Age Determination, Growth and Reproduction in the Lesser-spotted Dogfish, *Scyliorhinus canicula* (L.)

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Abstract

Successful fisheries management is based on the knowledge of species-specific life history data, comprising age and general morphometric information. This study presents such information for the lesser-spotted dogfish (*Scyliorhinus canicula*).

Four samples of *S. canicula,* totalling 745 individuals (310 males and 435 females), were collected by fisheries scientists from research and commercial vessels in ICES areas VIIa and VIIg, over the period November 1999–November 2000. A further 10 hatchling specimens (5 males and 5 females), from a commercial aquarium, were also collected. The total body length range for males was from 10.4 cm to 71.0 cm and for females was 10.3 cm to 70.0 cm.

A total of 706 specimens (301 male and 405 female) were aged using crystal violet stained sagittal sections of vertebral centra. Centrum length grew in proportion to total body length for males and females. Age estimates ranged from 0 years (hatchlings) to 11 years for males and 0 years to 12 years for females. Annual periodicity of growth increment deposition was suggested following analysis of the centrum edge characteristics of a subsample of specimens by all three readers. The von Bertalanffy growth parameters L_∞, K and t_0 were estimated for males (L_∞ = 87.42 cm, K = 0.118, t_0 = -1.09) and females (L_∞ = 75.14 cm, K = 0.15, t_0 = -0.96) separately. The length at 50% maturity for males was 53.5 cm and for females was 57.0 cm. These findings increase the life history data available for *S. canicula* and form a valuable contribution to the implementation of basic management measures to ensure the sustainability of catches of this by-catch species.

Key words: age estimates, annual periodicity, crystal violet, length at 50% maturity, sagittal sections, *Scyliorhinus canicula*, von Bertalanffy growth parameters

Introduction

The lesser-spotted dogfish, *Scyliorhinus canicula*, is a temperate, bottom-dwelling elasmobranch (Wheeler, 1969; Compagno, 1984), which is considered to be the most abundant species of catshark in European inshore waters (Ellis and Shackley, 1997). Despite its abundance, this species has never had a high commercial value in Ireland. It is caught as by-catch in demersal fisheries and is mainly used for bait in crab and whelk fisheries (Clarke, 1999; Fahy, 1999).

Efficient fisheries management requires biological information on the life history of target and non-target stocks for the assessment of a species' growth and mortality rates, recruitment, age-at-maturity and overall life-span (Ricker, 1975; Hoenig and Gruber, 1990; Anon., MS 1999). It is acknowledged that the life history traits of elasmobranchs (longevity, slow growth rates and late sexual maturation) make them susceptible to overfishing, which results in the lack of sustainability of many directed

and by-catch elasmobranch fisheries (Hoenig and Gruber, 1990; Bonfil, 1994; Camhi *et al*., 1998).

Some problems have arisen in the acquisition of this life history information in many elasmobranch species. These problems are mostly related to the difficulties in accurately ageing elasmobranchs, which unlike teleost fish do not possess otoliths or conventional scales (Holden, 1974; 1977). As a result, elasmobranch ageing studies have been based on a variety of different techniques including, length frequency analysis (Brander and Palmer, 1985; Rodríguez-Cabello *et al*., 1997), tooth replacement rates (Moss, 1972), eye lens weight (Siezen, 1989), X-radiography (Ferreira and Vooren, 1991; Officer *et al.*, 1996) and the enumeration of growth increments on dorsal spines (Holden and Meadows, 1962) and caudal thorns (Gallagher and Nolan, 1999). Most elasmobranch ageing studies are, however, based on the analysis of periodic growth increments within vertebral centra (Cailliet *et al.*, 1986).

Although the demographic and ecological information for *Scyliorhinus canicula* in the Northeast Atlantic was considered fragmentary (Pawson and Vince, 1999), recent studies have begun to provide increased information on the reproduction and growth of *S. canicula* in the waters around Ireland (Ellis and Shackley, 1997; Ivory, MS 1999; Henderson and Casey, 2001). The von Bertalanffy growth parameters (L_∞, K and t_0) previously estimated for *S. canicula* (Table 1) were derived using the analysis of length frequency data (Rodríguez-Cabello *et al.*, 1997), vertebral age determination (Henderson and Casey, 2001) and from unpublished data (Jennings *et al.*, 1999).

Numerous studies have also assessed different aspects of the reproductive biology of this species in the Mediterranean and different parts of the Atlantic (Table 2) but only recently have such reproductive characteristics been related to the age and growth of this species (Henderson and Casey, 2001). Different lengths at first maturity for *S. canicula* have been recorded and related to latitudinal variation (Rodríguez-Cabello *et al.*, 1998). The majority of the largest specimens of *S. canicula* caught are usually male, which is suggested to be due, at least in part, to a differential growth rate between the sexes (Rodríguez-Cabello *et al.*, 1998). The lack of sufficient data prior to this study has, however, precluded the estimation of separate growth curves for male and female *S. canicula*.

This study examines the age, growth and reproductive biology by sex of *S. canicula* within the Irish and Celtic Sea areas, with the aim of increasing the species specific information available for this non-target species.

Materials and Methods

Four samples of *Scyliorhinus canicula,* totalling 745 individuals, were obtained by fisheries scientists from research and commercial vessels in ICES areas VIIa (the Irish Sea) and VIIg (the Celtic Sea), over the period November 1999 to November 2000 (Table 3). Each sample consisted of the entire catch of *S. canicula* for a given haul, with all specimens being frozen (at -23ºC) for storage.

TABLE 1. The von Bertalanffy growth parameters for *S. canicula* from Atlantic waters; L_∞ = theoretical asymptotic length, K = the Brody growth coefficient and t_0 = the theoretical age at zero length.

Study	L_∞	K	t_0
Henderson and Casey (2001)	82.7	0.15	-1.36
Jennings *et al.* (1999)	88.0	0.20	–
Rodríguez-Cabello *et al.* (1997)	88.8	0.13	–

The ageing study also involved 10 hatchlings of known age, obtained from a commercial aquarium (*Exploris*, Portaferry, Co. Down, Northern Ireland).

Prior to processing, specimens were thawed until the body could be manipulated for accurate total length (cm) and bodyweight (g) measurement. The clasper length (mm) was measured in male specimens from the point where the clasper attaches to the pelvic fin to its tip. The assignment of maturity was based on the results of an examination of the testes, the size and condition of the claspers and the *vasa deferentia* in the males; and on the size of the ovary and oocytes along with the size, condition and colouration of the nidamental glands and oviducts in females based on indices modified from Stehmann (1987) (Table 4).

A segment of the vertebral column was removed from each specimen, from a site just anterior to the pectoral girdle (above the thoracic cavity) to the beginning of the abdominal cavity, with each segment containing between 10 and 12 vertebral centra. Vertebral centra from this region are recommended for age analysis because they are the largest of the centra and are generally easier to read than smaller centra (Taylor and Holden, 1964; Cailliet *et al.*, 1983; Officer *et al.*, 1996). The excised segment of the vertebral column was initially cleaned of any loose flesh with a scalpel, and was then placed in a 5% solution of trypsin (from hog pancreas, 101 units/mg, Fluka Chemie GmbH. Chemical abstract registry no. 9002-07-7) in a drying oven at 40°C for 24 hr. This incubation period removed the neural and haemal arches and the intervertebral connective tissue allowing the separation of the individual centra. The centra were then rinsed thoroughly in tap water and allowed to air dry for 48 hr.

The segment of the vertebral column was removed from the hatchling specimens in the same way as for the larger specimens. Due to their small size (<1 mm in length) and delicacy, hatchling vertebrae were cleaned and separated by heating in water, rather than a trypsin solution, until the flesh was loose enough to be removed with a forceps, and the centra could be separated easily.

The two largest centra from each segment of the vertebral column were ground to a medial, longitudinal, section on medium grained, aluminium oxide, abrasive paper (P600 grade, 1913 siawat plain, www.sia-abrasives.ch, Swiss Industrial Abrasives Ltd.) followed by polishing on fine grained aluminium oxide abrasive paper (P1200) using distilled water as a lubricant.

