Age and growth estimates for the starry smoothhound (*Mustelus asterias*) in the Northeast Atlantic Ocean

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Age, growth, and longevity were estimated for the starry smoothhound (*Mustelus asterias*), based on the interpretation of sectioned vertebrae of 106 males (35–104 cm stretch total length, STL) and 114 females (44–112 cm STL). Growth curves were fitted to length-at-age data using von Bertalanffy and Gompertz models. The three-parameter von Bertalanffy growth function (VBGF) provided the best statistical fit to the male data ($L_\infty = 103.7$ cm STL, $L_0 = 38.1$ cm STL, $k = 0.195$ year^{-1}). The Gompertz growth function provided the best statistical fit to the female data, although the estimated parameters were biologically unreasonable. Therefore, the three-parameter VBGF was also accepted for females ($L_\infty = 123.5$ cm STL, $L_0 = 34.9$ cm STL, $k = 0.146$ year^{-1}). Longevity was estimated to be 13 and 18.3 years for males and females, respectively. The length–weight relationship is also presented for 304 male and 424 female *M. asterias*. The von Bertalanffy model was fitted to the weight-at-age data. These estimates can form the basis of future work on the assessment and management of this species.

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Introduction

The vulnerability of elasmobranchs to overexploitation has been linked to their life history (Stevens *et al.*, 2000). Many are late maturing with low fecundity and slow population growth rates, rendering them more susceptible to fishing mortality than most teleost species (Stevens *et al.*, 2000). Growth rate is a critical component of the life history of all species (Musick, 1999), and detailed knowledge is required to provide sound scientific advice for the implementation of conservation and management strategies.

The von Bertalanffy growth function (VBGF) is the most widely used model describing vertebrate growth, but the use of multiple growth functions is important in characterizing the growth of a species effectively (Cailliet *et al.*, 2006). Models such as the Gompertz growth function (GGF) can provide better fits for some species or sexes (Neer and Thompson, 2005; Natanson *et al.*, 2006). Moreover, two-parameter variations of the models have been used with a fixed length-at-birth (L_0) in an attempt to provide more biologically reasonable growth estimates and to fill in sample gaps of the youngest age classes (Cailliet *et al.*, 2006; Romine *et al.*, 2006). However, this can cause a decrease in the theoretical asymptotic length (L_∞) and an increase in the mean-square error and the standard error of the estimate of the function (Cailliet *et al.*, 2006). A one-parameter version with both L_0 and L_∞ fixed at observed levels would preclude underestimating L_∞ by taking into account maximum observed lengths even if they are not part of the vertebrae sample set. Only one example of a one-parameter version could be found in the elasmobranch literature

(Natanson *et al.*, 2006) and, although it was not the accepted model in this instance, its utility is worth investigating further.

The starry smoothhound (*Mustelus asterias*) is a relatively small demersal shark that is found in inshore temperate waters of the Northeast Atlantic Ocean and Mediterranean Sea (Compagno, 1984). Despite long-standing commercial interest in it by several western European countries, little is known of its basic biology in the NE Atlantic, largely because of the confusion concerning its discrimination from the common smoothhound (*Mustelus mustelus*), whose range partially overlaps with *M. asterias*. The confusion is mainly attributable to the variation in appearance of the traditionally diagnostic white spots of *M. asterias*. However, the recent development of a molecular genetic-identification technique (Farrell *et al.*, 2009) allows for quick and reliable identification of the Northeast Atlantic *Mustelus* species and will permit detailed studies on the genus.

The aforementioned confusion has prevented the collation of species-specific landings and survey data, so information on stock status of the two species in the NE Atlantic use aggregated data under the generic heading *Mustelus* spp. (ICES, 2007). *Mustelus* spp. have been reported to be locally extinct or depleted in many parts of the Mediterranean Sea where they were previously considered abundant, including the Gulf of Lions, the upper Tyrrhenian Sea, and the Adriatic Sea (Aldebert, 1997; Jukic-Peladic *et al.*, 2001; Ferretti *et al.*, 2005). Italian landings of *Mustelus* spp. peaked in 1994 at 9999 t, then declined to ~462 t by the turn of the century (FAO, 2000). Similar decreases in landings and local extinctions have been reported in Portuguese

waters and in the southern Bay of Biscay (Quero, 1998; Correia and Smith, 2003). Despite this, survey data suggest that *Mustelus* spp. abundance has increased in recent years in the Bristol Channel, the Celtic Sea, and the North Sea and that it has remained stable in the Irish Sea (ICES, 2007). Although reported landings of *Mustelus* spp. in the NE Atlantic have concurrently been increasing steadily, available data consist primarily of French landings, which have climbed to some 2640 t year^{-1} (FAO, 2000). There are no management or conservation measures in place for the fishery.

No studies have been published that fully describe the age and growth of *M. asterias* in the NE Atlantic. Estimates for female *M. asterias* of a Brody growth coefficient (*k*) of 0.22–0.24 year^{-1} have been made based on data from the Mediterranean, including gestation period, length-at-birth, and maximum observed length (Quignard and Capapé, 1972; Francis, 1981). These data suggest that *M. asterias* is fast-growing and early-developing. However, such extrapolation can be misleading because the growth rates of different life stages vary (Cailliet *et al.*, 1986), and there is also a strong possibility that such estimates may have been confounded by historical misidentification (Farrell *et al.*, 2009). Further, preliminary age determination of three female *M. asterias* based on the observations of pairs of vertebral bands suggests that Francis (1981) may have overestimated *k* and that the age-at-length may be twice that predicted (Henderson *et al.*, 2003). This lack of certainty and paucity of basic biological information means that there is no basis for the development of management or conservation measures.

