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Life history of a wide-ranging deepwater lantern shark in the north-east Atlantic, *Etmopterus spinax* (Chondrichthyes: Etmopteridae), with implications for conservation

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In this paper, the population biology of the velvet belly lanternshark *Etmopterus spinax* was studied and life-history coefficients determined. Age was estimated from sections of the second dorsal spine and validated by marginal increment analysis. Males attained a maximum age of 8 years while 11 year-old females were found. Several growth models were fitted and compared for both size-at-age and mass-at-age data, showing that even though this is a small-sized species, it has a relatively slow growth rate. This species matures late, specifically at 49·6 and 42·5% of the maximum observed ages for males and females, respectively. It has a low fecundity, with a mean ovarian fecundity of 9·94 oocytes and a mean uterine fecundity of 7·59 embryos per reproductive cycle. This species seems to have a long reproductive cycle, and even though no conclusive data were obtained, a 2–3 year cycle is possible. The estimated coefficients indicate that this species has a vulnerable life cycle, typical of deepwater squalid sharks. Given the high fishing pressures that it is suffering in the north-east Atlantic, this fish may already be facing severe declines or in risk of facing them in the near future.

Key words: age and growth; elasmobranch; fisheries management; population dynamics; reproduction; species conservation.

INTRODUCTION

The velvet belly lantern shark *Etmopterus spinax* (L.) is a small-sized deepwater squalid shark, that occurs in the eastern side of the Atlantic Ocean, from Iceland and Norway (Compagno *et al.*, 2005) to South Africa (Compagno, 1984), including the Azores (Santos *et al.*, 1997), the Canaries (Brito *et al.*, 2002) and the Cape Verde Islands (Reiner, 1996). It also occurs in the western and central Mediterranean Sea (Serena, 2005), including the Ionian, the lower Adriatic and the Aegean Seas (Notarbartolo di Sciara & Bianchi, 1998). This species lives mainly in the outer continental and insular shelves and upper slopes, at depths

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from 70 to 2000 m, but mostly between 200 and 500 m, near or well above the bottom (Compagno *et al.*, 2005).

In Portugal, the genus *Etmopterus* is a common-caught by-catch and discard of several deepwater fisheries that operate in the area, namely the bottom trawl fishery targeting Norway lobster *Nephrops norvegicus* (L.), deepwater rose shrimp *Parapenaeus longirostris* (Lucas) and red shrimp *Aristeus antennatus* (Risso) (Monteiro *et al.*, 2001) and the deepwater longline fishery targeting wreckfish *Polyprion americanus* (Bloch & Schneider), European conger *Conger conger* (L.) and European hake *Merluccius merluccius* (L.) (Coelho *et al.*, 2005). Even though *Etmopterus* species are caught in large quantities, their commercial value is small or none, therefore, they are usually discarded (Monteiro *et al.*, 2001). Thus, *E. spinax* is never landed and is never accounted for in the official fisheries statistics, limiting the availability of data for monitoring its fishing mortality and assessing its population status.

Although *E. spinax* is a relatively common species, information on its biology is limited. Preliminary length at maturity was reported by Coelho & Erzini (2005) for this aplacental viviparous species, while Sion *et al.* (2000) made a first attempt at age estimation in the Mediterranean population from dorsal spines. Neiva *et al.* (2006) studied the feeding ecology of the Atlantic population and Atkinson & Bottaro (2006) correlated the ampullatory distribution of the pores with the predatory lifestyle. Other studies that mention this species deal mainly with its distribution (Capape *et al.*, 2000; Massuti & Moranta, 2003) or focus on fishery aspects (Carbonell *et al.*, 2003).

Given the relatively high levels of fishing mortality that this species is currently suffering, the lack of previous studies and the fact that deepwater squalid sharks in general are characterized for having vulnerable life cycles and are among the most vulnerable of elasmobranchs, there is a need for population dynamics studies on this species. The objectives of this study were to estimate various population characteristics of *E. spinax*, specifically regarding age, growth, maturity, reproduction and fecundity. The data presented here will be useful for modelling purposes, for monitoring population variation in the future and may serve as a basis for comparison with other studies on this species in other areas.

MATERIALS AND METHODS

BIOLOGICAL SAMPLING

Specimens were caught in all months, except March 2003, from February 2003 to April 2004, as by-catch of deep-water trawlers and longliners. The commercial longliners usually operated near rocky bottoms to catch demersal bony fishes such as *P. americanus* and *C. conger*, while the commercial trawlers fished on muddy and sandy bottoms, targeting crustaceans such as *N. norvegicus*, *P. longirostris* and *A. antennatus*. In addition, some specimens were obtained during the Portuguese Fisheries Institute (INIAP–IPIMAR) deep-water demersal trawl survey in the summer of 2003. Individuals were caught at depths from 245 to 745 m.

