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ORIGINAL PAPER

The potential use of caudal thorns as a non-invasive ageing structure in the thorny skate (*Amblyraja radiata* Donovan, 1808)

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Abstract The thorny skate, *Amblyraja radiata*, is the most widely distributed and abundant of all skate species worldwide, found on both sides of the north Atlantic Ocean. Large inter-regional size differences exist for this species and the few age and growth studies undertaken have revealed marked differences in life history traits for geographically distinct stocks. To facilitate the progression of further age and growth studies for this commercially important species, the effectiveness of caudal thorns as a rapid ageing tool was assessed. Twenty-eight male and 24 female thorny skates were collected off Greenland, covering the full size range of the species. Replicate age readings of crystal violet stained vertebral sagittal sections and whole silver nitrate stained caudal thorns revealed mean intra-reader age reading precision was higher for caudal thorns (Covariance (CV): reader 1 = 9.07, reader 2 = 9.73) than vertebrae (CV: reader 1 = 14.91, reader 2 = 14.27). Age bias plots revealed minimal inter-structure bias, apart from a higher average thorn age reading of 0.76 years from age classes 5–11 years for reader 1. Minor inter-reader bias was evident for vertebrae only; averaging 0.90 years higher for reader 1 from age classes 11 to 15 years. Preliminary evidence suggests caudal thorns could prove an effective non-invasive ageing tool for thorny skates.

Keywords Skate · Age · Caudal thorns · Vertebrae · Bias

Introduction

Amblyraja radiata (Donovan, 1808), commonly known as the thorny skate or starry ray, has an almost ubiquitous boreal distribution, spanning the northern Atlantic Ocean (Bigelow and Schroeder 1954). In the eastern North Atlantic Ocean, it is distributed from east Greenland, Iceland, the Barents Sea, Baltic Sea and as far south as the mid-North Sea and southern English Channel (Stehmann and Burkel 1984). In the western North Atlantic Ocean, it can be found from off the west Greenland coast, Hudson Bay, Canada to South Carolina (Bigelow and Schroeder 1954; Compagno et al. 1989). This species accounts for over 80% of the estimated biomass of all skates in the North Sea, east coast of Greenland (Rätz 1992, 1999), Barents Sea (Dolgov 2004), and Grand Banks (Kulka and Mowbray 1999).

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Despite widespread abundance, marked contrasts in levels of commercial interest are evident for the thorny skate, particularly between the Northwest and Northeast Atlantic. In the North Sea (NE), it is discarded due to its small size (maximum size 54 cm total length [TL]) (Walker 1999). However, in the Grand Banks directed skate fishery (NW), the large growing thorny skates (maximum size 108 cm [TL]) is the most important component of directed and by-catch skate fisheries landing approximately 12,000 t annually (Kulka and Miri 2003).

Inter-regional heterogeneity in life history traits for thorny skates also appear to exist possibly due to a combination of both differing environmental conditions (Templeman 1987; Del Río 2002) and compensatory responses to intense exploitation (Walker and Hislop 1998). Therefore, robust area-specific age and growth studies are a basic requisite to enable meaningful assessments and subsequent management strategies to be implemented (Anderson 1990; Frisk et al. 2001). Despite being the most studied skate species, only a relatively small number of age and growth studies have been undertaken (Vinther 1989; Walker 1999; Sulikowski et al. 2005). In part, the paucity of age and growth studies can be attributed to the use of vertebrae for age assessment of skates, which is labour intensive and necessitates dissection for removal, cleaning, separation, and often the subsequent application of various enhancement techniques to improve band resolution (Cailliet 1990, Cailliet and Goldman 2004). Additionally, interpretation problems can often arise with reduced band resolution both at the focus and at the periphery of these structures, particularly for larger specimens (Cailliet et al. 1990; Francis and O'Maolagain 2005). These problems have also been encountered in a northeast Atlantic Ocean population of thorny skates using vertebrae as the ageing structure, which has lead to, in part, uncertainties in their derived growth data (Walker 1999). Gallagher and Nolan (1999) presented an alternative ageing technique using caudal thorns, which proved both rapid and reliable. Close association between vertebral and thorn band estimates was evident for four commercial skate species from the Falkland Islands and derived growth rate data (Gallagher 2000) were substantiated in a subsequent study utilizing caudal thorns (Hendersen et al. 2004).