Several studies have demonstrated that the age of *Mustelus* spp. can be successfully determined by enumerating band pairs in the vertebral centra (Tanaka and Mizue, 1979; Yudin and Cailliet, 1990; Moulton *et al.*, 1992; Officer *et al.*, 1996; Yamaguchi *et al.*, 1996; Goosen and Smale, 1997; Francis and Ó Maolagáin, 2000; Conrath *et al.*, 2002). Using these studies as a guide, we here report age and growth estimates for the starry smoothhound, *M. asterias*, based on the interpretation of band pairs in sectioned vertebrae. These estimates lay the basis for improved strategies for assessment and management of the species.

Material and methods

Mustelus asterias were collected between October 2006 and February 2009 from the Irish Sea, the Bristol Channel, the Celtic Sea, and west of Ireland (Figure 1). No commercial fishery targets the species in Ireland, so collection was necessarily opportunistic, and specimens consisted of the discards of commercial trawlers, gillnetters, and fisheries research vessels. Sex was recorded, stretch total length (STL) was measured (to the centimetre below) in a straight line from the tip of the snout to the tip of the upper caudal lobe in a stretched position, and weight was determined in kilogrammes. In addition to the samples for age analyses, further length–weight data were recorded over the same period from "catch and release" *M. asterias* taken during fishery surveys and by recreational anglers and charter boats. Because of the potential for misidentification, all fish were identified genetically using the method of Farrell *et al.* (2009).

The relationship between weight and STL was calculated for males and females by fitting data to the power equation $W = aL^b$, where W is the weight (kg), L the STL (cm), a the intercept, and b the slope.

Preparation and interpretation of vertebrae

A section of ten vertebrae was excised from each fish from beneath the first dorsal fin so as to minimize variation in counts (Officer

et al., 1996), and stored at $-20°$C until processing. The section was then thawed and three vertebrae dissected out, carefully separated, and excess connective tissue, including the neural and haemal arches, removed by placing them in a 5% solution of sodium hypochlorite. Vertebrae were left in this solution for 5–30 min depending on their size, smaller vertebrae requiring only a short soak time, scrubbed to remove any remaining tissue, then rinsed in running water for 30–60 min. The vertebrae were then dried in air for 24–48 h, again depending on size, and sectioned sagittally through the focus with a low-speed Isomet Rotary Diamond saw (Buehler). The sections were 0.5 mm thick, fixed to glass microscope slides with mounting medium, then viewed unstained under a binocular dissecting microscope (Olympus SZX9) with transmitted light. Measurements were made at ×20 magnification with an ocular micrometer.

The radius of each sectioned vertebra was measured from the focus to the distal margin of the corpus calcareum (Figure 2). STL was plotted against vertebral radius (VR) to determine whether vertebral growth was proportional to somatic growth.

Before reading the vertebrae, the definition of band pairs and the interpretation of the vertebrae were agreed by all authors. The first and third authors carried out preliminary age readings, and because they shared the same interpretation of band formation, the first author conducted further age readings. To be considered an annulus, each band pair had to be visible in the corpus calcareum and to traverse the intermedialia (Casey *et al.*, 1985). The age was estimated by enumerating the band pairs between the angle change and the centrum edge (Figure 2).

All vertebrae were read blind three times by the first author. This technique may minimize bias introduced by multiple readers (Sminkey and Musick, 1995), but strict adherence to the criteria defined has to be observed. The clarity of band pairs was assessed and categorized as I, high clarity; II, medium clarity; III, low clarity. Category III vertebrae were not included in the age analyses, and category II were only included if at least two counts were equal. Verification of the periodicity of band deposition was attempted, but fish were not available for all months of the year owing to the opportunistic nature of the sampling. The centrum edge was assessed and categorized as either opaque, narrow translucent, or broad translucent, and only high and medium clarity (categories I and II) were included in the edge analyses.

Data analysis

Age-bias plots of the counts were generated to check for systematic bias (Campana *et al.*, 1995). The precision of the counts was measured by calculating the index of average percentage error (IAPE), the coefficient of variation (*CV*), and the percentage agreement (PA; Table 1; Beamish and Fournier, 1981; Chang, 1982).

Two growth models were fitted to the length-at-age data and one to the weight-at-age data. The first was the original VBGF, with size at birth L_0 (von Bertalanffy, 1938):