In the laboratory, total length (L_T), fork length (L_F), pre-caudal length (L_{PC}) and body girth (G_{IR}) were recorded to the nearest lower mm. Total mass (M), eviscerated mass (M_E) and the mass of the gonads (M_G) and the liver (M_L) were recorded to the

nearest 0·01 g. Male clasper length, the diameter of female uterus, the diameter of ripe oocytes in mature females and the L_T and M of embryos in pregnant females were recorded to the nearest 0·01 mm using digital calipers and digital scales with 0·01 g precision. All morphometric measurements were taken according to the specification presented in Coelho & Erzini (2007).

MORPHOMETRIC RELATIONSHIPS

Linear regression was used to explore the relationships between the independent variable L_T and each of the dependant variables L_F, L_{PC} and G_{IR} without any data transformation, and between the independent variable L_T and the ln transformed variables M and M_E. The S.E. were calculated for all the estimated coefficients, along with the coefficient of determination (r^2) of each regression. Linear regressions were carried out for males and females separately, with ANCOVA, using L_T as the covariate used to compare the two sexes (homogeneity of the regressions).

AGE ESTIMATION AND VALIDATION

Preliminary tests on vertebrae showed that no bands were visible, even after using the alizarin red S band enhancing technique (La Marca, 1966). Thus, these structures were abandoned in favour of the dorsal spines. The relationship between individual growth in length (L_T) and first and the second dorsal spine growth namely total spine length (S_{TL}, mm), measured from the spine tip to the anterior side of the spine base, the external spine length (S_{EL}, mm), measured as the distance between the tip and point of entry of the spine into the body, the external spine width (S_{EW}, mm), measured as the width of the spine at the point of entry into the body and the base spine width (S_{BW}, mm), measured as the diameter of the spine at its base (Clarke & Irvine, 2006), was explored by linear regression. Linear regression was also used to explore the relationship between ln transformed L_T and spine mass (M_S, mg). The S.E. were calculated for all the estimated coefficients and r^2 values determined. Separate analyses were carried out for males and females and ANCOVA with L_T as the covariate used to compare the sexes. All spine measurements were taken with digital calipers with 0·01 mm precision and mass recorded using electronic precision (0·1 mg) scales.

Annual bands formed in the inner dentine layer of the second dorsal spines and defined as pairs of opaque and translucent bands were counted in order to estimate age. The spines were cleaned, embedded in epoxy resin and cut in 0·5 mm sections with a low-speed saw (Buehler Isomet, Lake Bluff, IL, U.S.A.) with a series 15LC diamond blade. A binocular microscope (Zeiss, Halbergmoos, Germany) was used to observe the sections mounted on microscope glass slides with DPX at ×100 amplification under transmitted white light. The spine sections were digitally photographed and the software Image Pro Plus 4.5 (Media Cybernetics, Bethesda, MD, U.S.A.) used for image analysis. A complete protocol of spine cleaning, sectioning, photographing and visualization is described in Coelho & Erzini (2007). Spine radius in the area where the bands were observed was measured and linear regression used to explore the relationships between variables for each sex and ANCOVA using L_T as the covariate to compare sexes.

Three independent readings, at least 1 month apart, of each structure were made by a single reader who had no information regarding specimen characteristics or the results of previous readings. Age was attributed only when at least two of the three age readings were in agreement.

The accuracy of the age estimates (Campana, 2001) was evaluated by the per cent agreement, the average per cent error (A_{PE}) defined by (Beamish & Fournier, 1981) and the coefficient of variation (C.V.) and the index of accuracy (D) defined by (Chang, 1982).

Marginal increment analysis (M_{IR}) was used to validate the periodicity of band pattern formation: $M_{IR} = (R - R_n)\,(R_n - R_{n-1})$, where R is the radius of the structure, R_n is

the distance to the outer edge of the last complete band and R_{n-1} is the distance to the outer edge of the next-to-last complete band. Seasonal values of M_{IR} were plotted to determine the annual pattern of band formation. A two-way ANOVA was used to test for differences in the M_{IR} values along the year and between the different age classes. This test was chosen after an initial check for normality of the data and homogeneity of the variance.