The thorny skate, as its name implies, has a spinulose covering, distributed both dorsally and ventrally that vary in abundance depending on size, sex and maturity status (Bigelow and Schroeder 1954; Stehmann and Burkel 1984; Templeman 1987). Of importance however, is a distinct row of approximately 10 median caudal thorns that are consistently present from pre-hatching through adulthood (Berestovskii 1994; Stehmann and Merrett 2001). If these caudal thorns prove effective as a non-invasive, rapid ageing tool it would undoubtedly enable the proliferation in necessary age and growth studies for this ubiquitous species. This study set out to ascertain the effectiveness of these structures in this regard for the thorny skates by comparing thorn and vertebral band data from multiple readers.

Materials and methods

Sample collection

In October 2004, 52 thorny skates were collected onboard the 'Walther Herwig III', a German research vessel undertaking an annual groundfish survey off Greenland. Samples collected using otter trawl gear to a maximum depth of 400 m were labelled, blast frozen onboard, and subsequently transported to Ireland for further analysis.

Sample processing

In the laboratory each skate was sexed, TL (mm) (straight line distance from the tip of the rostrum to the end of the tail) and disc width (mm) (straight line distance between the tips of the widest portion of the pectoral fins) were measured. A vertebral segment containing approximately 10 vertebrae was extracted from each specimen from the abdominal cavity region. An incision was made under the thorn base tissue of the anterior caudal thorns towards the tail region, which enabled the removal of 7–10 caudal thorns. Excess tissue was removed from both vertebrae and thorns by immersion in hot water (circa. 70–85°C) followed by a light scraping with a fine scalpel. Both sets of structures were air-dried and then immersed in a 5% solution of trypsin (hog pancreatin) at 35–40°C for 24 h to remove neural and haemal arches and connective tissues from vertebrae and remove remaining tissue from caudal thorns. Following this process, centra and thorns were washed for 30 min in running water and stored in 70% industrial methylated spirits. For each sample, a single vertebra and thorn was selected. Vertebral and caudal thorn processing followed the protocol of Gallagher and Nolan (1999). Sagittal vertebral sections were stained with crystal violet and whole caudal thorns were stained with silver nitrate.

Age reading

For age reading purposes, a growth increment or 'band' on vertebral sagittal sections was defined as a translucent unstained band appearing at relatively regular intervals along the corpus calcareum, and separated by an opaque band (Fig. 1). As the intermedialia was often over-stained or ground away, the majority of band counts were derived from counts of the heavily stained bands on the corpus calcareum. The birth or hatching mark (age zero) was defined as the first mark after the change in the angle of the corpus calcareum. All age readings were made from the focus towards the distal edge on a single axis exhibiting greatest resolution. Band counts were corroborated with readings made along the remaining three axes. For whole caudal thorns, bands were defined as concentric surface ridges separated by broader bands, distal to the base of the birth-mark ridge (Fig. 2). Caudal thorn band counts were made from the tip towards the distal margins. The location of the birthmark (Fig. 3) was defined by the examination of a recently hatched juvenile of 11.3 cm (TL). Three non-consecutive band counts were made independently by two readers for each vertebral section and caudal thorn without prior knowledge of the specimen's details.

A dissecting microscope (magnification 6-40×) was used to view both sets of structures. A fibre-optic source facilitated the illumination of vertebral sections with transmitted light, and whole thorns were viewed under both reflected and transmitted light. Each vertebral section was measured from focus to distal margin, and the base of each thorn was measured from anterior to