$$L(t) = L_\infty - (L_\infty - L_0)e^{-kt}, \qquad (1)$$

where $L(t)$ is the length as a function of time t, L_∞ the theoretical asymptotic length, L_0 the length at birth, and k a rate constant (year^{-1}). Three variations of the model were used: three-parameter calculation estimating L_∞, L_0, and k; two-parameter calculation estimating L_∞ and k and using an observed L_0 of 30 cm
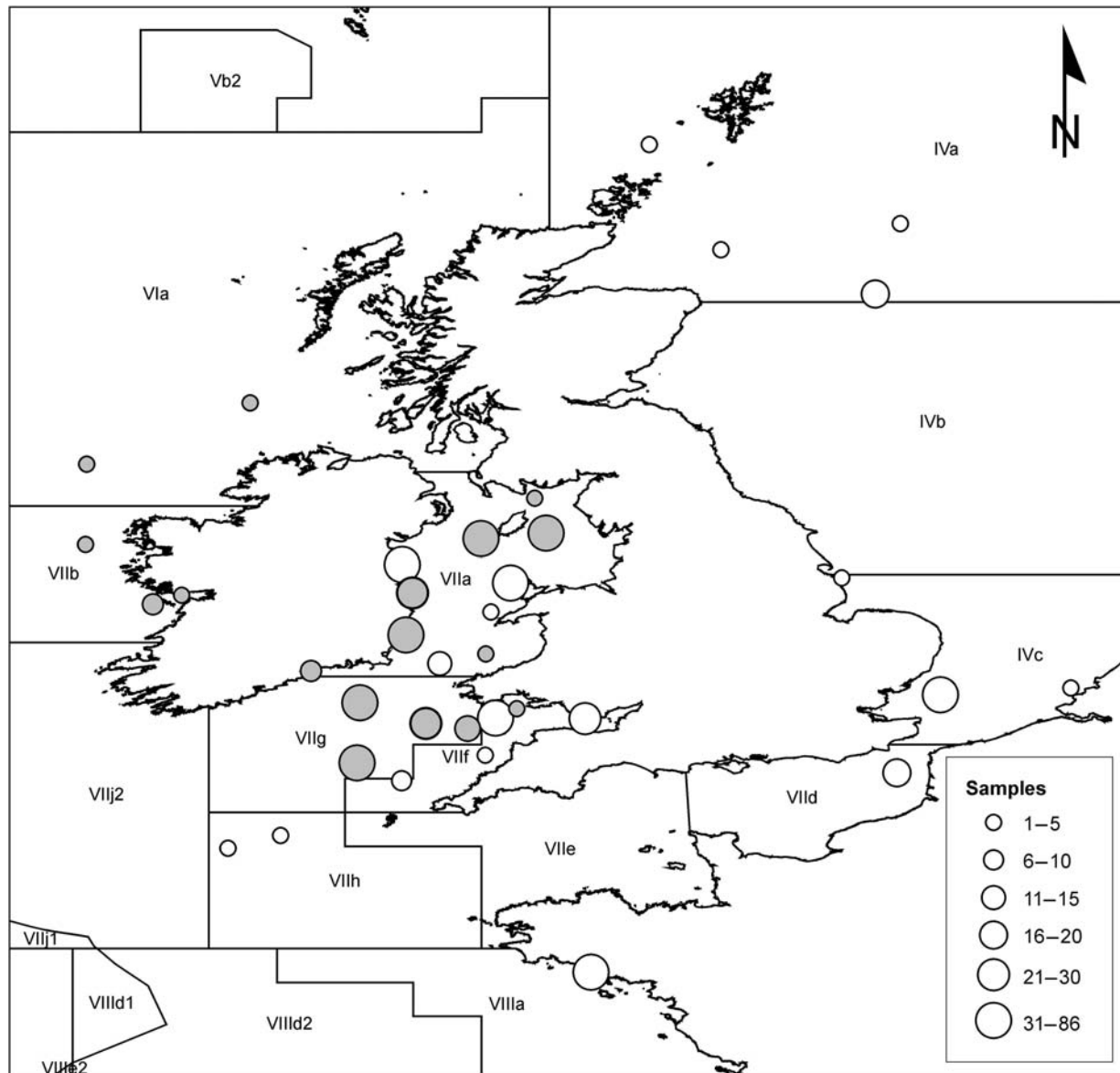
Figure 1. The distribution of *M. asterias* samples collected from the Northeast Atlantic Ocean during the study. All samples shown were included in the length–weight analyses, and the vertebrae of the samples highlighted grey were also sectioned for age analyses. Roman numerals indicate ICES assessment areas.

STL; one-parameter calculation estimating k with observed values of L_0 of 30 cm STL and L_∞ of 104 and 133 cm STL for males and females, respectively. The STL at birth was based on the average STL of the smallest free-swimming individual caught during the study (28 cm), and the largest embryo found *in utero* (32 cm; EDF, pers. obs.). The maximum STL values were based on reliably identified specimens from the NE Atlantic (EDF, pers. obs.; J. R. Ellis, pers. comm.).

The second model used was a modified version of the GGF (Romine *et al.*, 2006):

$$L(t) = L_0(e^{G(1-e(kt))}),\qquad(2)$$

where $G = \ln(L_\infty/L_0)$. Three variations of this model were also used with either unconstrained parameters or the same parameters set for the VBGF.

Weight-at-age data were also modelled with a modified von Bertalanffy equation (Beverton and Holt, 1957):

$$W(t) = W_\infty(1 - e^{-k(t-t_0)})^3,\qquad(3)$$

where $W(t)$ is the weight as a function of time (t), W_∞ the theoretical asymptotic weight, t_0 the theoretical time at zero length, and the value 3 indicates isometric conditions. A two-parameter variation of the model was also used with W_∞ fixed for males and females at 5 and 11.5 kg, respectively. The values for W_∞ were the maximum weights observed for each sex of genetically confirmed *M. asterias* recorded during the study. An allometric variation of this model was also applied to the weight-at-age whereby the isometric condition (3) was replaced with specific male and female b-exponents of the length–weight relationship, determined from the power functions.
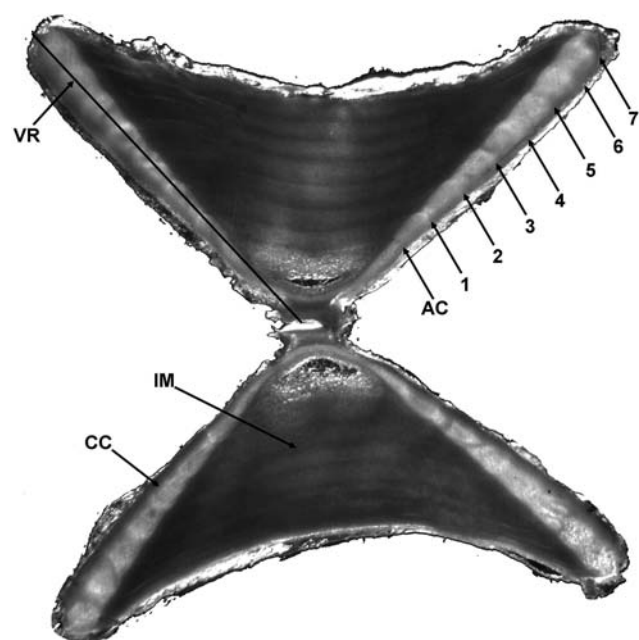
Figure 2. A sectioned *M. asterias* vertebra with seven band pairs. VR, vertebral radius; CC, corpus calcareum; IM, intermedialia; AC, angle change.