GROWTH MODELLING

The von Bertalanffy growth function (VBGF), a modified version of the VBGF with known size at birth, the Gompertz growth model and the logistic equation were used to model growth in L_T. The VBGF is expressed as: $L_t = L_\infty(1 - e^{-K(t-t_0)})$, where L_t is the L_T-at-age t, L_∞ is the maximum asymptotic length, K is the growth coefficient and t_0 is the theoretical age when $L_t = 0$. The VBGF with a fixed intersect of the length axis [known size at birth (L_0)] is given by: $L_t = L_\infty\ (1 - be^{-Kt})$, where $b = (L_\infty - L_0)L_\infty^{-1}$ and L_0 is the size at birth, that in this species was measured to be 107 ± 9 mm L_T (mean ± S.D., $n = 34$), based on observations of totally formed embryos occurring in late-term pregnant females. The Gompertz growth model is expressed as: $L_t = L_\infty e^{-e^{[-g(t-t_0)]}}$, where g is the Gompertz growth coefficient. The logistic equation can be expressed as: $L_t = L_\infty\{[1 + (L_\infty - L_0)L_0^{-1}]e^{-rt}\}$, where L_0 is the theoretical length at birth and r is the logistic growth coefficient.

Mass-at-age data were modelled using the VBGF and the Gompertz models. While for the latter the same model is used for mass-at-age, the VBGF for mass is: $M_t = M_\infty(1-e^{-K(t-t_0)})^b$, where M_t is total mass at age t, M_∞ is the maximum asymptotic mass and b is the allometric growth coefficient from the L_T and M relationship (3·092 and 3·290 for males and females, respectively).

Coefficients and associated S.E. of all the models were estimated for males and females separately by non-linear least squares regression with the STATISTICA 6 software (StatSoft, Tulsa, OK, U.S.A.). The maximum likelihood test (Kimura, 1980) was used to compare male and female growth coefficients.

Model comparison and selection was based on the small sample corrected form of the Akaike information criterion (A_{IC}) (Shono, 2000). For the least squares fit, this is given by: $A_{IC} = R_{SS}\ n^{-1} + 2k\ (k + 1)\ (n - k - 1)^{-1}$, where R_{SS} is the residual sum of squares, n is the number of observations and k is total number of estimated regression coefficients. The smallest A_{IC} value was the criterion used to select the 'best' model (A_{ICmin}) and the differences between this 'best' model and all others (i) expressed as: $\Delta i = A_{IC,i} - A_{ICmin}$.

MATURITY

Mature specimens were those considered able to reproduce or that had already reproduced in the past (Conrath, 2004). A two-way ANOVA was used to test for differences in mean sizes and ages of mature and immature males and females.

Age at maturity (A_{50} at which 50% of the individuals are mature) was estimated by fitting maturity ogives to the proportion of mature individuals by 1 year age classes. Non-linear least squares regression, implemented in the STATISTICA 6.0 software (StatSoft, 2004) was used to estimate the coefficients and associated S.E. and 95% CI of the logistic model: $P_{A_i} = (1 + e^{-b(A_i - A_{50})})^{-1}$, where P_{A_i} is the proportion of mature individuals in the age class A_i and b is the slope. The maximum likelihood test (Kimura, 1980) was used to test for differences between sexes in the estimated parameters.

Sexual characters such as clasper length in males and uterus width in females were used to confirm the maturity estimated by the ogives. ANCOVA tests, using L_T as the covariate, were used to assess if there were differences between these paired structures. Once it was determined that there were no differences, the left side clasper length and the left side uterus width of each male and female, respectively, was plotted against L_T.

REPRODUCTIVE CYCLE

Macroscopic observations of the reproductive organs of the specimens were used to define male and female maturity stages according to the scale proposed by Coelho & Erzini (2007) for other *Etmopterus* species. According to that scale, four stages were used to describe males, where stages 1 and 2 represent immature, stage 3 mature and stage 4 actively mating specimens, while females were divided in seven stages, where stages 1 and 2 represent immature, stage 3 mature, stages 4 to 6 pregnant and stage 7 resting females. The percentage of each maturity stage throughout the year for both males and females was plotted in order to assess if different stages were occurring predominantly during a specific season or period.

The gonado-somatic index (I_G) and the hepato-somatic index (I_H) were calculated for all specimens and the means for each maturity stage in each sex plotted. These indices were calculated as: $I_G = 100M_G M_E^{-1}$ and $I_H = 100M_L M_E^{-1}$.

The evolution of the I_G for stage 3 mature females was plotted for the different seasons throughout the year and tested with an ANOVA.

Kruskal–Wallis and pair-wise Dunn tests were used to test if significant differences occurred between I_G and I_H values for the different maturity stages. These non-parametric tests were chosen due to the lack of normality of the data and of homogeneity of the variance.

FECUNDITY

The number of oocytes in maturity stage 3 females and the number of mid-term embryos in stage 5 pregnant females were counted to determine total fecundity. Given the possibility that some of the pups may have already been born at the time of capture, pregnant females in stage 6, with near-term embryos were excluded from the fecundity study.