The polished face of each centrum was mounted onto a glass slide using "Resin C" (Scott Bader Company

TABLE 2.   A summary of the length (cm) at 50% maturity data available for *Scyliorhinus canicula* from different parts of its geographical range.

Author	Sampling Area	Male	Female
Jennings *et al.* (1999)	Atlantic (North Sea)	58.0	58.0
Henderson and Casey (2001)	Atlantic (Ireland)	57.5	58.1
Ellis and Shackley (1997)	Bristol Channel	52.0	55.0
Ford (1921)	English Channel	57.0–60.0	57.0–60.0
Leloup and Olivereau (1951)	English Channel	52.0–60.0	52.0–60.0
Fauré-Frémiet (1942)	Atlantic (France)	52.0–60.0	52.0–60.0
Rodríguez-Cabello *et al.* (1998)	Atlantic (Spain)	–	54.2
Capapé *et al.* (1991)	Mediterranean (France)	44.0	41.0–47.0
Leloup and Olivereau (1951)	Mediterranean	37.0–44.0	37.0–44.0
Capapé (1977)	Mediterranean (Tunisia)	40.0	40.0–45.0

TABLE 3.   The composition by sex of *S. canicula* for each sample in this study. *Hatchling specimens of known age (Exploris aquarium, Portaferry, Co. Down, Northern Ireland). M = male and F = female.

Sampling Date	No. of Males	No. of Females	Total	Ratio (M:F)
November 1999	155	196	351	1:1.26
February 2000	65	79	144	1:1.22
July 2000	18	84	102	1:4.67
November 2000	72	76	148	1:1.01
November 2001*	5	5	10	1:1.00
Total	315	440	755	1:1.40

Ltd., www.scottbader.com) and ground to an "X-shaped" longitudinal cross-section and polished as above. Small vertebral centra, with a diameter of less than 4 mm, were mounted whole onto glass slides and the exposed surface was ground and polished to a half centrum section in the same manner as the larger vertebrae.

In order to read the growth increments deposited within the centra, sagittal sections were enhanced by staining with crystal violet (Schwartz, 1983, modified by Ivory, MS 1999). Immersion of the sagittal sections in a 0.0025% crystal violet solution for periods of between 1.5 hours to 7 hours, was found to give the most effective increment resolution. Sections were checked after an initial staining period of 1 hour to 1.5 hours and thereafter every hour until the stain was incorporated into the entire surface of each section. For the majority of sections, the best increment definition was reached when the section was overstained and then destained using 70% ethanol applied with a cotton tipped rod ("cotton bud") to the desired degree of intensity (Schwartz, 1983). Stained sections were finally immersed for 1 minute in distilled water to rinse off any excess crystal violet.

The total length (mm) of each centrum was compared to the total body length (TL) (cm) of each specimen. This relationship was determined for male and female specimens separately, using regression analysis. With the exception of the hatchling specimens, the relationship between the distance (μm) from the focus of the centrum to the hatching mark (HM) with total body length (TL) (cm), was also determined for each specimen. This analysis was carried out to verify that the position of this mark was constant, thus justifying its use as a reference point for the increment counts. The hatchling specimens were omitted from this analysis as their growth and development was considered to be influenced by their captivity in an aquarium.

Increments on centrum sections were read using an *Olympus* stereomicroscope at magnifications between 6.7× and 40×. A fibre optic light source (20 volt, 150

TABLE 4. Maturity Indices (modified from Stehmann, 1987) used to assign maturity to the male and female *S. canicula* specimens.

Male	Female
1. **Juvenile** Claspers very soft and less than the length of the pelvic fins. Testes undeveloped, thread-like. *Vasa deferentia* undeveloped.	1. **Juvenile** Ovary thin. Oocytes extremely small and often not visible to the naked eye. Nidamental glands undeveloped and not differentiated from the thread-like oviducts.
2. **Adolescent, maturing** Claspers still soft and flexible and usually less than the length of the pelvic fins. *Vasa deferentia* beginning to coil.	2. **Adolescent, maturing** Ovary still with mainly small oocytes. Nidamental glands opaque and small but differentiated from the thin oviducts.
3. **Adult, mature** Claspers rigid and generally longer than the pelvic fins. Tips of claspers sometimes red and swollen. Testes swollen. *Vasa deferentia* extremely coiled at proximal end of ducts.	3. **Adult, mature** Ovary large containing oocytes at different stages of development. Nidamental glands large and developed, white and opaque. Oviducts thickened.
4. **Adult, running** Claspers rigid and longer than pelvic fins. Claspers often swollen and reddened. *Vasa deferentia* extremely coiled with sperm present throughout their length. Sperm flows with pressure on the cloaca. Testes swollen.	4. **Adult, laying, resting** Ovary large, with oocytes ranging from small to fully formed. Nidamental glands fully developed, large, white and opaque, sometimes containing developing egg cases. Oviducts large and thick and often containing fully formed egg cases.

Watt) was used to illuminate the vertebral sections from below and obliquely until the optimum resolution of each section was achieved. A growth increment on a centrum section was defined as a heavily stained opaque zone with an adjoining lighter stained translucent zone, appearing at intervals along the *corpus calcareum* (diagonal axis) of a given section.

Each section was read from the focus to the distal margin of the *corpus calcareum* on the axis with the best resolution of the stained increments (the primary axis). The three remaining axes on each section were used to corroborate the increment counts on the primary axis.

Vertebral sections were read on 3 independent occasions by the primary reader (senior author) without prior knowledge of fish the section was taken from, thus fulfilling the criteria for a blind study (Officer *et al.*, 1996). If at least two of the increment counts of an individual reader agreed, then the section was assigned an age on the basis of the modal age of these readings (Eltink, 2000). If the three increment counts did not agree but the counts only disagreed by 1 increment around the mean, then the mean reading was assigned as the age. If all three counts differed by greater than 1 increment around the mean, the section was rejected.

A subsample of 50 vertebral sections was read independently by two additional readers, reader 2 (R2) and reader 3 (R3), as well as by the primary reader to provide a comparison. The two readers were trained separately to use the same reading protocol as the primary reader. Reader consistency was tested using age bias plots of the mean age ($\pm$2 standard deviations) against the modal age. This comparison is usually made under the assumption that the modal age is an accurate approximation of the actual age of the fish. In the absence of age validation in this study (e.g. tag recapture, chemical marking) age bias plots were used to determine the relative bias, defined as the difference between the estimate of the mean age and the modal age, of each set of readings to the modal age (Eltink, 2000).

Centrum increment count precision was assessed for all sections read by the primary reader and for the subsample of 50 sections read by all three readers, using percent agreement, coefficient of variation (CV) and index of precision (D) (Chang, 1982).

Centrum edge analysis was used as a method of verifying the periodicity of increment deposition within the centra, by examining the type of growth zone forming at the distal edge of the primary axis of a given section and relating this growth zone characteristic to the time of year the specimen was caught. This analysis was carried out on the subsample of 50 sections read by each of the three readers.

The growth zone structure developing at the distal edge of each section was categorised using a modification of the grading system described by Yudin and Cailliet (1990):

Grade 1.   Narrow opaque zone forming at the edge of the section

Grade 2.   Opaque zone well formed at the edge of the section

Grade 3.   Narrow translucent zone forming at the edge of the section

Grade 4.   Translucent zone well formed at the edge of the section.

The sections were read three times by each of the three readers and assigned a centrum edge grade, i.e. Grade 1, 2, 3 or 4, each time depending on the extent of the growth zone that was developing. The final centrum edge grade of a given section was the most frequently assigned grade from all the readings combined. The different readers did not always discern the same edge zone developing in a given section and, thus, in some cases more than one grade type was assigned in the course of the readings. If the readers identified the edge zone as being opaque but consensus was not reached on the degree of development of this edge zone, that section was designated as being Grade 1/2 and similarly if the edge zone was identified as translucent but assigned Grades 3 and 4 equally by the readers, it was designated as Grade 3/4. Finally for some sections no consensus was possible as the all the readers determined different edge zones developing and for these sections the edge zones were classed as Undetermined.