Table 1. Measures of precision for comparing inter- and intra-reader vertebrae readings.

Statistic or index	Count 2 vs. Count 1 ($n = 220$)	Count 3 vs. Count 1 ($n = 220$)	Count 3 vs. Count 2 ($n = 220$)
Correlation coefficient (r)	0.9979	0.9983	0.9990
CV	2.17	1.85	1.36
IAPE	1.53	1.31	0.96
PA	89.5	91.1	93.4
PA $\pm$ 1 year	98.1	97.3	99.4

Growth models were evaluated for goodness of fit with the Akaike Information Criterion (AIC) and Akaike weights (w_i; Akaike, 1974; Burnham and Anderson, 2002). However, utilizing goodness of fit alone may result in the incorrect model being chosen (Haddon, 2001; Cailliet *et al.*, 2006; Romine *et al.*, 2006), so a combination of fit and biological interpretation of parameters was used. Longevity was estimated as the time taken to attain 95% of L_∞ and W_∞ (Taylor, 1958; Natanson *et al.*, 2006). All statistical analyses were preformed with the Solver function and the data analysis tool of Microsoft Excel.

Results

In all, 232 *M. asterias*, 113 males (35–104 cm STL) and 119 females (44–112 cm STL), were collected for age determination (Figure 1). Overall, though, i.e. including the "catch-and-release" fish measured, 728 *M. asterias*, 304 males (28–104 cm STL) and 424 females (30–124 cm STL), were recorded for the length–weight relationship (Figures 1 and 3).

Vertebrae

The relationships between STL and VR for males and females were not significantly different (ANCOVA, $F = 1.4$, df $= 1$, $p > 0.05$),
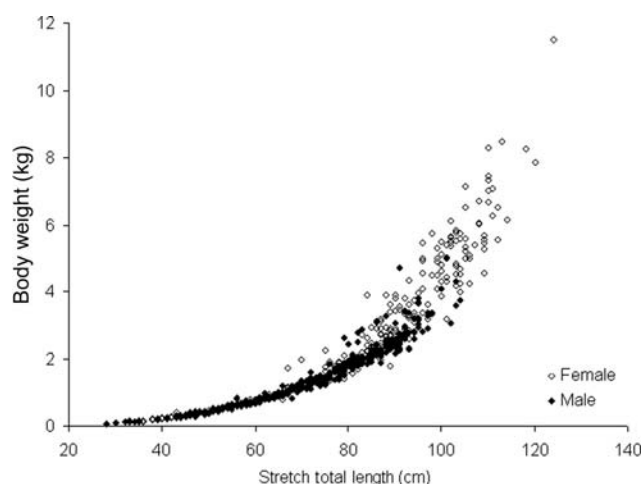

Figure 3. Relationship between body weight and STL for male and female *M. asterias*.
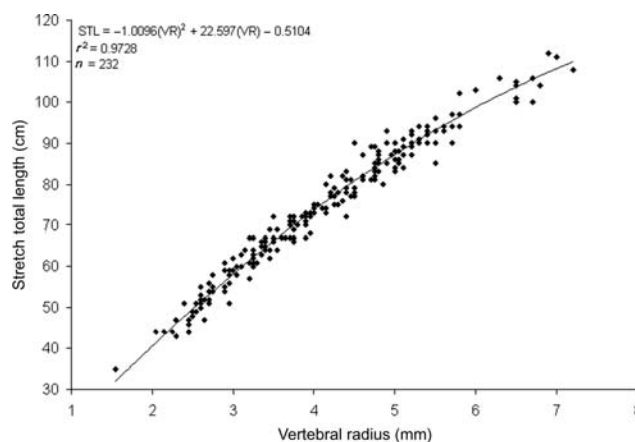

Figure 4. Relationship between VR and STL for combined male and female *M. asterias*.

so the data for both sexes were combined (Figure 4). The relationship between STL and VR was curvilinear:

$$STL = -1.0096(VR)^2 + 22.597(VR) - 0.5104. \qquad (4)$$

Of the original 232 individuals, 12(5%) had category III vertebrae and were removed from age analyses. The remaining 220 sectioned vertebrae, 106 males and 114 females, had a clear pattern of band pairs each consisting of a narrow opaque and a wider translucent band (Cailliet *et al.*, 2006). A distinct angle change was present in the intermedialia between the focus and the first band pair (Figure 2); this was not observed in embryonic vertebrae, but it was visible in pups aged as 0, and as such was considered to be the birth mark.