RESULTS

BIOLOGICAL SAMPLE

A total of 795 specimens (485 females and 310 males) were caught and processed in the laboratory. Undamaged spines for age and growth were collected from 790 specimens. For some morphometric relationships, specifically for the length and mass relationships, 494 additional specimens (218 males and 276 females) caught outside the sampling period were also used. Both male and female samples had a wide length range, with females attaining substantially larger sizes than males. Specifically, females varied from 91 to 411 mm L_T, while males ranged from 102 to 338 mm L_T. Females also had a wider age range than males. Estimated ages of females varied from 0 to 11 years, while males ranged from 0 to 8 years (Fig. 1).

MORPHOMETRIC RELATIONSHIPS

The morphometric relationships are presented in Table I. No significant differences between sexes were detected for the L_T and L_F (ANCOVA, d.f. = 1,364, $P > 0{\cdot}05$) and L_T and L_{PC} (ANCOVA, d.f. = 1,364, $P > 0{\cdot}05$) relationships, and therefore regressions for both sexes were combined. For all other regressions, significant differences were detected between sexes (ANCOVA, L_T and G_{IR}, d.f. = 1,352, $P < 0{\cdot}05$; ANCOVA, L_T and M, d.f. = 1,1286, $P < 0{\cdot}05$; ANCOVA, L_T and M_E, d.f. = 1,854, $P < 0{\cdot}05$).

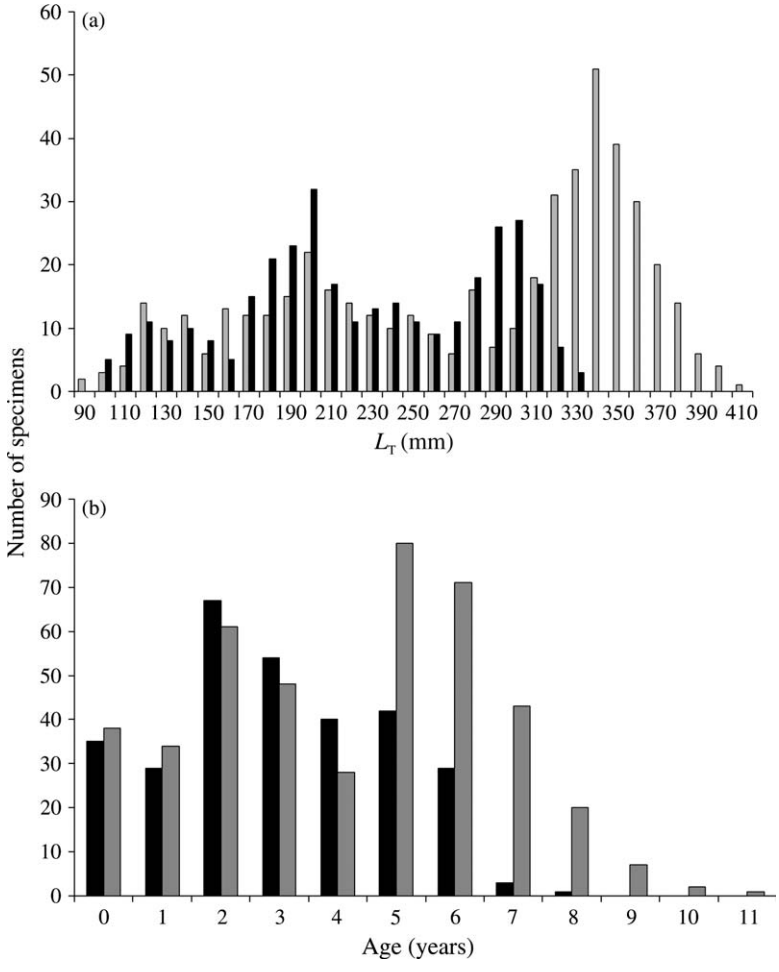

FIG. 1. (a) Total length and (b) age distributions of the male (■) and female (▒) sample of *Etmopterus spinax* used in this study.