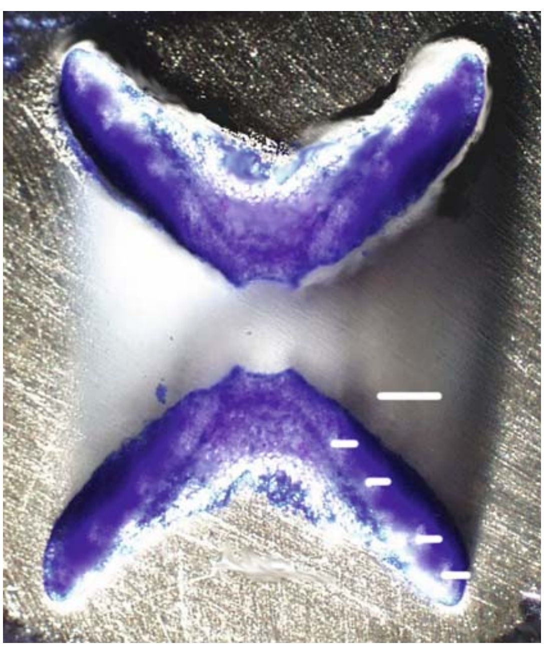

Fig. 1 Sagittal section of crystal violet stained vertebral centra from a thorny skate *A. radiata* measuring 356 mm TL estimated to be 4 years (scale bar = 0.8 mm)

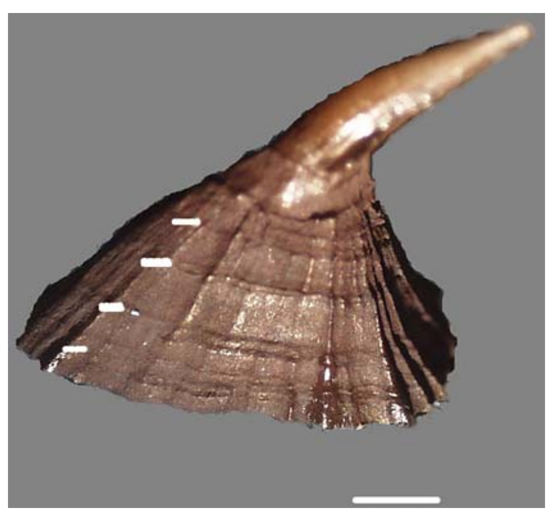

Fig. 2 A whole silver nitrate stained caudal thorn from a thorny skate *A. radiata* measuring 316 mm TL estimated to be 4 years (scale bar = 1.1 mm)

Fig. 3 A whole un-stained caudal thorn from a recently hatched thorny skate *A. radiata* measuring 113 mm TL (scale bar = 0.9 mm)

posterior using a graticule on the microscope, to relate structural to somatic growth.

Precision and bias

Coefficient-of-variation (CV) (Chang 1982) was used to assess precision, described as

$$\mathrm{CV} = 100x\frac{\sqrt{\sum_{i=1}^{R}\frac{(X_{ij}-X_j)^2}{R-1}}}{X_j}$$

where X_{ij} is the ith age determination of the jth fish, X_j the mean age estimate of the jth fish, and R is the number of times each fish is aged. Age bias plots were used to assess intra reader bias between structures and inter-reader bias within structures, as recommended by Campana et al. (1995). This form of graphical representation allows the plotting of one set of readings versus a second set of readings with reference to an equivalence line. Two forms of bias were assessed;

- intra-reader bias between structures: ager X structure 1 = ager X structure 2
- inter-structure bias assessment within readers: ager X = ager Y

The age readings of ager Y, or ager X structure 2 are presented as the mean and 95% confidence interval corresponding to each of the age categories reported by ager X or ager X structure 1 (Campana et al. 1995).

Results

Structure growth and band morphologies

A strong linear relationship was evident (r^2 = 0.93) for vertebral radius and TL (mm) (Fig. 4), whereas thorn length and TL was weaker and was best described by a logarithmic relationship (r^2 = 0.67) (Fig. 5).

Overall, band resolution on vertebral sections was reasonable. However variable stain uptake presented problems on occasion, necessitating de-staining and re-staining. In addition, locating the birth-mark near the focus and crowding of bands towards the periphery was evident for a small number of samples of vertebral sections. Although band resolution was generally very good on caudal thorns from juveniles (< 30 cm TL), thorn-wear near the tip in larger specimens (>45 cm TL) tended to occlude resolution in this region and in addition bands near the periphery were, on occasion, split or crowded.

