn shrinkage after preservation, and allometric change in thorn size between neonate and juvenile stages. The latter situation applies in another deepwater skate, *Bathyraja brachyurops* (Gallagher et al., 2005), so allometric change may offer the best explanation.

Comparison of 50 thorns x-rayed before and after trypsin cleaning showed that although the presence of a skirt of skin around the base of the thorn, and the cartilage plug inside the thorn, reduced the clarity of the bands, they had no effect on the band counts. X-rays of caudal thorns all showed some banding structure, but they varied markedly in band clarity (one of the clearer thorns is shown in Figure 2a). Some bands were clear and unambiguous, while others were diffuse and indistinct; frequently it was difficult to determine



Figure 2: Four images of a caudal thorn from SRR 197, a 73 cm female *Amblyraja georgiana*. Star shapes in x-ray are skin denticles. Thorn base length = 13.2 mm; final band count = 11; readability = 1. (a) X-ray, vertical view; (b) reflected light, oblique view; (c) transmitted light, vertical view; (d) transmitted light, oblique view.

whether a thorn zone comprised a small number of broad bands or a larger number of narrow bands (Figures 2b, d).

Thorn bands viewed under transmitted white light (Figure 2c) were usually more distinct, though still difficult to count. Changing the orientation of the thorn relative to the light angle, and in some cases the addition of dim reflected light, helped visualise and count the bands.

Band counts

Band counts made from thorn x-rays were highly variable between readings and, when plotted against skate length, there were numerous outliers. More importantly, comparison of counts from x-rays with counts from thorns examined under transmitted white light revealed that one or more bands near the apex of the thorn were being overlooked in the x-rays because they were obscured by other bands in vertical view. It was concluded that the x-ray band counts were unreliable, and consequently they are not presented in this report.

Instead, band counts from thorns viewed with white light were used to develop a final set of age estimates. The ability to rotate thorns in three dimensions relative to the incident white light angle allowed much more flexibility and greatly enhanced band interpretation. Nevertheless, band counts were still difficult. Of 151 aged thorns, 14 (9%) were judged unreadable. The readability of most thorns (80%) was scored as 3 or 4; few thorns (11%) were scored as having a readability of 1 or 2. The final sample size of aged thorns was 137. Repeatability of counts was poor: the mean CV of two readings was 17.4% and the IAPE was 12.3%. CVs in elasmobranch ageing studies are rarely less than 10% (Campana, 2001), but the CV was considerably higher than this, and precision was therefore low.

An age-bias plot indicated that the second reading produced slightly lower band counts than the first reading (Figure 3). This is likely to have resulted from the reader having gained experience from the previous count. The second white light count from thorns was therefore adopted as the most realistic band count. Nothing is known about



Figure 3: Within-reader comparison of thorn band counts for *Amblyraja georgiana*. Numbers represent number of skates, and dots with error bars are the mean count of reading 2 (\pm 2 standard errors) relative to reading 1 (offset by +0.1 bands for clarity). The diagonal line indicates the expected relationship. *N* = 119.

the time of hatching or the time of deposition of growth bands in *A. georgiana*, so no adjustments were made for these factors. Therefore the second band count was used as the best estimate of skate age.

Plots of PL versus estimated age revealed 10 outliers (circled in Figures 4a, b). The thorn bands for these fish were recounted, and in all cases the result was similar (\pm 1 band) to the original count. Furthermore, most of the outliers were judged to be easy to read, with five skates having readability scores of 1–2, four with scores of 3, and one with a score of 4. There are many possible explanations for these outliers, including data errors (e.g. length recording error, specimen mix-up in the laboratory), counting errors (split bands being counted separately instead of being combined, or bands being overlooked), and true growth variability. The causes could not be determined and any errors could not be corrected.