AGE ESTIMATION AND VALIDATION

A clear relationship between the growth in mass and size of the spines (1, first and 2, second) with L_T of specimens was observed (Table II). Differences between sexes were detected for most of the relations, namely for the L_T and S_{EL1} (ANCOVA, d.f. = 1,701, $P < 0{\cdot}05$), L_T and S_{BW1} (ANCOVA, d.f. = 1,744, $P < 0{\cdot}05$), L_T and M_{S1} (ANCOVA, d.f. = 1,736, $P < 0{\cdot}05$), L_T and S_{TL2} (ANCOVA, d.f. = 1,758, $P < 0{\cdot}05$), L_T and S_{EW2} (ANCOVA, d.f. = 1,767, $P < 0{\cdot}05$), L_T and S_{EW2} (ANCOVA, d.f. = 1,728, $P < 0{\cdot}05$) and L_T and M_{S2} (ANCOVA, d.f. = 1,759, $P < 0{\cdot}05$). Differences between sexes were not detected in the L_T and S_{TL1} (ANCOVA, d.f. = 1,735, $P > 0{\cdot}05$), L_T and S_{EW1} (ANCOVA, d.f. = 1,711, $P > 0{\cdot}05$) and L_T and S_{EL2} (ANCOVA, d.f. = 1,712, $P > 0{\cdot}05$), and in these cases a regressions for sexes combined was carried out.

TABLE I. Linear regressions between total length (L_T) and fork length (L_F) pre-caudal length (L_{PC}), body girth (G_{IR}), total mass (M) and eviscerated mass (M_E) in *Etmopterus spinax*, indicating the total sample (n), the type of data transformation, the range of the independent variable and the intersect (a) and the slope (b) of the linear regression, with the respective S.E. The coefficient of determination (r^2) of each regression is also given

			Sample characteristics		Regression coefficients				
Relationship	Transformation	Sex	n	Range in L_T (mm)	a	b	S.E. of a	S.E. of b	r^2
L_T and L_F	None	Males	112	106–338	−1·008	0·865	0·132	0·006	0·997
		Females	255	91–407	−1·344	0·866	0·111	0·004	0·997
		Combined	367	91–407	−1·104	0·865	0·077	0·003	0·998
L_T and L_{PC}	None	Males	112	106–338	−1·565	0·762	0·263	0·013	0·989
		Females	255	91–407	−4·115	0·775	0·211	0·008	0·989
		Combined	367	91–407	−4·491	0·776	0·120	0·007	0·991
L_T and G_{IR}	None	Males	103	106–338	7·797	0·282	0·374	0·139	0·808
		Females	252	120–407	−20·032	0·418	0·691	0·058	0·820
L_T and M	ln	Males	528	102–338	−13·021	3·092	0·062	0·020	0·979
		Females	761	91–411	−14·058	3·290	0·060	0·018	0·977
L_T and M_E	ln	Males	344	102–338	−12·947	3·038	0·054	0·017	0·989
		Females	513	91–411	−12·944	3·038	0·051	0·016	0·987

TABLE II. Linear regressions between total length (L_T) of specimens and several spine measurements, total spine length (S_{TL}), external spine length (S_{EL}), external spine width (S_{EW}) and base spine width (S_{BW}), and spine mass (M_S) for both the first (1) and second (2) dorsal spines of *Etmopterus spinax*. The total sample size (n), the type of data transformation, the range of the explanatory variable and the intersect (a) and the slope (b) of the linear regression, along with the respective S.E. and the coefficient of determination (r^2) of each regression are given

			Sample		Regression coefficients				
Relationship	Transformation	Sex	n	Range of L_T (mm)	a	b	S.E. of a	S.E. of b	r^2
L_T and S_{TL1}	None	Males	301	102–338	1·901	0·053	0·238	0·010	0·900
		Females	437	91–411	2·547	0·050	0·285	0·010	0·861
		Combined	738	91–411	2·269	0·052	0·185	0·007	0·886
L_T and S_{EL1}	None	Males	281	102–338	2·029	0·024	0·195	0·008	0·745
		Females	426	91–411	1·384	0·028	0·184	0·006	0·827
L_T and S_{BW1}	None	Males	302	102–338	−0·123	0·012	0·053	0·002	0·893
		Females	445	91–411	0·111	0·010	0·056	0·002	0·868
L_T and S_{EW1}	None	Males	281	102–338	0·334	0·011	0·077	0·003	0·803
		Females	433	91–411	0·353	0·012	0·072	0·002	0·834
		Combined	714	91–411	0·291	0·012	0·050	0·002	0·845
L_T and M_{S1}	ln	Males	300	102–338	−4·230	2·141	0·087	0·028	0·951
		Females	439	91–411	−3·941	2·046	0·079	0·024	0·943
L_T and S_{TL2}	None	Males	307	102–338	2·887	0·773	0·259	0·011	0·941
		Females	454	91–411	3·930	0·729	0·275	0·009	0·929
L_T and S_{EL2}	None	Males	284	102–338	3·768	0·377	0·243	0·010	0·824
		Females	431	91–411	4·470	0·356	0·245	0·008	0·806
		Combined	715	91–411	4·136	0·365	0·167	0·006	0·830
L_T and S_{BW1}	None	Males	310	102–338	−0·152	0·108	0·050	0·002	0·893
		Females	460	91–411	0·010	0·101	0·039	0·001	0·923
L_T and S_{EW2}	None	Males	288	102–338	0·391	0·102	0·065	0·003	0·822
		Females	443	91–411	0·609	0·092	0·054	0·002	0·851
L_T and M_{S2}	ln	Males	306	102–338	−4·090	2·346	0·082	0·027	0·962
		Females	456	91–411	−3·726	2·222	0·071	0·022	0·959