Precision and bias

Mean CV estimates were similar for both readers, being consistently lower for thorn readings, at 9.07% and 9.73%, than vertebral readings at,

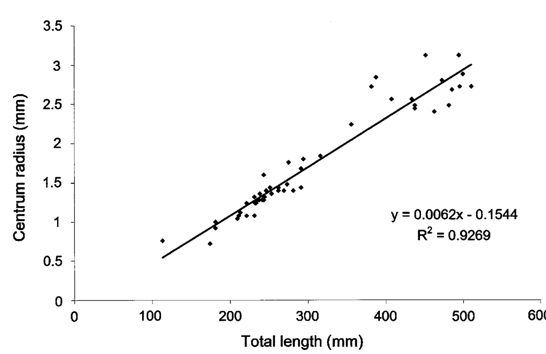

Fig. 4 The relationship of TL (mm) to centrum radius (mm) for combined sexes of thorny skate *A. radiata*. n = 52

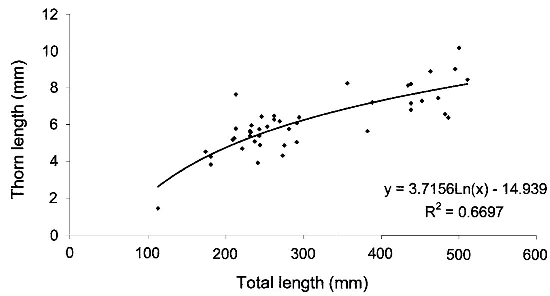

Fig. 5 The relationship of TL (mm) to thorn length (mm) for combined sexes of thorny skate *A. radiata*. $n = 52$

14.93% and 14.23%, for reader 1 and reader 2, respectively.

Age bias plots revealed no appreciable inter-structure bias (Figs. 6 and 7), apart from a higher average reading of 0.76 years for thorns compared to vertebrae for reader 1 between age classes 5–11 years (Fig. 6). Intra-reader bias for each structure was also minimal, with the largest bias evident for vertebral age readings, with reader 1 presenting 0.90 years higher ages than reader 2 between age classes 11–15 years (Fig. 7).

Discussion

Although relatively commonplace for commercial teleost species (Casselman 1983; Beamish and McFarlane 1987), inter-structure comparative age reading studies for elasmobranchs are rare (Gallagher and Nolan 1999; Francis and O'Maolagain 2005; Smith et al. 2005), mainly because few elasmobranchs, apart from skates, possess secondary calcified structures that can be used for age assessment purposes. Even when well established for certain teleosts, inter-structure age reading agreements across an entire size range for a given species are seldom achieved, especially for the larger size classes (Beamish and McFarlane 1987). Results from this study suggest that caudal thorns prove effective as an ageing alternative for thorny skates or serve as a useful form of age verification for vertebral age determination, given the similarity of age readings from both novel and conventional structures. Precision estimates for thorns were relatively reasonable for both readers, considering that over 90% of elasmobranchs studies returned CV estimates in excess of 10% (Campana 2001). CV estimates for vertebral age readings were higher for both readers, revealing less precision than thorns and were in line with precision estimates from other elasmobranch studies utilising vertebrae (Cailliet et al. 1990; Campana 2001; Francis et al. 2001). Consistent bias was not prevalent apart from slightly higher inter-reader vertebral age estimates for reader 1. This may in part be explained by the fact that unlike reader 2, reader 1 had previous experience at elasmobranch vertebral age reading, and generally more experienced age readers tend to resolve more bands in ageing structures (Officer et al. 1996). It is however difficult to ascertain which structure or indeed which reader presents the most accurate age estimates without knowing the true age of structures examined (Cailliet and Goldman 2004).

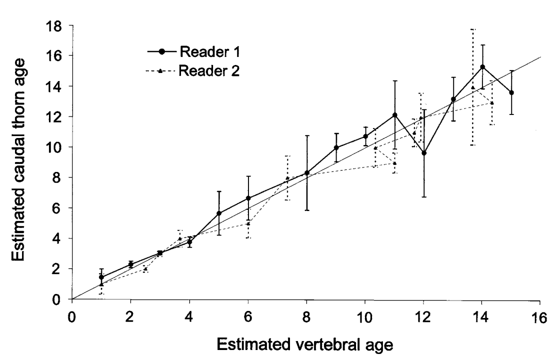

Fig. 6 Inter-structure age bias plot for the thorny skate *A. radiata*. Each error bar represents the 95% confidence interval for the mean caudal thorn age estimate, around that of a given vertebral age estimate by readers 1 and 2. The straight line represents the 1:1 equivalence line. $n = 52$