The von Bertalanffy growth parameters (L_∞, K and t_0) were derived for both sexes using *FISHPARM* (Prager *et al.*, 1987), which implements Marquardt's algorithm (Marquardt, 1963) for nonlinear, least squares parameter estimation. The growth of *S. canicula* was then characterised by comparing the von Bertalanffy curve constructed from the derived parameters of L_∞, K and t_0, with the total length (cm) plotted against the observed age data. Differences between male and female growth curves were tested by comparing the derived von Bertalanffy growth parameters, L_∞, K and t_0 using

Hotelling's T^2, modified to an F statistic (Bernard, 1981). If the T^2 statistic was significant, Roy-Bose simultaneous confidence intervals around differences between the parameter values were produced to elucidate which parameter contributed most to the statistical significance (Morrison, 1976). The intervals around the difference between the pair of parameter values being compared (e.g. L_∞) were significant if they failed to include zero. If this occurred then the parameter had a significant influence on the difference in growth between the two groups of fish being compared.

Once each individual was assigned a maturity stage, based on the visual inspection of the reproductive system (Table 4), the length at 50% maturity was determined by sex. Maturity ogives were constructed using the percentage of mature individuals in each total length size-class (cm) (FISHPARM; Prager *et al.*, 1987). Clasper length (mm) in males and nidamental gland width (mm) in females, were plotted against total length (cm) to assess the growth of these structures relative to the assigned state of general morphological maturity.

Results

The sex ratio for the total sample, including hatchlings was 315 males to 440 females (M:F, 1:1.4), with significantly more females present (χ^2 value = 28.80, degrees of freedom (df) = 3, $p \leq 0.0001$). The overall length range of individuals examined was similar for both male and female specimens (Fig. 1). Males ranged from 10.4 cm to 71.0 cm TL ($\bar{x}$ = 53.7 cm), whilst the range for females was 10.3 cm to 70.0 cm TL ($\bar{x}$ = 51.2 cm). Although, male and female specimens covered generally similar length ranges, the actual distribution of lengths within these ranges were significantly different (Kolmogorov-Smirnov (K–S) test, D = 0.1583, n = 755, p = 0.0002). These differences were due, in part, to the presence of a greater number of large (>61.0 cm TL) male specimens than females in the overall sample.
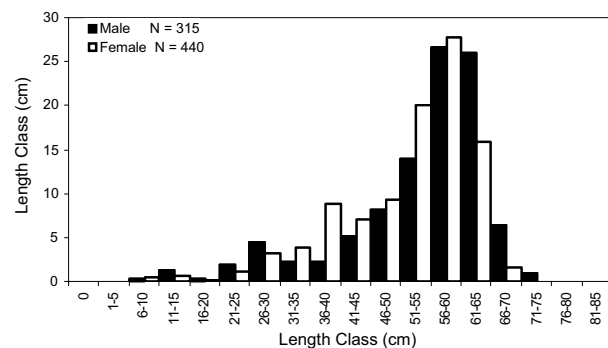

Fig. 1.   The length frequency distribution, by 5 cm size-class, of male and female *S. canicula*.

A power function described the relationship between centrum length (mm) and total length (cm) for both sexes (Fig. 2: $r^2 = 0.98$ for both males and females). The interaction between sex and total length and the influence of these parameters on centrum length was compared using ANCOVA, on log transformed data. Differences between males and females were not significant ($p > 0.05$), which indicated that at the same total length, centrum length was similar for males and females. The relationship between the distance from the focus of each section, to the hatching mark (HM) (μm) and total length was not significant for either male or female individuals ($p > 0.05$ in both cases), indicating that the position of the HM was independent of length ($r^2 = 0.02$ for males and 0.04 for females) (Fig. 3).

Ages were estimated using sagittal sections of vertebral centra from 301 males and 405 females. Males ranged in age from 0 years (hatchling) to 11 years and females from 0 years (hatchling) to 12 years (Fig. 4). All the hatchling specimens were just two weeks old and were classed as age 0 years.
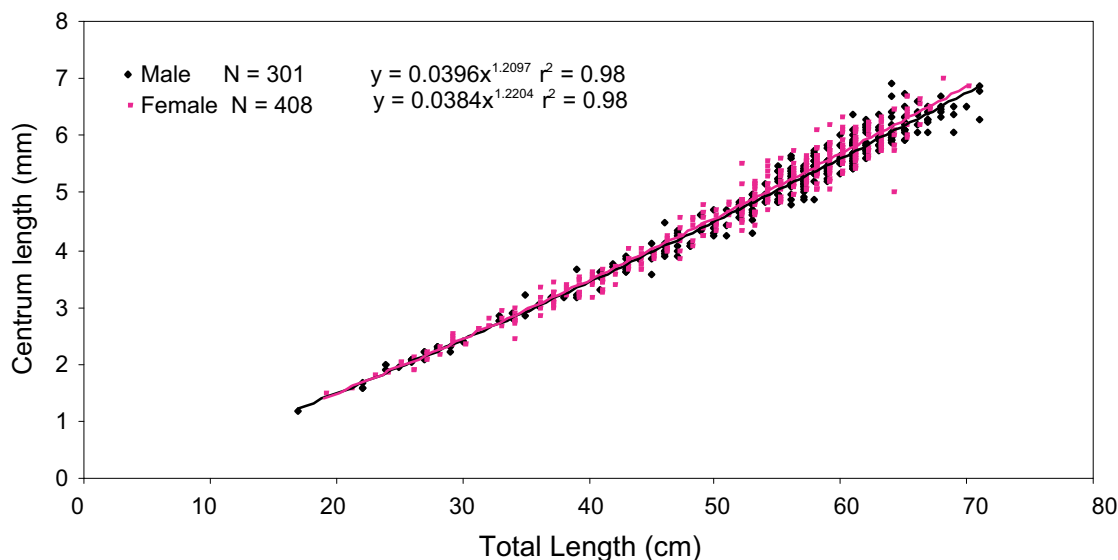

Fig. 2.   The relationship between centrum length and total length in male and female *S. canicula*.
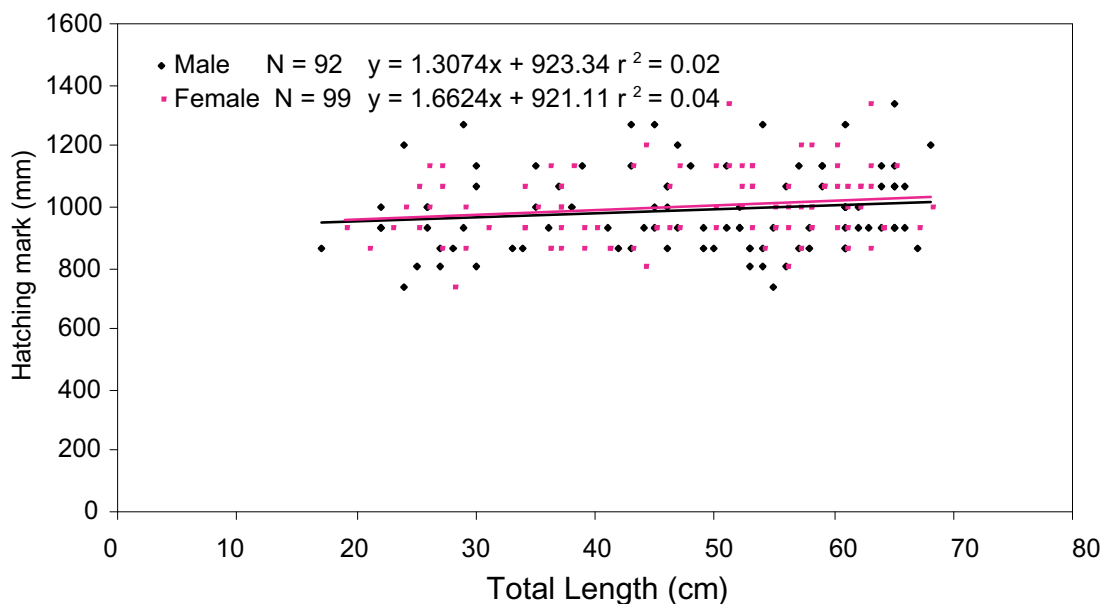

Fig. 3.   The relationship between the distance from the focus to the hatching mark and total length for male and female *S. canicula*.
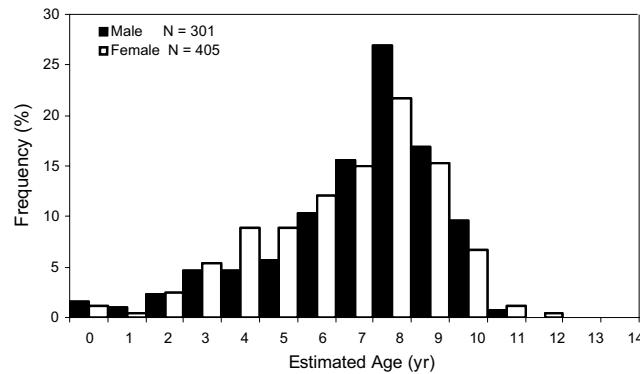
Fig. 4.   The age frequency distribution of male and female
S. canicula.