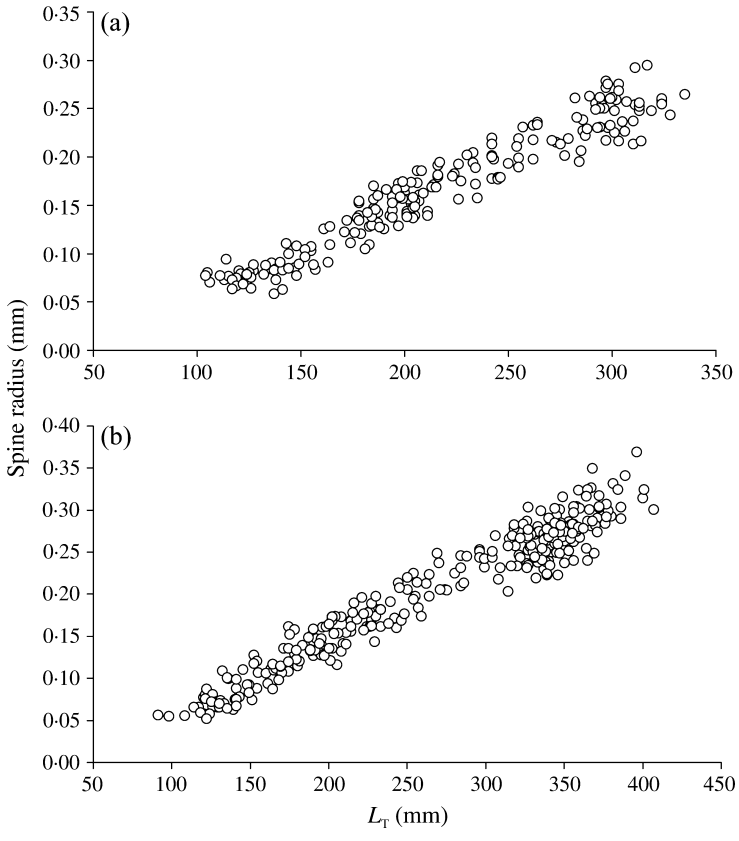

FIG. 2. Relationships between total length (L_T) and radius of the spine sections where age was estimated for both (a) males and (b) females of *Etmopterus spinax*.

The linear relationships between L_T and the radius of the spine section where age was estimated was significant for both males (ANOVA, d.f. = 1,205, $P < 0{\cdot}05$) and females (ANOVA, d.f. = 1,304, $P < 0{\cdot}05$) (Fig. 2), with differences detected between sexes (ANCOVA, d.f. = 1,512, $P < 0{\cdot}05$).

A clear pattern of alternating translucent and opaque band formation was visible on the spine sections (Fig. 3). A total of 733 of 790 specimens were successfully read (92·8%), with poor band discrimination (32 specimens) and lack of concordance (25 specimens) accounting for the remainder. The percentage of concordant readings in 0, ±1, ±2 and ±3 years was 89·0, 9·0, 2·0 and 0·0% for males and 85·2, 11·8, 2·8 and 0·2% for females. The A_{PE}, C.V. and D precision indices obtained were, respectively, 9·93, 9·23 and 5·33 for males and 17·58, 18·22 and 10·52 for females.

In general, no significant differences in the mean L_T at age between sexes were detected for the younger age classes, while significant differences were detected for the older age classes. Specifically, while no differences were found for age-classes 0, 1, 2 and 4 years, there were differences for age-classes 3, 5, 6 and 7 years (Table III). Differences for older specimens were not tested due to small sample size (age-class 8 years) or due to the complete lack of males (age-classes 9, 10 and 11 years).