As with most elasmobranchs studied to date, the periodicity of band formation has not been comprehensively validated for the thorny skate (Sulikowski et al. 2005). However a comparison of tag-recaptures and vertebral age estimates in the North Sea (Walker 1999) and a study of marginal vertebral increments undertaken on samples collected in the Gulf of Maine (Sulikowski et al. 2005) support an annual band pair deposition cycle, as has been documented for other skate species (Holden and Vince 1973; Gallagher et al. 2005a). In addition, the oldest age

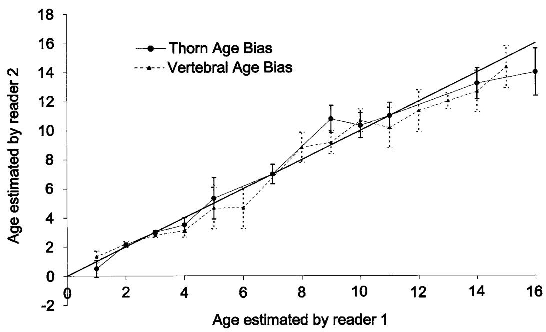

Fig. 7 Inter-reader caudal thorn and vertebral age bias plot for the thorny skate *A. radiata*. Each error bar represents the 95% confidence interval at the mean of reader 2's age estimate around that of a given age estimate by reader 1. The straight line represents the 1:1 equivalence line. n = 52

suggested by Sulikowski et al. (2005) for vertebral band counts of 16 years is comparable to 15 and 16 years for vertebral and caudal thorn band counts respectively in this study. Furthermore, Templeman's (1984) long-term tagging studies also revealed that the thorny skate has a longevity of at least 20 years.

Plotting of vertebral radius versus TL revealed a strong linear relationship (r^2 = 0.93), indicating that vertebral growth correlates well with somatic growth for the thorny skate. Gallagher et al. (2005b) demonstrated a strong logarithmic relationship between thorn height and TL for the white tipped skate *Bathyraja brachyurops*. However, thorn wear and proto-thorn damage was evident for several specimens in this study and precluded the effective use of this measurement. Thorn length versus TL was used instead, however the derived logarithmic relationship was relatively poor (r^2 = 0.67), largely due to the variability in intra specimen thorn size. It is probable that selection of a larger sample of specimens where thorn wear was not evident and measurement of thorn height would reveal allometric growth, as has previously been observed for caudal thorns (Gallagher et al. 2005b).

For elasmobranchs, there remains uncertainty about the causal factors of band formation processes and the link between environmental and physiological cues (Officer 1995; Cailliet and Goldman 2004). Natanson (1993) revealed that holding little skate, *R. erinacea*, under a constant temperature environment did not influence the rate of vertebral band formation, but did however influence band morphology. As initially postulated for dorsal fin spines (Holden and Meadows 1962), Gallagher et al. (2005b) suggested that surface defined ridges on caudal thorns are the external expressions of bases of successive cones that form with the cessation in somatic growth as a result of a marked annual cyclical reduction in seawater temperature. Although we collected samples within a narrow time period (October 2004), the majority of vertebral samples had either a fully formed opaque band or had initiated the formation of a translucent band, which concurs with the timing of vertebral band formation of other skate species in the north east Atlantic (Holden and Vince 1973; Gallagher et al. 2005a). In addition, for caudal thorns either a fully formed broad band or the initiation of a surface ridge was evident, which coincides with the initiation of the annual winter cycle of seawater temperature reduction (Rätz 1999), and also the movement of thorny skates into deeper colder water at this time of year in this area (>400 m) (Rätz 1999).

Not all skate species possess suitable caudal thorns for age assessment. The apparent absence of surface band patterns on caudal thorns from four temperate skate species from Irish coastal waters was attributed to a lack of a marked seasonal drop in seawater temperatures (Gallagher et al. 2005b). It has also been suggested that surface band patterns on caudal thorns were not evident on thorny skates collected off New England (Sulikowski personal communication). This was however a preliminary appraisal and it was acknowledged that further study was required to verify this (Sulikowski personal communication). It is clear that the cues for band formation warrant further investigation in this novel structure particularly if intra-specific regional differences exist. Of importance is the need for additional work on thorn growth processes through detailed analysis of the underlying band structures utilizing available technologies (e.g. histology, electron microscopy, laser ablation, electron microprobe, X-ray analysis) in conjunction with captive rearing trials.