Of the 220 vertebrae included in the centrum edge analyses only 200 had an edge sufficiently clear to categorize. The centrum edge of older fish was particularly difficult to interpret because of the proximity of the band pairs. Attempted verification of the annual periodicity of band-pair deposition did not reveal a definite pattern, although there was a trend for the edges to be opaque in the first half of the year, and translucent in the fourth quarter (Figure 5).

Precision analyses

Comparisons of the three blind readings by the first author showed no systematic bias (Figure 6, Table 1). The level of precision was highest in the third count of the vertebrae ($CV = 1.36\%$, IAPE $= 0.96\%$, PA $= 93.4\%$, PA ± 1 year $= 99.4\%$), so these data were used for further analyses (Table 1).

Growth functions

The VBGF and GGF curves fitted the length-at-age data to varying degrees, depending on the number of parameters estimated (Table 2, Figure 7). For both males and females, the three-, two-, and one-parameter versions of the GGF produced higher estimates of k than the respective VBGF models.

The three-parameter VBGF provided the best statistical fit for males and the three-parameter GGF the best statistical fit for females. These were the models with the lowest AIC values and highest Akaike weights. The resulting growth coefficients for males and females were $k = 0.195$ year^{-1} and $k = 0.241$ year^{-1},
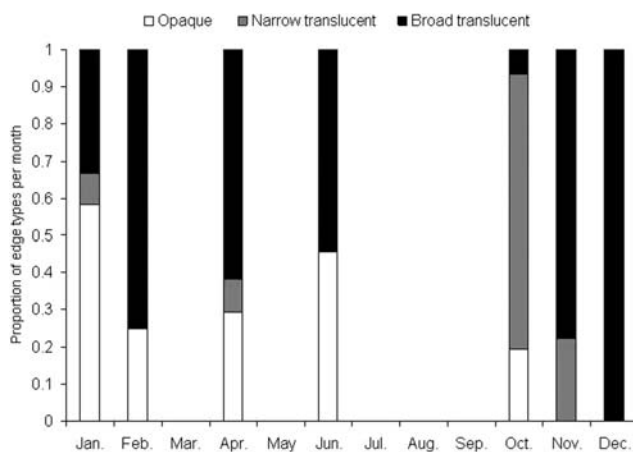

Figure 5. Monthly variations in the proportions of each of the three centrum edge types.
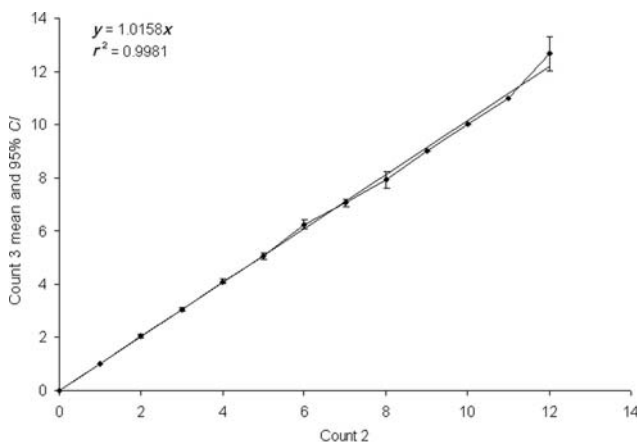

Figure 6. Age-bias graph for the pairwise age comparison of 220 *M. asterias* vertebrae from counts 2 and 3 by the first author. Each error bar represents the 95% confidence interval (*CI*) about the mean age assigned by reading 3 for all fish assigned a given age by reading 2. The 1:1 equivalence (solid line) is also indicated. No age estimation bias is present.

respectively. The estimated L_∞ for males of 103.7 cm was biologically reasonable because the maximum observed was 104 cm, but the L_0 of 38.1 cm was higher than the observed average length-at-birth of 30 cm. For females, the GGF-estimated L_∞ of 113 cm was significantly lower than the observed value of 133 cm, whereas the value of L_0 was similar to that of males. Although not statistically selected as the best fit for the data by the AIC or the Akaike weights, the three-parameter VBGF for females provided the biologically most-reasonable estimates of L_∞ and L_0, 123.5 and 34.9 cm, respectively. The Akaike weight (0.23) also reveals some support for this model, suggesting a value of k for females of 0.146 year^{-1}.

The two-parameter models produced higher values of k than the other models (Table 2), but they are likely, in terms of observed data, to be overestimated because L_0 is fixed and L_∞ is not. This caused the models to climb too quickly to an unrealistically low value of L_∞. The one-parameter models had the highest AIC values and little or no support from Akaike weights (Table 2). They also produced comparatively high values of k for males and low values for females.

The weight-to-length relationships for *M. asterias* were

$$W = 3 \times 10^{-6} L^{3.05} \ (r^2 = 0.98) \ \text{for males}, \tag{5}$$

$$W = 1 \times 10^{-6} L^{3.27} \ (r^2 = 0.98) \ \text{for females}. \tag{6}$$

At $\sim$80 cm STL, the slope of the relationship differed significantly between sexes ($F = 98.2$, df $= 1$, $p < 0.001$), the rate of increase in weight of females appearing to rise (Figure 3), perhaps indicating the onset of maturity.

The AIC values and Akaike weights for weight-at-age data suggest that the three-parameter allometric model produced the statistically best fit for males, $k = 0.199$ year^{-1} (Table 3). However, the estimated W_∞ of 3.8 kg was an underestimate because the maximum observed weight was 5 kg. The two-parameter isometric model provided the best statistical fit for females, $k = 0.101$ year^{-1}. The growth in the body weight of male and females was similar up to 3 years of age, after which female body weight increased faster than that of males (Figure 8). At the maximum observed age of 13, the body weight of females was approximately twice that of males.