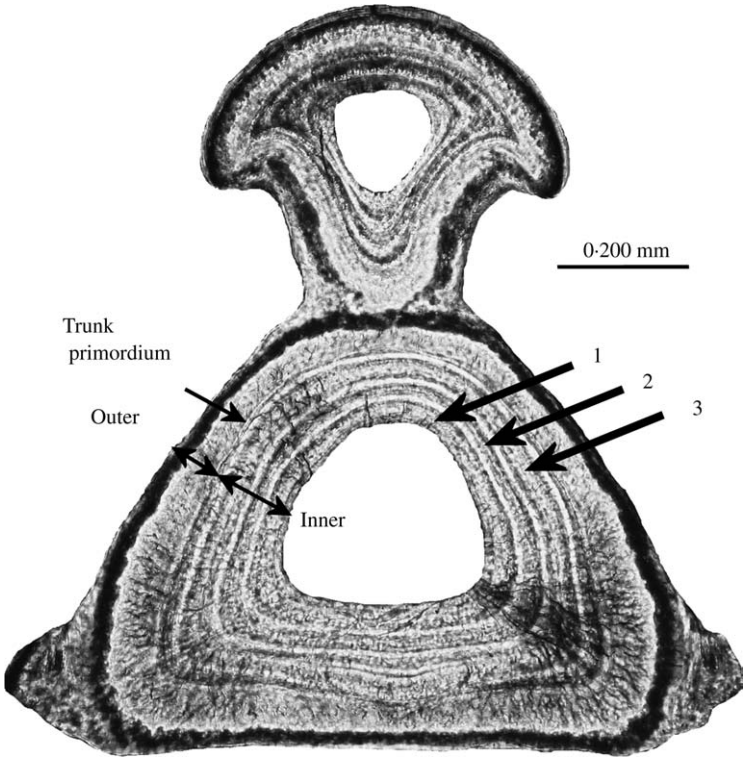

FIG. 3. Microphotograph of a sectioned dorsal spine of a male *Etmopterus spinax*, 234 mm total length and an estimated age of 3 years. It is possible to distinguish the inner trunk layer where the annual bands were counted and the outer trunk layer (without any growth bands and already present in late-term embryos), as well as the trunk primordium.

A total of 395 specimens were used for age validation by M_{IR} analysis. A clear annual pattern of band formation was observed, with the marginal increment showing higher values during the warmer months and lower values during the colder months (Fig. 4). This pattern was observed in all age classes for which this analysis was performed (between ages 3 and 7 years), while for the other age classes this analysis was not performed due to low sample size. Significant differences were found between mean M_{IR} values along the different seasons but not between mean M_{IR} values for the different age-classes within each season (two-way $ANOVA_{season}$, d.f. = 3,290, $P < 0{\cdot}05$; two-way $ANOVA_{age}$, d.f. = 4,290, $P > 0{\cdot}05$).

GROWTH MODELLING

In general, the four models used gave good fits to the L_T-at-age data and produced relatively similar curves, both in the case of males and females. In all cases, the estimated L_∞ values were higher for females, except for the VBGF where the opposite situation was observed (Fig. 5).

Between sexes comparison for each length-based model showed significant differences between male and female growth curves (maximum $likelihood_{VBGF}$,

TABLE III. Comparison of the mean ± S.D. total length (L_T) between male and female *Etmopterus spinax* for each age group. *n* refers to the sample size and S.D. to the standard deviation. The *P*-value and the decision (differences significant or not significant) of the Student *t*-statistic are also given

	Females		Males		*t*-test
Age (years)	*n*	Mean L_T (mm) ± S.D.	*n*	Mean L_T (mm) ± S.D.	*P*
0	38	126·4 ± 14·4	35	123·2 ± 12·7	>0·05
1	34	163·4 ± 16·2	29	160·0 ± 14·6	>0·05
2	61	199·1 ± 15·5	67	195·2 ± 12·4	>0·05
3	48	234·7 ± 18·0	54	223·8 ± 17·1	<0·05
4	28	277·6 ± 24·5	40	268·7 ± 19·1	>0·05
5	80	324·2 ± 20·3	42	295·1 ± 13·3	<0·05
6	71	345·5 ± 14·5	29	310·7 ± 10·2	<0·05
7	43	360·9 ± 12·4	3	311·0 ± 0·7	<0·05
8	20	372·5 ± 12·6	1	335·0	
9	7	390·0 ± 12·1			
10	2	396·0 ± 21·2			
11	1	407·0			

n, sample size.

d.f. = 2,3, $P < 0{\cdot}05$; maximum likelihood$_{\text{VBGF known}L_0}$, d.f. = 2,2, $P < 0{\cdot}05$; maximum likelihood$_{\text{logistic}}$, d.f. = 2,3, $P < 0{\cdot}05$; maximum likelihood$_{\text{Gompertz}}$, d.f. = 2,3, $P < 0{\cdot}05$). Between sexes comparisons for each mass-based model also showed significant differences between male and female growth curves (maximum likelihood$_{\text{VBGF}}$, d.f. = 2,3, $P < 0{\cdot}05$; maximum likelihood$_{\text{Gompertz}}$, d.f. = 2,3, $P < 0{\cdot}05$).