The need for future research on thorn and band growth processes should not preclude their application as valid ageing tools for the thorny skate. Particularly since much remains unresolved regarding our understanding of vertebral growth band formation processes, the commonly used ageing tool for elasmobranchs (Cailliet and Goldman 2004). Caudal thorns offer a number of distinct advantages over conventional vertebral ageing including ease of removal and preparation for ageing (which results in minimal commercial loss). More importantly specimens do not need to be sacrificed, which is vital either in tag-recapture studies, where thorns can be removed at tagging and recapture for age validation, or where biological information is required for depleted stocks without further impacting on their status. This preliminary study has revealed that caudal thorns from thorny skates possess a surface band pattern that relates to vertebral band formation and thus can be used for age assessment purposes.

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References

Anderson ED (1990) Fishery models as applied to elasmobranch fisheries. In: Pratt HL, Gruber SH, Taniuchi T (eds) Elasmobranchs as living resources: advances in the biology, ecology, systematics and the status of the fishery. NOAA Technical Report NMFS 90, pp 473–484

Beamish RJ, McFarlane GA (1987) Current trends in age determination methodology. In: Summerfelt RC, Hall GE (eds) Age and growth in fish. Iowa State University Press, Ames, USA pp 15–42

Berestovskii EG (1994) Reproductive biology of skates of the family Rajidae in the seas of the far north. J Ichthyol 34:26–37

Bigelow HB, Schroeder WC (1954) Fishes of the western north Atlantic, part II. Sawfishes, guitarfishes, skates, rays, chimaeroids. Sears Foundation, Bingham Oceanographic Laboratory, New Haven, 588 pp

Cailliet GM (1990) Elasmobranch age determination and verification: an updated review. In: Pratt HL, Gruber SH, Taniuchi T (eds) Elasmobranchs as living resources: advances in the biology, ecology, systematics and the status of the fisheries. NOAA Technical Report NMFS 70, pp 157–165

Cailliet GM, Goldman KJ (2004) Age determination and validation in Chondrichthyan fishes. In: Carrier J, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press LLC, Boca Raton, Florida pp 339–447

Cailliet GM, Yudin KG, Tanaka S, Taniuchi T (1990) Growth characteristics of two populations of *Mustelus manazo* from Japan based upon cross-readings of vertebral bands. In: Pratt HL, Gruber SH, Taniuchi T (eds) Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. NOAA Technical Report NMFS 90, pp 167–176

Campana SE (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 SE, Annand MC, McMillan JI (1995) Graphical and statistical methods for determining the consistency of age determinations. Trans Am Fish Soc 124:131–138

Casselman JM (1983) Age and growth assessment of fish from their calcified tissue-techniques and tools. In: Prince ED, Pulos LM (eds) Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes and sharks. NOAA Technical Report NMFS 8, pp 157–166

Chang WYB (1982) A statistical method for evaluating the reproducibility of age determination. Can J Fish Aquat Sci 39:1208–1210

Compagno LJV, Ebert DA, Smale MJ (1989) Guide to sharks and rays of southern Africa. New Holland Publishers, London, 158 pp

Del Río JL (2002) Some aspects of the thorny skate, *Amblyraja radiata*, reproductive biology in NAFO Division 3N. NAFO SCR Document 02/118, serial no. N4739, 14pp

Dolgov AV (2004) Feeding and food consumption by the Barents sea skates. J Northw Atl Fish Sci 35: http://www.journal.nafo.int/35/34–dolgov.html

Francis MP, O'Maolagain C, Stevens D (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

Francis MP, O'Maolagain C (2005) Age and growth of the Antartic skate, *Amblyraja georgiana*, in the Ross Sea. CCAMLR Sci 12:183–194

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

Gallagher MJ, Nolan CP (1999) A novel method for the estimation of age and growth in rajids using caudal thorns. Can J Fish Aquat Sci 56:1590–1599

Gallagher MJ (2000) The fisheries biology of commercial ray species from two geographically distinct regions. Ph.D. Thesis, Department of Zoology, University of Dublin, Trinity College, Dublin 2, Ireland