The primary reader exhibited differences in reading consistency between the three reading rounds. Analysis of the age bias plot, in the first reading round, revealed that the majority of the mean ages derived, were higher than the corresponding modal age (Fig. 5). It was clear that the mean ages in the second reading round agreed more closely with the modal age, and there was also less variation around the majority of these mean age estimates than in first reading round. The third reading round exhibited the least amount of relative bias overall, and a reduction in the variation around each of the estimated mean ages.

For the subsample of 50 sections, reader consistency was tested by comparing the increment counts for each section, read by a given reader, to the modal age for that section. It should be noted, that the modal age was calculated for each section from the combined readings (N = 9) of the three readers.

Differences in reading consistency between the three reading rounds were recorded for the primary reader reading the subsample of 50 sections (R1). Analysis of the age bias plots, for the three reading rounds, indicated a general improvement in the agreement between the mean ages and the modal ages, although the standard deviations around the mean age estimates varied more for certain ages than for others, between the rounds (Fig. 6).

There was considerable inconsistency in the standard deviations, around the mean ages, generated during the different reading rounds by the second reader (R2). This suggested that, although there was a reduction in the absolute amount of bias at most modal ages with experience, there was still sizeable variation in some of the increment counts at specific modal ages (Fig. 7).

Age estimates determined by the third reader (R3) also exhibited variation around the derived mean age estimates in each of the reading rounds. This suggested that, although the relative bias improved moderately with experience, repeated increment counts were not wholly consistent (Fig. 8).

The precision between the increment counts of the primary reader and the estimated modal age for each sagittal section was high, with a coefficient of variation (CV) of 7.6%, an index of precision (D) of 4.4% and percentage agreement of 75.0% (Table 5). The low CV, and high percentage agreement, implied that there was little variation between the increment counts for a given section, whereas the low value of D suggested that increment counts for a given section contributed little error to the mean age for that section. In the case of the subsample of 50 sections, precision was estimated between the increment counts of each reader, and the modal age calculated for each section, from the combined readings (N = 9) of the three readers. Differences in precision were evident between the readers of the subsample of 50 sections, with greater variation and less precision in the increment counts made by the second and third readers (R2 and R3), than that evident in those made by the primary reader (R1). Of the two less experienced readers, the third reader (R3) was more precise. These results indicate that practiced, experienced readers give more precise increment counts, than trained readers with limited familiarity of the ageing structures.

Analysis of the structure of the centrum edge of the subsample of 50 sections gave some indication of the temporal periodicity of increment deposition. Sections from November had a high proportion of both Grade 1 (28.6%) and Grade 2 (35.7%) opaque edge zones, with
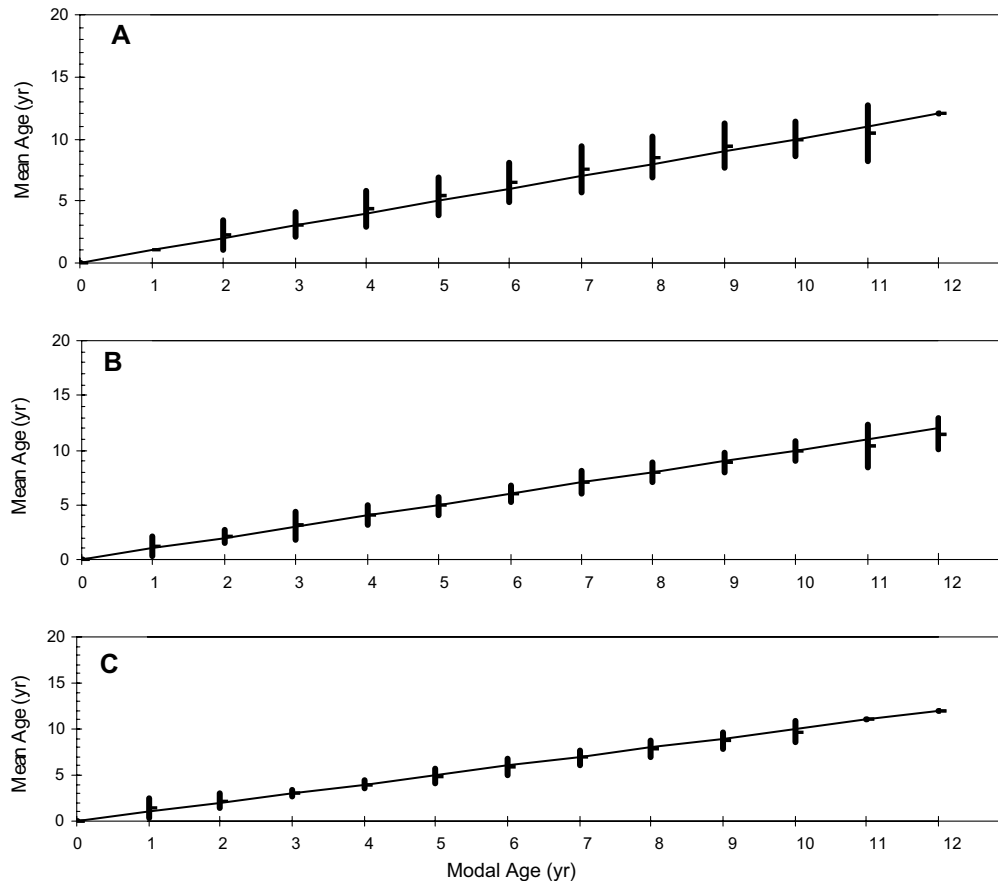
Fig. 5.   Age bias plots of the mean age (yr) (±2 standard deviations) against the modal age (yr) for the primary reader for: (**A**) reading round 1, (**B**) reading round 2 and (**C**) reading round 3. N = 706 for each reading round. The estimated mean age corresponds to the model age, if it lies on the 1:1 equilibrium line (solid line). Relative bias is measured as the difference between the estimated mean age and the modal age.

only a limited proportion of Grade 3 translucent zones forming (3.6%) at the centrum edge (Fig. 9 and Table 6). There were also a low proportion of Grade 1/2 (7.1%) and Grade 3/4 (7.1%), though the edge zone of some sections was considered Undetermined (17.9%).

By February there was an increase in the proportion of translucent edge zones, with 25.0% Grade 3 and 8.3% Grade 4. There were still opaque zones, 25.0% Grade 2 zones and 16.7% Grade 1/2 zones, suggesting that late winter and early spring may be the changeover period from opaque to translucent deposition. This change from opaque to translucent zone deposition was further evidenced by the high proportion of Undetermined (25.0%) edge zones.

In July there was a high proportion (40.0%) of fully formed translucent zones (Grade 4) at the centrum edge as well as many newly forming Grade 1 zones (30.0%). There was also only a small percentage of Undetermined edge zones, which implied that during this period the deposition pattern was more definitive.