The thorns from a 17.8 cm neonate skate were difficult to clean of adhering flesh (the museum fixation process meant that trypsin cleaning was ineffective), and the largest thorns were poorly calcified and fragile. Dark material was apparent near the skirt of the thorn, but it was not clear whether this constituted the band that was counted

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as the first band in thorns from larger skates, or whether it was a partially formed band or a lighting artifact. Thorn base length at the location of the first growth band was measured in 10 larger skates, and it averaged 3.7 mm (range 3.3–4.2 mm). Therefore, the base length of the largest neonate thorn (4.6 mm) was larger than the average base length at time of deposition of the first band, suggesting that the neonate had recently formed its first band.

Most skates in our sample had estimated ages of 2–9 years. The maximum age estimates were 12 years for males and 14 years for females (Figure 4).

Growth curves

Von Bertalanffy growth curves were fitted to the data, both with and without the outliers (Figure 4). The outliers made little difference to the fitted curves for males and both sexes combined. For females, the curve without the outliers was implausible, intersecting the x-axis at about one year. Thus no advantage was seen in deleting the outliers. Table 1 provides von Bertalanffy parameter estimates for the datasets including outliers.

Sex	Sample size	$L_{\infty} \pm SE$ (cm)	$K \pm SE$ (year ⁻¹)	$t_0 \pm SE$ (years)
Females	77	69.2 ± 3.1	0.402 ± 0.169	-0.73 ± 1.13
Males	58	79.9 ± 14.5	0.163 ± 0.106	-2.41 ± 1.85
Both sexes	137	70.8 ± 3.2	0.308 ± 0.089	-1.10 ± 0.78

Table 1: Von Bertalanffy growth curve parameters by sex. SE – standard error.



Figure 4: Von Bertalanffy growth curves for (a) females, (b) males, and (c) both sexes combined, fitted to age estimates obtained from thorn band counts. Growth curves are also shown for datasets from which 10 outliers (circled) were removed. *N* = sample size.



Figure 5: Von Bertalanffy growth curves by sex, and for both sexes combined. Curves were fitted to datasets that included outliers identified in Figure 4.

The growth curves for the two sexes were similar (Figure 5). Because of the high uncertainty in the individual age estimates, and the broad scatter of data points about the fitted sex-specific growth curves, a formal significance test of the difference between the two sexes is not warranted. However, the data do not provide any indication that growth rates vary by sex. The von Bertalanffy growth curve for the two sexes combined therefore provides the best available representation of growth in *A. georgiana*.

The combined-sexes growth curve intersects the y-axis at about 20 cm PL (Figure 5). There is no information on the length of A. georgiana when they hatch from their egg cases. Several small specimens of A. georgiana are held in the Museum of New Zealand collection (NMNZ P38580, P37774, P38588): they had been removed from toothfish stomachs and they measured 11.5, 12.3 and 13.5 cm PL respectively after correction for preservation shrinkage. The smallest of these specimens had a 4 mm long umbilical scar, indicating that its yolk sac had recently been absorbed; the two larger specimens had no umbilical scars. These data suggest that young skates hatch from their egg cases at 10-12 cm PL. The y-axis intersection point of the growth curve therefore appears too high, possibly because the age estimates were not corrected for the time elapsed between hatching and first band deposition, or between the timing of the last band deposition and capture. An increase of 0.5 years for all age estimates would move the growth curve sufficiently to the right for it to intersect the y-axis at about 10 cm.

Discussion

Estimating the age of A. georgiana proved difficult. Caudal thorns viewed obliquely using transmitted white light provided the clearest banding patterns, and they were used to estimate skate ages. However, the reading precision of thorns was low, and the high variability in the length-atage data may reflect the high uncertainty in ageing individual skates. Age estimates in this study are unvalidated, and it is simply assumed that the thorn bands are formed annually. Gallagher and Nolan (1999) presented data (from marginal state analysis and oxytetracycline injection) consistent with annual deposition of thorn bands in several species of Bathyraja from the Falkland/Malvinas Islands, but their results did not convincingly validate thorn ageing. Proper validation is required before the results of this study can be considered a true description of growth patterns in A. georgiana. In particular, the possibility that thorn growth ceases in large individuals must be investigated before confident statements can be made about longevity; if band deposition ceases at the thorn margin of large skates, or if bands become too narrow to be resolved, then the ages of large skates may be underestimated. The fact that thorn size