Gallagher MJ, Nolan CP, Jeal F (2005a) Age, growth and maturity of the commercial ray species from the Irish Sea. J Northw Atl Fish Sci 35:47–66

Gallagher MJ, Nolan CP, Jeal F (2005b) Structure and growth processes of caudal thorns. J Northw Atl Fish Sci 35:125–129

Henderson AC, Arkhipkin AI, Chtcherbich JN (2004) Distribution, growth and reproduction of the white-spotted skate *Bathyraja albomaculata* (Norman, 1937) around the Falkland Islands. J Northw Atl Fish Sci 35: http://www.journal.nafo.int/35/1-henderson.html

Holden MJ, Meadows PS (1962) The structure of the spine of the spur dogfish (*Squalus acanthias*) and its use for age determination. J Mar Biol Assoc U K 42:179–197

Holden MJ, Vince MR (1973) Age validation studies on the centra of *Raja clavata* using tetracycline. Journal du Conseil International pour l'Exploration de la Mer 35:13–17

Kulka DW, Miri CM (2003) The status of thorny skate (*Amblyraja radiata* Donovan, 1808) in NAFO Divisions 3L, 3N, 3O and subdivisions 3Ps. Canadian Science Advisory Secretariat Research Document—2003/031

Kulka DW, Mowbray FK (1999) An overview of the grand banks skate fishery. In: Shotton R (ed) Case studies of the management of elasmobranch fisheries. FAO Fisheries Technical Paper, Rome pp 47–73

Natanson LJ (1993) Effect of temperature on band deposition in little skate. Copeia 1:199–206

Officer RA (1995) Vertebral mineralisation patterns in gummy and school sharks and their utility for age determination. Ph.D Thesis, University of Melbourne, Victoria, Australia

Officer RA, Gason A, Walker TI, Clement JG (1996) Sources of variation in counts of growth increments in vertebrae from gummy shark, *Mustelus antarcticus*, and school shark, *Galeorhinus galeus*: implications for age determination. Can J Fish Aquat Sci 53:1765–1777

Rätz HJ (1992) Decrease in the fish biomass of West Greenland (Subdivisions 1B-1F), continued. NAFO SCR 92/40, serial no. N2088

Rätz HJ (1999) Structures and changes of the demersal fish assemblage off Greenland, 1982–96. NAFO Sci Coun Studies 32:1–15

Smith WD, Perez CR, Ebert DA (2005) Growth of the California skate, *Raja inornata*: assessment of multiple aging structures and somatic growth models. In: Abstract. American Society of Ichthyologists and Herpetologists/American Elasmobranch Society/Annual Meeting. Tampa, FL

Stehmann M, Burkel DL (1984) Rajidae. In: Whitehead PJP, Bauchot ML, Hureau JC, Nielson J, Tortonese E (eds) Fishes of the north-eastern Atlantic and the Mediterranean, vol 1. UNESCO, Paris, pp 163–196

Stehmann MFW, Merrett NR (2001) First records of advanced embryos and egg capsules of Bathyraja skates from the deep north-eastern Atlantic. J Fish Biol 59:338–349

Sulikowski JA, Kneebone J, Elzey S, Jurek J, Danley PD, Howell WH, Tsang PCW (2005) Age and growth estimates of the thorny skate (*Amblyraja radiata*) in the western Gulf of Maine. Fish Bull 103:161–168

Templeman W (1984) Migrations of thorny skate, *R. radiata*, tagged in the Newfoundland area. J Northw Atl Fish Sci 5:55–63

Templeman W (1987) Length–weight relationships, morphometric characteristics and thorniness of thorny skate (*Raja radiata*) from the northwest Atlantic. J Northw Atl Fish Sci 7:89–98

Vinther M (1989) Some notes on the biology of the starry ray *Raja radiata*, in the North Sea. Working Document for ICES study group on elasmobranch fisheries, April 1989, 20p

Walker PA, Hislop JRG (1998) Sensitive skates or resilient rays? Spatial and temporal shifts in ray species composition in the central and north-western North Sea between 1930 and the present day. ICES J Mar Sci 55:392–402

Walker PA (1999) Fleeting images dynamics of north sea ray populations. Ph.D. Thesis, University of Amsterdam