A comparison of the von Bertalanffy growth curves fitted revealed a variance in the growth parameters (L_∞, K and t_0) between males and females (Fig. 10). Male *S. canicula* appear to have a slower growth rate (K) and a greater asymptotic length (L_∞) than females. Comparison of the von Bertalanffy growth parameters (L_∞, K and t_0) derived for males and females indicated that the growth of male and female *S. canicula* specimens was
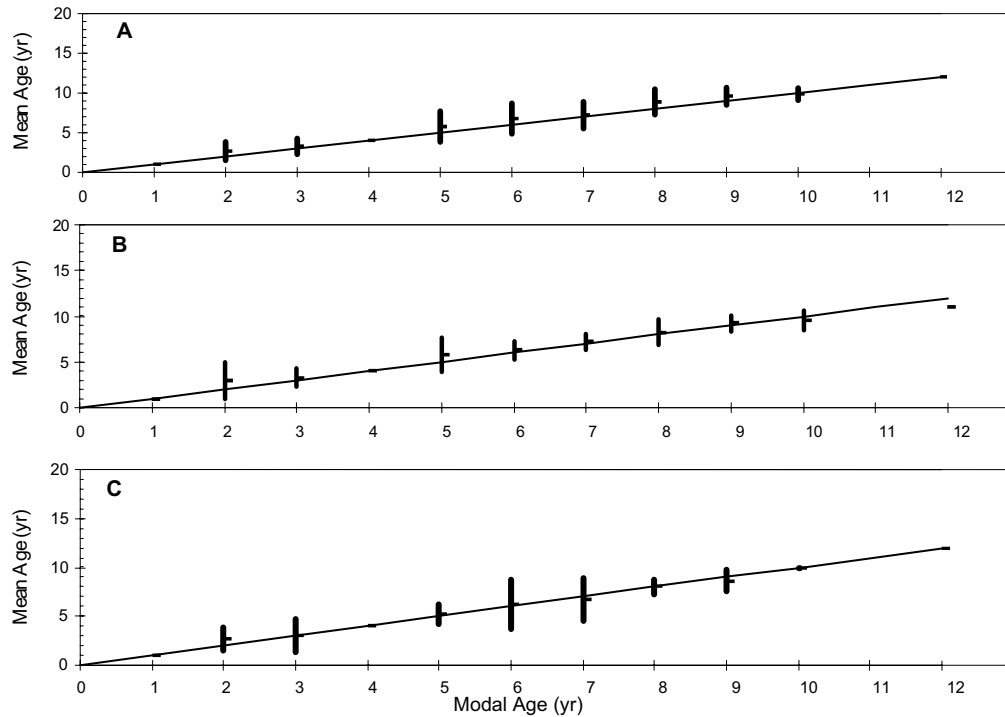
Fig. 6. Age bias plots of the mean age (yr) (±2 standard deviations) against the modal age (yr) for the primary reader (R1) of subsample of sections for: (**A**) reading round 1, (**B**) reading round 2 and (**C**) reading round 3. N = 50 for each reading round. The estimated mean age corresponds to the model age, if it lies on the 1:1 equilibrium line (solid line). Relative bias is measured as the difference between the estimated mean age and the modal age.

significantly different (Hotelling's $T^2 = 1084.97, p < 0.05$). The Roy-Bose simultaneous confidence intervals were non-zero and positive for L_∞ and non-zero and negative for both K and t_0 indicating that all of the parameters had a significant influence on the differences in growth between the sexes.

Males matured at a smaller size than females, reaching first maturity at 49.0 cm TL and 50% maturity at 53.5 cm TL, whereas females reached first maturity at 52.0 cm TL and 50% maturity at 57.0 cm TL (Fig. 11). Lengths at 100% maturity, calculated from the maturity ogives were 62.0 cm TL for males and 69.0 cm TL for females. Males also reached maturity faster than females, with an age at 50% maturity of 6.6 years against that of 7.9 years in females.

Clasper length (mm) increased with total length (cm) (Fig. 12), and this increase was most rapid between 46 cm and 55 cm TL. This period of rapid clasper growth incorporates the length at 50% maturity for males. The width of the nidamental gland (NGW) (mm) also increased with total length (cm) (Fig. 13), exhibiting rapid growth between 54 cm and 60 cm TL. The length at 50% maturity

for females was reached during this period of rapid nidamental gland growth.

Discussion

There were significantly more female than male individuals observed during this study, due mainly to the dominance of females in the July 2000 sample. Females are known to predominate in July samples from the Cantabrian Sea (Rodríguez-Cabello *et al.*, 1998) and other summer samples from Plymouth waters (Ford, 1921), with males being more common in Plymouth waters during winter (Ford, 1921). These differences in the sex ratio are thought to be related to breeding behaviour and are likely to result in unisexual aggregations in certain areas at different times of the year (Harris, 1952; Wheeler, 1969; Compagno, 1984; Ellis and Shackley, 1997).

Although, the maximum length for both male and female *S. canicula* in Atlantic waters has been documented as 100 cm TL (Compagno, 1984; Quero, 1984), specimens exceeding 80 cm TL are rarely observed (Vas, 1991; Rodríguez-Cabello *et al.*, 1997). In addition, the maximum length attained is influenced by latitudinal variation, with
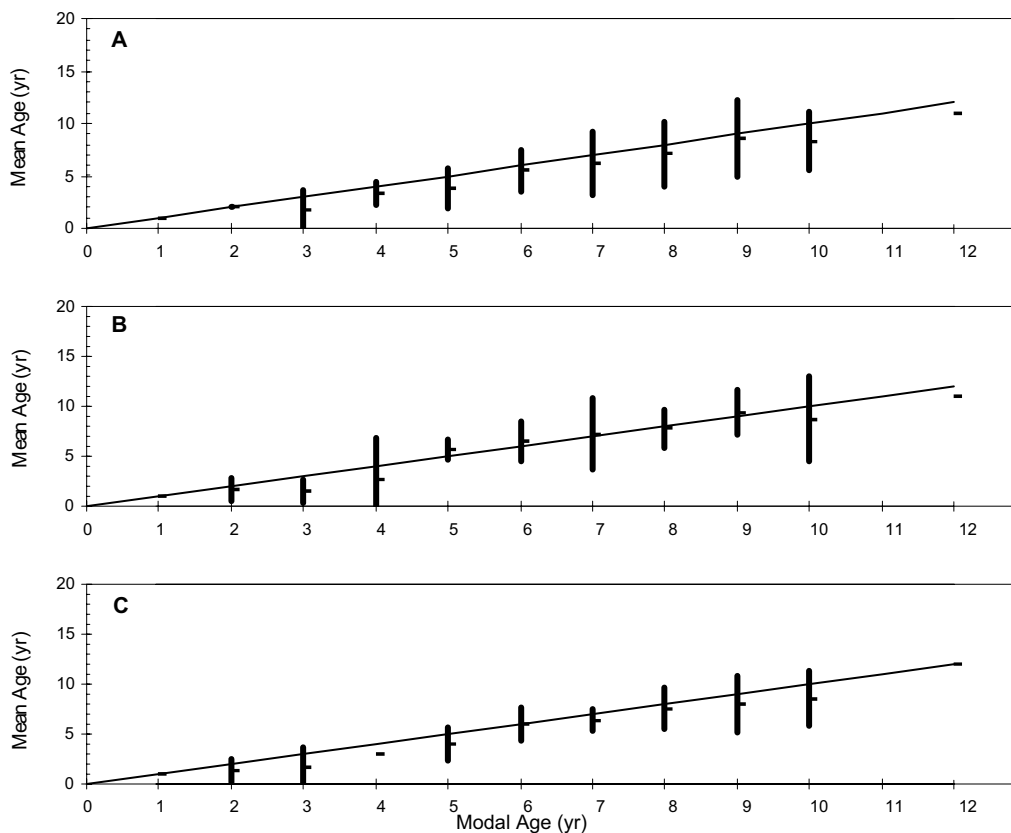
Fig. 7. Age bias plots of the mean age (yr) (±2 standard deviations) against the modal age (yr) for the reader 2 (R2) for: (**A**) reading round 1, (**B**) reading round 2 and (**C**) reading round 3. N = 50 for each reading round. The estimated mean age corresponds to the model age, if it lies on the 1:1 equilibrium line (solid line). Relative bias is measured as the difference between the estimated mean age and the modal age.

specimens from warmer Mediterranean waters reaching a smaller size than those from the northern parts of this species' geographical range (Leloup and Olivereau, 1951; Compagno, 1984). Furthermore, the fact that the majority of the larger (>60 cm) *S. canicula* specimens examined are usually male (Lyle, 1983; Capapé *et al*., 1991; Rodríguez-Cabello *et al*., 1998), as was the case in the current study, could indicate a differential growth rate between the sexes (Rodríguez-Cabello *et al*., 1998).