Longevity

The maximum observed ages based on sectioned vertebrae of males and females were both 13 years. Longevity (T_{max}) estimates for males ranged from 7.3 to 13 years and for females from 9.9 to 20.2 years. For both males and females, the three-, two-, and one-parameter versions of the GGF produced lower estimates than the respective VBGF models. The T_{max} for males, according to the statistically best fitting model, the three-parameter VBGF, was 13 years (Table 2). T_{max} for females, according to the statistically best fitting model, the three-parameter GGF, was 12.8 years (Table 2). The estimate of T_{max} for males was in line with observed values, but for females it was an underestimation. However, according to the biologically most-reasonable model for females, the three-parameter VBGF, T_{max} was 18.3 years. Note that T_{max} was estimated as the time taken to attain 95% of L_∞, so there are likely to be older fish in the population. The weight-at-age data suggested that the T_{max} for males and females was 17.4 and 31.9, respectively (Table 3). Such higher estimates, especially in females (see lack of a defined asymptote in Figure 8), are probably related to the

Table 2. VBGF and GGF parameters for stretched total length.

| Method	Sex	L_∞ (cm)	L_0 (cm)	k (year^{-1})	n	T_{max} (year)	AIC	w_i
VBGF three-parameter	Male	103.7	38.1	0.195	106	13.0	426.78	0.45
VBGF two-parameter	Male	96.9	30[a]	0.274	106	9.6	429.67	0.11
VBGF one-parameter	Male	104.0[a]	30[a]	0.224	106	11.8	431.49	0.04
GGF three-parameter	Male	100.0	40.5	0.270	106	10.6	426.99	0.40
GGF two-parameter	Male	92.3	30[a]	0.425	106	7.3	436.52	0.00
GGF one-parameter	Male	104.0[a]	30[a]	0.318	106	10.0	448.13	0.00
VBGF three-parameter	Female	123.5	34.9	0.146	114	18.3	467.49	0.23
VBGF two-parameter	Female	116.0	30[a]	0.182	114	14.9	467.42	0.24
VBGF one-parameter	Female	133.0[a]	30[a]	0.136	114	20.2	471.67	0.03
GGF three-parameter	Female	113.0	37.2	0.241	114	12.8	466.16	0.45
GGF two-parameter	Female	105.3	30[a]	0.324	114	9.9	470.19	0.06
GGF one-parameter	Female	133.0[a]	30[a]	0.217	114	15.5	502.53	0.00

[a]A fixed parameter based on observed values.
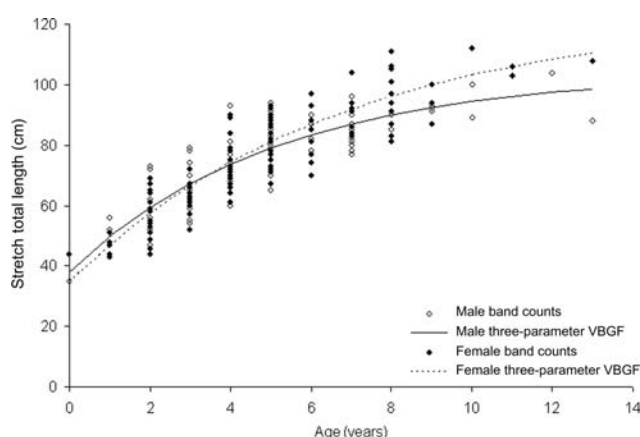
Figure 7. The VBGF with three-parameter estimation for male (L_∞ = 103.7 cm STL, L_0 = 38.1 cm STL, k = 0.195 year^{-1}) and female (L_∞ = 123.5 cm STL, L_0 = 34.9 cm STL, k = 0.146 year^{-1}) *M. asterias* in the Northeast Atlantic Ocean. Only fish used for age determination were used in developing these relationships, not those used in length–weight analysis.

higher variability in the weight parameter, which—contrary to length—is hugely influenced by feeding activity and reproductive status (i.e. presence, number, and size of embryos).

Discussion

This study has provided estimates of age and growth for a species of shark that has been exploited over much of its distribution (Aldebert, 1997; Quero, 1998; Jukic-Peladic et al., 2001; Correia and Smith, 2003; Ferretti et al., 2005), but is currently seemingly becoming more abundant in the NE Atlantic. Consequently, efforts to increase the knowledge of the population biology of *M. asterias* are needed to ensure its sustainable management. This is the first comprehensive study of age and growth in this species in the NE Atlantic.

Although age estimates were not validated, vertebral ageing has been validated in another white-spotted aplacental species of *Mustelus*, *Mustelus antarcticus* (Officer et al., 1997), and has been verified in *Mustelus manazo* (Tanaka and Mizue, 1979; Yamaguchi et al., 1996). Annual band-pair deposition has also been verified in two unspotted placental species of *Mustelus*,

M. mustelus and *Mustelus canis* (Goosen and Smale, 1997; Conrath et al., 2002). Although not yet verified or validated, enumeration of vertebral band pairs has also been applied to age studies for *Mustelus lenticulatus*, *Mustelus californicus*, and *Mustelus henlei* (Yudin and Cailliet, 1990; Francis and Ó Maolagáin, 2000). The opportunistic nature of the sampling in the current study precluded a collection of representative specimens from each month of the year and inhibited verification of annual band-pair deposition (Figure 5). However, trends suggest that the opaque band is produced in the first half of the year.