shows no evidence of reaching an asymptote in the largest skates (Figure 1) suggests that band compression near the thorn margin may not be a major issue, although poor resolution of marginal bands has been reported in the thorns of another deepwater skate (Gallagher and Nolan, 1999). The maximum estimated age of 14 years found in this study should be regarded as a conservative estimate of longevity in the species.

If the estimated ages and growth curves are valid, *A. georgiana* grows moderately fast compared with other skates. Using the von Bertalanffy growth curve for both sexes combined (Table 1), this species reaches PLs of 44 and 51 cm by ages 2+ and 3+ respectively. In comparison, New Zealand's rough skate (*Dipturus nasutus*) reaches 37 and 45 cm, and the smooth skate (*D. innominatus*) reaches 38 and 48 cm, by the same ages (Francis et al., 2001).

The estimated lengths at maturity of *A. georgiana* for males and females are 64 and 66–69 cm PL respectively (Francis, 2003). Using the 'combined sexes' growth curve, the estimated ages at maturity are 6–7 years for males and 8–11 years for females. These estimates are near the middle to upper end of the range of ages at maturity for skates worldwide. For example, females of New Zealand's rough and smooth skates mature at about 6 and 13 years respectively (Francis et al., 2001). There appear to be no published estimates of growth rates or age-at-maturity for Antarctic or Arctic skates (Cailliet and Goldman, 2004), although studies are currently under way on skates from the Gulf of Alaska and the Falkland/Malvinas Islands.

A reviewer of this paper questioned whether skates living in cold Antarctic waters could reach such a large size in just 2-3 years. Previous literature on the growth of Antarctic and sub-Antarctic species suggests that fishes from this region exhibit a wide range of growth rates, comparable with those found elsewhere. Patagonian and Antarctic toothfish (Dissostichus eleginoides and D. mawsoni respectively) reach about 30-35 cm total length at age 2+ (Horn, 2002), compared with A. georgiana which grows to about 44 cm PL at the same age (this study). D. mawsoni occupies the same habitat and environment as A. georgiana. However the ageing of *D. mawsoni* has not been validated, although the ageing of *D. eleginoides* has (Horn, 2002). Kock and Everson (1998) reviewed the age and growth of Antarctic notothenioid fishes and reported that their growth performance was similar to that of fishes from the North Sea. It seems that food availability and reproduction may limit the growth of Antarctic fishes more than environmental conditions such as depth and temperature (Kock and Everson, 1998).

Nevertheless, caution is required in the use of age and growth estimates from this study, until further work has been carried out. That work should include the use of a second reader to estimate between-reader variability; examination of thorns from different parts of the body to confirm that age estimates are independent of location; and validation of the thorn ageing technique. Thorn sectioning (Gallagher et al., 2005) may clarify the bands and lead to greater counting precision. Obtaining samples of small skates (PL less than 30 cm) would considerably aid the interpretation of early band formation near the apex of thorns.

Conclusions

Caudal thorns viewed with transmitted white light had growth bands that were counted to produce age estimates. However, reading precision was low, producing uncertain age estimates, and the method has not been validated. Thus caution is required in using these preliminary results. The maximum estimated age was 14 years, but this is a conservative estimate of longevity. There was no obvious difference in growth between the sexes, so the von Bertalanffy curve for both sexes combined provides the best description of growth: $L_t = 70.8 \left(1 - e^{-0.308[t+1.10]}\right)$, where L_t is the PL in centimetres at age *t* years. Estimated ages at sexual maturity were 6–7 years for males and 8–11 years for females.