A curvilinear relationship exists between vertebral centrum length and TL, indicating that centra grow in proportion to dogfish length over all the size-classes sampled, making this structure useful for age analysis. *S. canicula* was previously found to exhibit a linear relationship between vertebral centrum diameter and TL (Henderson and Casey, 2001), however, the length range of the specimens involved did not include immature fish below 41 cm TL. The presence of both mature and immature individuals, in the present study, enabled the non-linear relationship between vertebral centrum growth

and somatic growth to be predicted as found for the tiger shark (*Galeocerdo cuvieri*) (Branstetter *et al*., 1987) and for the school shark (*Galeorhinus galeus)* (Ferreira and Vooren, 1991).

Crystal violet was used successfully to enhance the growth increments on the, excised and cleaned, vertebrae of the *Scyliorhinus canicula* specimens, examined in this study. This staining method is known to enhance growth increments on vertebral centra of other elasmobranch and teleost species (Johnson, 1979; Schwartz, 1983; Gallagher, 2000) and has the advantage that, with only one stage to the staining protocol, the concentration and immersion times can be altered easily to give the desired staining resolution (Gallagher, 2000). This staining method was first attempted, with limited success, for sagittal sections of vertebral centra from *S. canicula* in a preliminary study (Ivory, MS 1999).

The distance to the HM on the vertebral centra did not change significantly with TL for either sex. The
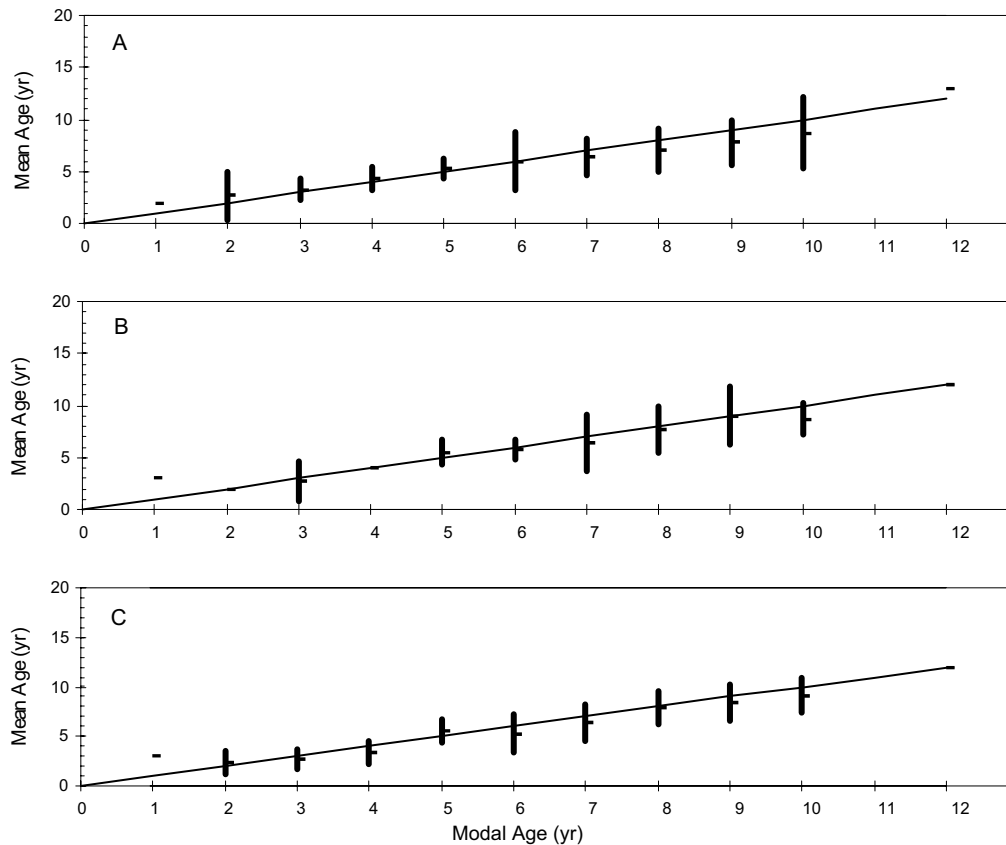
Fig. 8.   Age bias plots of the mean age (yr) (±2 standard deviations) against the modal age (yr) for the reader 3 (R3) for: (**A**) reading round 1, (**B**) reading round 2 and (**C**) reading round 3. N = 50 for each reading round. The estimated mean age corresponds to the model age, if it lies on the 1:1 equilibrium line (solid line). Relative bias is measured as the difference between the estimated mean age and the modal age.

TABLE 5.   A comparison of Chang's (1982) coefficient of variation (CV), index of precision (D) and percentage agreement with the modal age for increment counts from sagittal sections of S. canicula for the sexes combined. R1 = primary reader for the subsample of sections, R2 = reader 2, R3 = reader 3.

Reader	Primary	R1	R2	R3
N	706	50	50	50
CV (%)	7.6	9.5	20.6	14.2
D (%)	4.4	5.5	11.9	8.2
% Agreement	75.0	66.0	30.0	49.3

consistency in the position of this innermost increment, suggested that it was deposited soon after hatching and justified its use as the counting reference point on each of the centrum sagittal sections. Difficulties in identifying a counting reference point have been recognised as a problem in the ageing of other species, and are considered to affect the consistency and accuracy of the resulting age estimates (Stevens, 1975; Brander and Palmer, 1985).

The readings of the primary reader exhibited a general decrease in bias accompanied by an increase in precision with repeated readings for the total sample and also for the subsample of 50 sections. In the case of the inexperienced readers (R2 and R3) there was less consistency and precision when readings were compared with those of the primary reader (R1) for the same subsample of 50 sections. Overall, the additional readers exhibited a general increase in counting ability with increased readings indicating that the training period for these readers was valuable in helping familiarise them with the growth increment characteristics. This supports the conclusion that the experience of the reader in reading the increments of a given species is known to improve their precision and reduce their bias (Officer *et al.*, 1996).
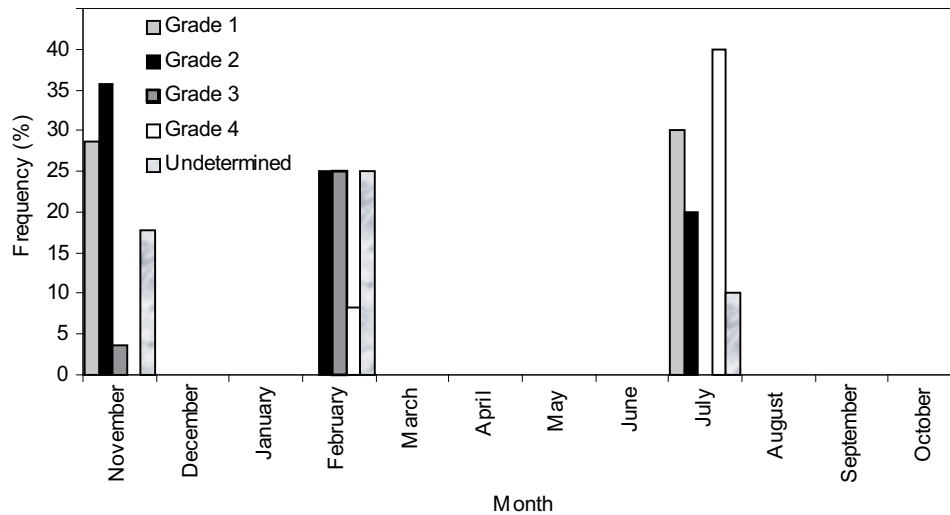
Fig. 9.   The percentage frequency, by month, of the centrum edge zone is assigned by the three
readers. Grade 1 = developing opaque edge zone, Grade 2 = well developed opaque edge
zone, Grade 3 = developing translucent edge zone, Grade 4 = well-developed translucent
edge zone and Undetermined = sections where the edge zone could not be agreed upon. N
= 50.