The results of the studies listed above suggest a propensity for *Mustelus* species, both white-spotted aplacental and unspotted placental, to form band pairs annually. Although the importance of verification and validation of age estimates is recognized (Cailliet, 1990), and absolute age determination and validation should be the goal of every study (Beamish and McFarlane, 1983), this is not always possible owing to time and sample availability. In the current study, the high level of precision between the three vertebral band counts coupled with the prior agreement of the authors on the defined criteria supports the interpretation of the vertebrae (Figure 6, Table 1). With this in mind and for the purposes of constructing growth curves, an annual deposition of band pairs in *M. asterias* is assumed, although further attempts at validation, including tagging and OTC marking, are currently being made.

The use of multiple growth functions is important in describing the growth of a species (Cailliet et al., 2006). The three models in this study were selected based on ease of use and their prevalence of use in the literature. The three-parameter VBGF provided the best statistical fit for males and a biologically reasonable estimate of L_∞ (Figure 7, Table 2). The overestimated length-at-birth is likely the consequence of there being no neonates in the samples. Only one fish <40 cm was aged, whereas the length-at-birth was 30 cm STL. The estimated longevity for males (13 years) also agreed with observed values.

The three-parameter GGF produced the best statistical fit for females, but the estimate of L_∞ (113 cm) was not biologically reasonable because the maximum observed STL was 133 cm (Table 2). This is probably the result of the small number of large females available for age analyses. The largest female collected, from survey and commercial boats, was only 112 cm STL, but larger females were regularly recorded in the "catch-and-release" data generated from anglers and charter boats. These animals were not sacrificed for the analyses, but

Table 3. VBGF parameters for weight.

Method	Sex	Growth	W_∞ (kg)	t_0	k (year^{-1})	n	T_{max} (year)	AIC	w_i
VBGF—W_t three-parameter	Male	Isometric 3	3.8	−2.37	0.198	106	17.6	−173.29	0.27
VBGF—W_t two-parameter	Male	Isometric 3	5[a]	−3.66	0.136	106	26.1	−172.90	0.23
VBGF—W_t three-parameter	Male	Allometric 3.05	3.8	−2.41	0.199	106	17.4	−173.30	0.28
VBGF—W_t two-parameter	Male	Allometric 3.05	5[a]	−3.73	0.136	106	26.1	−172.87	0.22
VBGF—W_t three-parameter	Female	Isometric 3	9.7	−2.49	0.118	114	27.4	−95.49	0.15
VBGF—W_t two-parameter	Female	Isometric 3	11.5[a]	−2.94	0.101	114	31.9	−97.29	0.37
VBGF—W_t three-parameter	Female	Allometric 3.27	9.4	−2.79	0.123	114	26.4	−95.43	0.14
VBGF—W_t two-parameter	Female	Allometric 3.27	11.5[a]	−3.36	0.104	114	31.4	−97.16	0.34

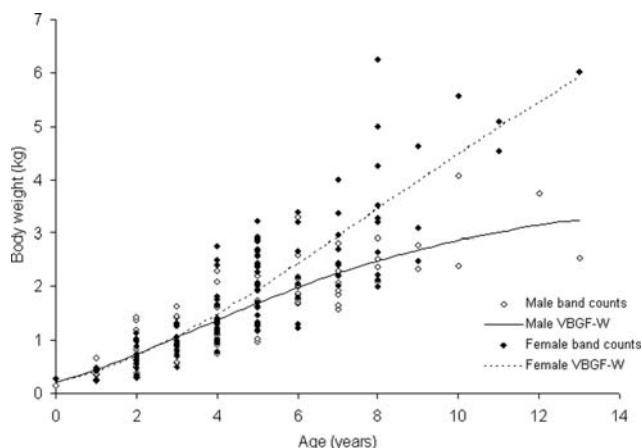[a]A fixed parameter based on observed values.

Figure 8. The VBGF for weight, for male and female *M. asterias* in the Northeast Atlantic Ocean. The three-parameter allometric model produced the best fit for males (W_∞ = 3.8 kg, t_0 = 2.41, k = 0.199 year^{-1}). The two-parameter isometric model with W_∞ fixed at 11.5 kg was the best fit for females (t_0 = 2.94, k = 0.101 year^{-1}).

were tagged and released unharmed. The longevity estimated by the three-parameter GGF (12.8) was also unreasonable because the oldest female sampled was 13 years at 108 cm STL. Given that the maximum observed STL was 133 cm, it is very likely that female longevity far exceeds the longevity estimated by this model. Hence, the value of k (0.241 year^{-1}) estimated by the GGF was considered to be an overestimate and was rejected in favour of the three-parameter VBGF.

Despite not being selected statistically as the best fit, the three-parameter VBGF for females produced biologically more-reasonable estimates for L_∞, L_0, and T_{max} of 123.5 cm, 34.9 cm, and 18.3 years, respectively (Figure 7, Table 2). The resulting value of k is significantly lower than that estimated by the GGF and is better supported by the estimated parameters. Therefore, we believe that the three-parameter VBGF provides a more reliable estimate of growth rate for females (k = 0.146 year^{-1}) and should be accepted as currently the most realistic model for *M. asterias*. Although it may be argued that the statistically best fitting model should always be chosen, rationality should also be employed and the biological parameters interpreted to ensure that the biologically most meaningful growth function is chosen (Haddon, 2001; Cailliet *et al.*, 2006). Romine *et al.* (2006) demonstrated this, when describing the growth of *Carcharhinus plumbeus*, by rejecting the best fitting statistical models in favour of those with the most meaningful estimates of biological parameters.