The results of this study are preliminary and should be used with caution. Further work is needed to determine whether the thorn ageing technique presented here produces reproducible and reliable age estimates.

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References

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

- Cailliet, G.M. and K.J. Goldman. 2004. Age determination and validation in chondrichthyan fishes. In: Carrier, J.C., J.A. Musick and M.R. Heithaus (Eds). *The Biology of Sharks and their Relatives*. CRC Press, Boca Raton, Florida: 399– 447.
- 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.
- Casey, J.M. and R.A. Myers. 1998. Near extinction of a large, widely distributed fish. *Science*, 281: 690–692.
- Daiber, F.C. 1960. A technique for age determination in the skate, *Raja eglanteria*. *Copeia*, 1960 (3): 258–260.
- Dulvy, N.K. and J.D. Reynolds. 2002. Predicting extinction vulnerability in skates. *Conserv. Biol.*, 16: 440–450.
- Dulvy, 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. *Conserv. Biol.*, 14: 283–293.
- Francis, M.P. 2003. Length-at-maturity of the Antarctic skates *Amblyraja georgiana* and *Bathyraja eatonii* in the Ross Sea. Document *WG-FSA*-03/42. CCAMLR, Hobart, Australia.
- Francis, M.P. and C. Ó Maolagáin. 2001. Age and growth of the Antarctic skates, *Bathyraja eatonii* and *Amblyraja georgiana*. Document *WG-FSA*-01/52. CCAMLR, Hobart, Australia.
- Francis, M.P. and N.W.McL. Smith. 2002. Morphometrics, maturity, and movement of the Antarctic skates *Amblyraja georgiana* and *Bathyraja eatonii* in the Ross Sea. Document *WG-FSA-02/42*. CCAMLR, Hobart, Australia.

- Francis, M.P., C. Ó Maolagáin and D. Stevens. 2001. Age, growth, and sexual maturity of two New Zealand endemic skates, *Dipturus nasutus* and *D. innominatus. N.Z. J. Mar. Freshwater Res.*, 35: 831–842.
- Gallagher, M. and C.P. Nolan. 1999. A novel method for the estimation of age and growth in rajids using caudal thorns. *Can. J. Fish. Aquat. Sci.*, 56 (9): 1590–1599.
- Gallagher, M.J., C.P. Nolan and F. Jeal. 2005. The structure and growth processes of caudal thorns. *J. Northwest Atl. Fish. Sci.*, 35.
- Holden, M.J. and M.R. Vince. 1973. Age validation studies on the centra of *Raja clavata* using tetracycline. *J. Cons. Perm. Int. Explor. Mer.*, 35: 13–17.
- Horn, P.L. 2002. Age and growth of Patagonian toothfish (*Dissostichus eleginoides*) and Antarctic toothfish (*D. mawsoni*) in waters from the New Zealand sub-Antarctic to the Ross Sea, Antarctica. *Fish. Res.*, 56 (3): 275–287.
- Kock, K.-H. and I. Everson. 1998. Age, growth and maximum size of Antarctic notothenioid fish – revisited. In: di Prisco, G., E. Pisano and A. Clarke (Eds). *Fishes of Antarctica: a Biological Overview*. Springer-Verlag, Milan: 29–40.
- Natanson, L.J. 1993. Effect of temperature on band deposition in the little skate, *Raja erinacea*. *Copeia*, 1993 (1): 199–206.
- Ryland, J.S. and T.O. Ajayi. 1984. Growth and population dynamics of three Raja species (Batoidei) in Camarthen Bay, British Isles. *J. Cons. Int. Explor. Mer*, 41: 111–120.
- Walker, P.A. and H.J.L. Heessen. 1996. Long-term changes in ray populations in the North Sea. *ICES J. Mar. Sci.*, 53 (6): 1085–1093.
- 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. *Sth Afr. J. Mar. Sci.*, 21: 165–179.

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