TABLE 6.   The percentage, by month, of each centrum edge zone as assigned by the three readers. Grade 1 = developing opaque
edge zone, Grade 2 = well developed opaque edge zone, Grade 1/2 = when Grade 1 and Grade 2 edge zones were as-
signed equally to a given section, Grade 3 = developing translucent edge zone, Grade 4 = well developed translucent
edge zone, Grade 3/4 = when Grade 3 and Grade 4 edge zones were assigned equally to a given section and Undeter-
mined = sections where the edge zone could not be agreed upon.

Month	N	Grade 1	Grade 2	Grade 1/2	Grade 3	Grade 4	Grade 3/4	Undetermined
November	28	28.6	35.7	7.1	3.6	0.0	7.1	17.9
February	12	0.0	25.0	16.7	25.0	8.3	0.0	25.0
July	10	30.0	20.0	0.0	0.0	40.0	0.0	10.0

Centrum edge analysis was used to verify the annual periodicity of deposition of growth increments (Brothers, 1983; Schwartz, 1983; Cailliet *et al.* 1986). Although there was a lot of variation in the centrum edge zones in each of the sample months, a general pattern of growth zone deposition was discernible. The change in the predominant edge zone visible in each of the sample months suggested a probable annual periodicity in growth zone deposition. In November (winter) opaque zones, specifically (Grade 2), were recorded suggesting that these zones had been forming during the autumn. By February (spring) there had been an increase in the proportion of translucent edge zones present, but the majority of these translucent zones were narrow and in the process of deposition (Grade 3). This suggests that a change from opaque to translucent deposition had begun during the winter and translucent zone deposition proceeded into the spring. The fact that the majority of the opaque zones identified were well formed and the presence of indeterminate centrum edge

zones would support the assumption of a changeover from opaque to translucent zone deposition from winter through to spring.

A large increase in the proportion of well formed translucent zones (Grade 4) was noted in July (summer) and also an increase in newly forming opaque zones (Grade 1). This suggested that translucent zones continued to be deposited at the centrum edge from the spring through to early summer, when the proportion of opaque zones began to increase again. The basic periodicity of these findings implies that opaque zones form at the edge of the vertebral centra from summer until approximately mid winter, followed by the deposition of translucent growth zones from late winter/early spring right through until the end of the summer.

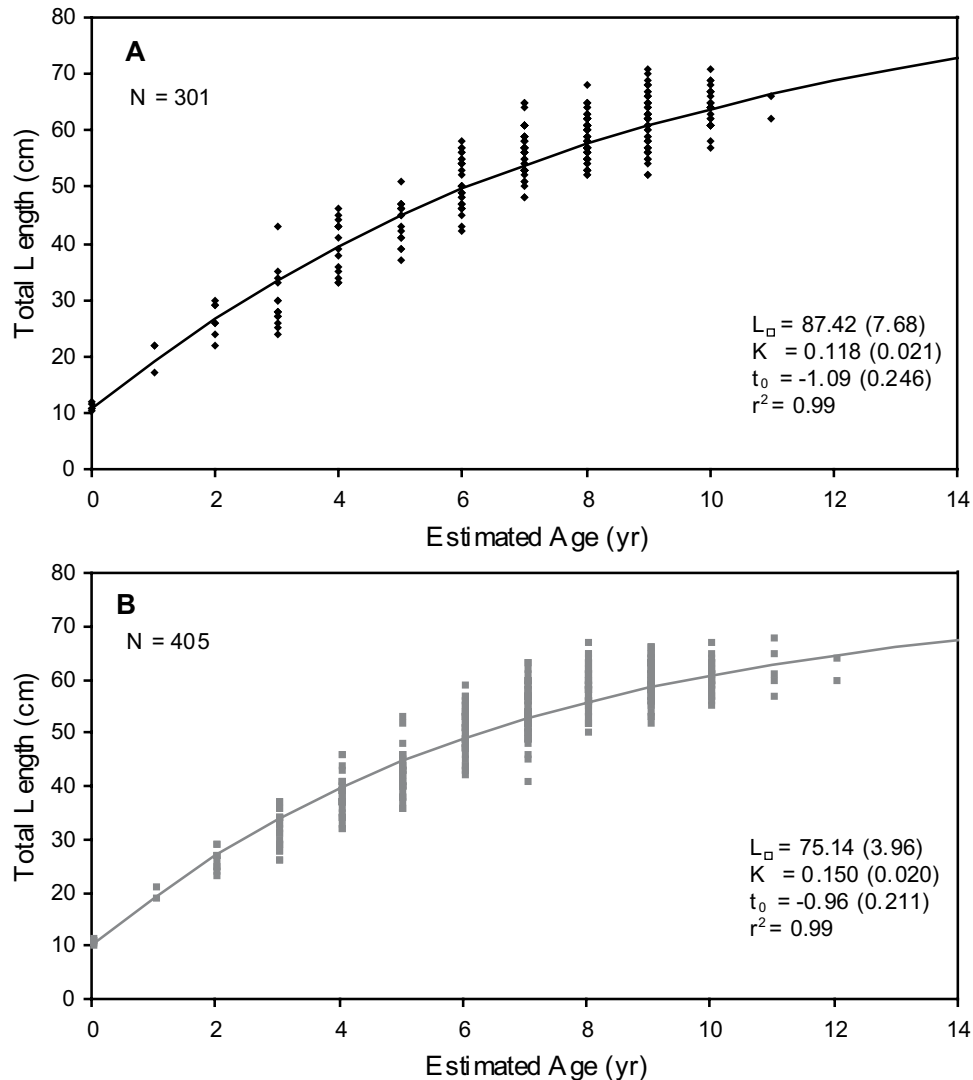A similar pattern of summer/autumn opaque and winter/spring translucent growth zone formation has

Fig. 10. The von Bertalanffy growth curves and parameters fitted to observed length-at-age data for: (**A**) male and (**B**) female *S. canicula*. The standard error of each parameter is given in parentheses.

been identified in other elasmobranch species, such as *Raja clavata* (Holden and Vince, 1973), *Raja erinacea* (Natanson 1993) and other rajid and bathyrajid species (Gallagher, 2000). Despite the favourable evidence for annual growth increment formation, the periodicity outlined here is not entirely unequivocal, as both edge zone types were found in specimens collected from each sample month. An assessment of the centrum edge characteristics from a larger sample size, during each month of the year is needed to identify the growth zone deposition periodicity accurately.