Perhaps, it can also be argued that the one-parameter model is the most suitable when dealing with a sample that does not have sufficient representative vertebrae from the smallest or largest fish but does have reliable observations of length-at-birth and maximum length. Fixing L_0, as here in the two-parameter models, however, can cause L_∞ to be underestimated. However, if L_∞ is also fixed at a reliable and accurate observed maximum and there are sufficient data for the middle length classes, then the resulting curve is forced to extend to a realistic L_∞, which will result in k being lower. In the current study, the Akaike weights provided little or no support for the one-parameter models, so they were not accepted (Table 2). However, the values of k and T_{max} estimated by the one-parameter models compared more favourably with the three-parameter model estimates accepted here than with the estimates from the two-parameter models. Only one example of a one-parameter version could be found in the literature (Natanson *et al.*, 2006). Those authors included a one-parameter VBGF and GGF in analysing the growth of *Isurus oxyrinchus*, but it was not the accepted model and received no further discussion. It is surprising that it has not been more widely used, however, because providing a model with more basic information than relying on statistical estimates alone would surely produce a more meaningful value of k.

The early growth in length of male and female *M. asterias* is broadly similar, but males appear to grow slightly faster (Figure 7). The higher growth coefficient (k) of males is largely the result of a slight plateau in their growth at ~5 years of age, whereas females of that age continued to grow (Figure 7). Similar patterns have been observed in other *Mustelus* species (Conrath *et al.*, 2002). This pattern was also evident in the weight-at-age model, but that model suggested slower growth rates for females (k = 0.101 year^{-1}) than the length-at-age model did (Tables 2 and 3, Figure 8). Weight, however, is a more variable parameter than STL because of changes in stomach content weight, which may be as much as 244 g, and also as a result of the presence and growth of embryos in females, which may account for as much as 1 kg of body weight (EDF, pers. obs.). The lack of a defined asymptote for females (Figure 8) is due to the scarcity of large females in the samples and the aforementioned variability in weight of larger females.

Studies of the age and growth of *Mustelus* species have estimated a wide range of values of k, from 0.1 to 0.695 year^{-1} for males and from 0.06 to 0.42 year^{-1} for females (Tanaka and Mizue, 1979; Yudin and Cailliet, 1990; Francis and Francis, 1992; Moulton *et al.*, 1992; Yamaguchi *et al.*, 1996; Goosen and Smale, 1997; Conrath *et al.*, 2002). Comparison of *M. asterias* growth rates from the current study with these literature values suggests that *M. asterias* is slow-growing. However, such

comparisons should be viewed with caution because the use of different growth models and their variations can have a significant effect on the resulting values of *k*, as illustrated here. Moreover, the genus *Mustelus* is not monophyletic and can be divided into two clades: white-spotted aplacental species and unspotted placental species (Lopez *et al.*, 2006). This may affect the growth rate of females in particular, owing to the energetic costs of the different levels of maternal investment in developing embryos (Wourms and Lombardi, 1992). Even within the two proposed clades, the individual species are widely distributed in both temperate and tropical waters (Compagno, 1984), and hence likely to be subjected to a wide range of environmental conditions that are also likely to affect growth rates.

Despite the differences in growth-model parameters and estimated growth rates (*k*), the primary findings of this study are clear: *M. asterias* in the NE Atlantic grow slower than previously believed generally. The findings support the view of Henderson *et al.* (2003), who suggested that the growth rate may be twice as slow as that estimated by Francis (1981). The implications of this may be profound and go some way towards explaining the species lack of resilience to exploitation in the Mediterranean, the southern Bay of Biscay, and on the Portuguese shelf.

Limited biological information for elasmobranchs has made it difficult to determine their vulnerability to exploitation and has subsequently hampered the implementation of conservation and management strategies (Frisk *et al.*, 2001). *Mustelus asterias* is currently classed as lower risk/least concern on the IUCN Red List of threatened species, largely because of the apparent increase in abundance in the NE Atlantic. However, in the Mediterranean, they are considered vulnerable and are probably locally extinct in several areas (Ellis, 2000; Serena, 2005). The data presented here suggest that management controls and conservation measures are needed for this species throughout its range. As previously mentioned, landings of *Mustelus* spp. in the NE Atlantic are currently increasing, mainly as a bycatch in mixed demersal fisheries. However, there is currently no management measure for *Mustelus* spp. in the area, and it is possible, indeed likely, that the dramatic declines and local extinctions seen in and around the Mediterranean will be repeated in the NE Atlantic generally. The mixed nature of the fishery makes management considerably more difficult, but introduction of landing limits may curtail the current upward trend. No nursery areas (Heupel *et al.*, 2007) have been described for the species, but abundances of juveniles (≤ 40 cm STL) are seasonally noted in the Bristol Channel, the Outer Thames Estuary (Ellis *et al.*, 2005), and on the southeast coast of Ireland (EDF, pers. obs.). Further study is needed to delineate potential nursery areas more accurately and to investigate whether their protection is possible. In the Irish Sea, large mature females (>90 cm STL), many showing obviously distended abdomens, are seasonally abundant in May off Holyhead, Wales (EDF, pers. obs.). Such aggregations are highly susceptible to exploitation, and seasonal closure of such areas to commercial fishing should be considered.

One positive aspect of work on the genus is that *Mustelus* spp. have been proven to support sustainable fisheries through the enforcement of strict management measures, based on sound scientific knowledge of life history, population structure, and movement patterns of the species in question (Walker, 1998). The findings here, though still requiring full validation, provide a first step towards this ideal. Further work on the reproductive biology and population structure of *M. asterias* in the NE Atlantic is already underway.

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