Females exhibited a broad age range (0 years to 12 years), which was similar to that of males (0 years to 11 years). Comparison of the estimated von Bertalanffy parameters, however, showed a difference in the overall growth of males and females. Male *S. canicula* were estimated to have a slower growth rate and attain a larger maximum size than females, with all the von Bertalanffy growth parameters (L_∞, K and t_0) being significantly different between the sexes. Due to limited sample sizes, especially for male specimens, previous growth studies on this species (Rodríguez-Cabello *et al.*, 1997; Jennings
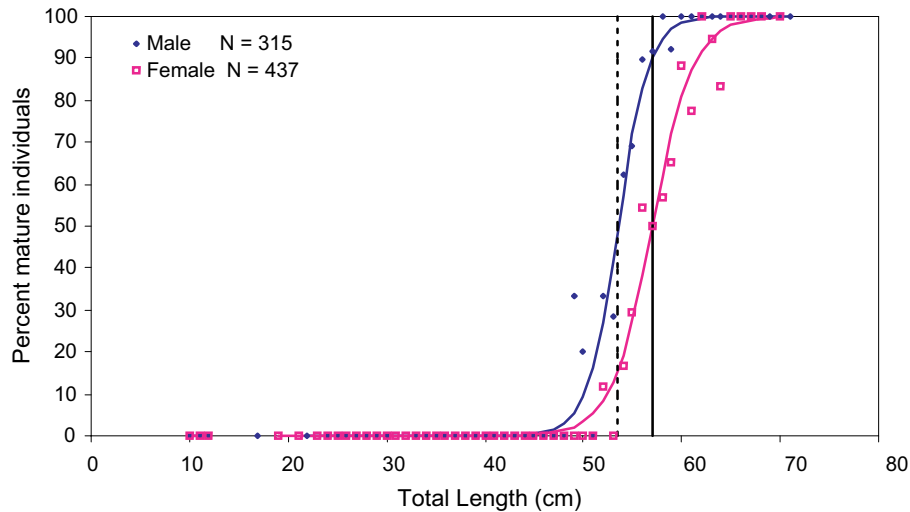
Fig. 11.   Maturity ogive relating the percentage of mature individuals and total length for male
and females *S. canicula*. The vertical dashed line represents the length at 50% maturity
for males. The solid vertical line represents the length at 50% maturity for females.
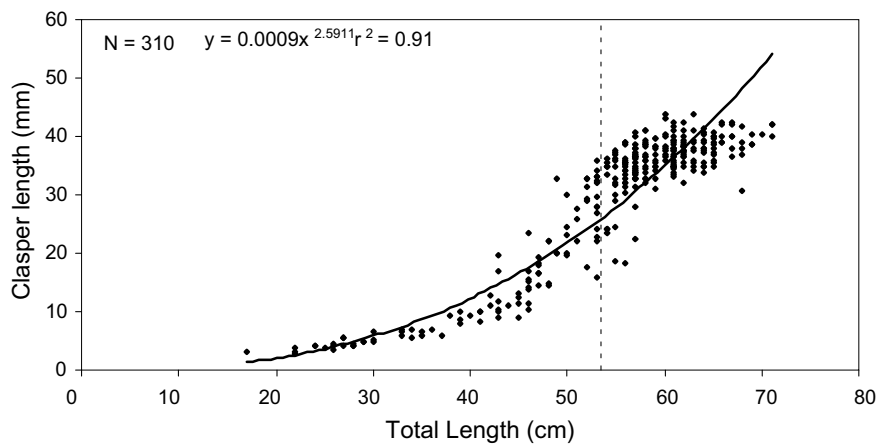

Fig. 12.   The relationship between clasper length and total length in male *S. canicula.* The
vertical dashed line represents the length at 50% maturity for males (53.5 cm
TL).

et al., 1999; Henderson and Casey, 2001) were only able
to estimate von Bertalanffy growth parameters for the
sexes combined.

The von Bertalanffy growth parameters estimated for
female *Scyliorhinus canicula* showed agreement with the
established data available on the growth of this species.
The L_∞ calculated for females was 75.14 cm, which is close
to the known maximum length of 80 cm for *S. canicula*
in Atlantic waters (Vas, 1991). Individual growth rates
have not been derived for the sexes of this species before
and this accounts for the slight deviation from previously
estimated values of *K*. The known size at hatching varies

from 8 cm to 11 cm throughout this species' geographical
range (Ford, 1921; Leloup and Olivereau, 1951; Collenot,
1966; Compagno, 1984; Mellinger *et al.*, 1984; Thomason
et al., 1996; Ellis and Shackley, 1997; Henderson and
Casey, 2001). The value of 10.06 cm estimated for L_0 for
females was within this range.

The calculated von Bertalanffy curve for males did
not estimate growth as well as that for females but it
provides the first estimates of growth for males of this
species. The L_∞ for males was greater than the maximum
length known for *S. canicula* and *K* was lower than
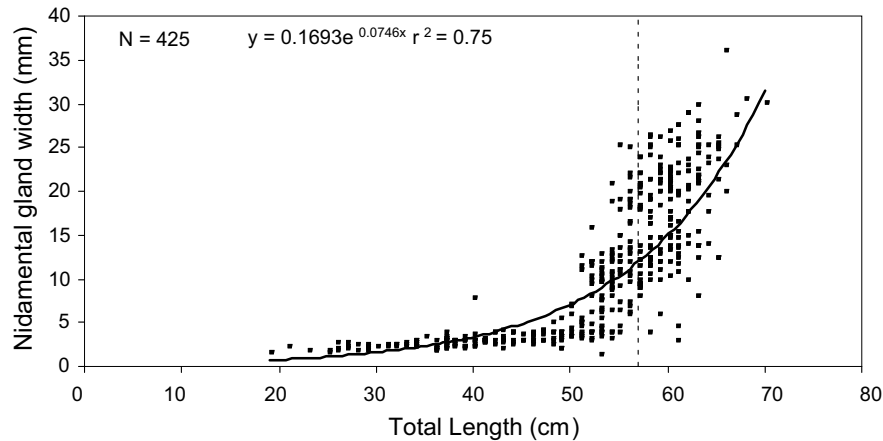previous estimates. These values are likely to have been

Fig. 13.   The relationship between nidamental gland width and total length in female *S. canicula*. The vertical dashed line represents the length at 50% maturity for females (57.0 cm TL).

influenced by the small number of older male specimens in the samples collected. As with the females, the L_0 for males (10.59 cm) was within the known range for the size at birth of this species.

This species is thought to have a relatively slow growth rate, with TL increasing from 15 cm after 1 year to 20 cm to 25 cm at 2 years, 30 cm to 35 cm at 3 years and 45 cm at 4 years (Collenot, 1966). These data were, however, observed in a captive environment with an unspecified sample size. This fact, in conjunction with the use of combined sex data in deriving the von Bertalanffy growth parameters for *Scyliorhinus canicula* previously, has precluded comparisons with growth parameters from the present study.

The length at 50% and 100% maturity in this species varies throughout its geographical range, with specimens from warmer waters (e.g. the Mediterranean) maturing at much smaller sizes than specimens from colder northern waters (Leloup and Olivereau, 1951; Compagno, 1984; Ellis and Shackley, 1997). The lengths at 50% maturity found in the current study are within the range found for specimens in the waters surrounding Britain and Ireland. In addition, females matured at a greater length than males, as observed previously for *S. canicula* specimens from other European waters (Fauré-Fremiet, 1942; Capapé, 1977; Capapé *et al*., 1991; Ellis and Shackley, 1997). Estimates of the age at 50% maturity also differ, as might be expected from the differences in length, with females maturing at a later age (7.9 years) than males (6.6 years). For both sexes the ages at 50% maturity estimated here were higher than the previous estimates of 5 years for both sexes combined (Jennings *et al*., 1999) and 6 years for females (Henderson and Casey, 2001).

Clasper length, in males, and nidamental gland width, in females, (NGW) both increased with increasing total length. The visually designated onset of maturity coincided with the most rapid increases in the size of these structures and the length range, over which maturation occurred, generally agreed with previous studies (Ellis and Shackley, 1997; Henderson and Casey, 2001).

The difference between the von Bertalanffy growth curves estimated for males and females is a reflection of the fact that the growth rate of *Scyliorhinus canicula* slows after maturity is reached (Leloup and Olivereau, 1951; Rodriguez-Cabello *et al*., 1997). Although males reach maturity at a younger age and smaller size than females, females, due to their oviparous reproductive strategy, invest more energy into egg development and ovulation as they mature. This results in a larger size and later age at maturity for females and slower overall growth particularly after maturity, whereas males maintain a more constant growth rate following maturity since their reproductive investment is not as large. Despite the majority of the largest specimens being male, they still exhibit a narrower age range than the females supporting the suggestion of a difference in the growth rate between the sexes. A greater sample size covering all size classes, especially the larger male and female specimens would help to confirm this finding.

As with all studies of age and growth, the periodicity of increment deposition requires validation (Beamish and McFarlane, 1983). Despite the lack of a validated age study, the general life history data now available for *Scyliorhinus canicula* could be used in the implementation of basic management measures in order to ensure the sustainability of catches of this non-target by-catch species.

Any fisheries management procedures established should, however, incorporate local management programmes to account for differences between populations of *S. canicula* from geographically distinct areas.

Acknowledgements

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