A considerable variability in L_∞ and M_∞ values was obtained depending on the growth model used. L_∞ values for males varied from 368·3 to 579·6 mm L_T and for females from 413·8 to 558·4 mm L_T, with the VBGF producing the

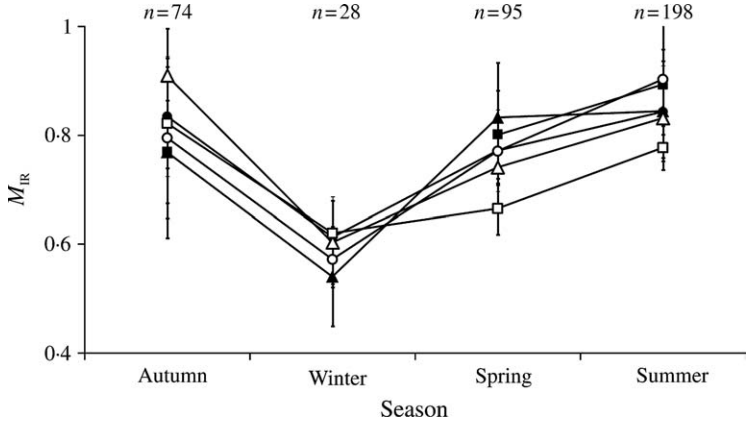

FIG. 4. Seasonal changes in the mean ± S.D. marginal increment (M_{IR}) both for all age-classes (●) combined and for each age-class separately[3 (▲), 4 (■), 5 (○), 6 (△) and 7 (□) years]. *n* = the total sample size in each season.

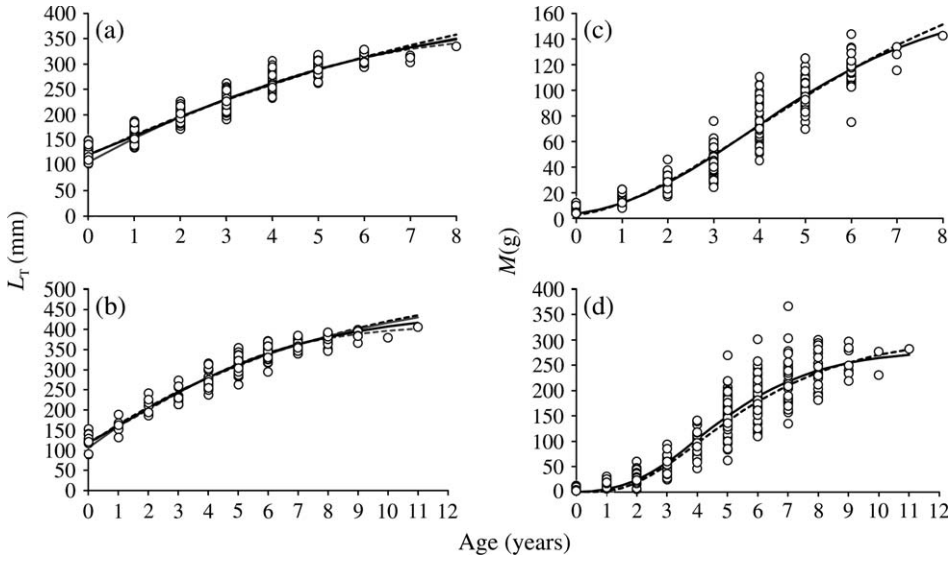

FIG. 5. (a), (b) Total length (L_T) at age and (c), (d) mass (M) at age for (a), (c) males and (b), (d) females of *Etmopterus spinax*, with the respective fitted growth models (○, observed data; ----, the fitted von Bertalanffy growth function; – – – –, the fitted logistic equation; ——, the fitted Gompertz model and ——, the fitted von Bertalanffy growth function with known size at birth).

highest values and the logistic equation the lowest. M_∞ values varied from 177·2 to 226·1 g for males and from 283·2 to 311·5 g for females, with the Gompertz producing the lowest estimated values and the VBGF the highest (Table IV).

For both sexes, the best model according both to A_{IC} and r^2 was the logistic model, followed by the Gompertz model, then the VBGF and finally the VBGF with known L_0. Given the low values of Δi (<2 in all cases), however, it was assumed that all models are valid and provide useful information. For mass-based data, the r^2 values were similar for both models and sexes, but according to the A_{IC}, the VBGF was more accurate than the Gompertz model (Table V).

MATURITY

In general terms, females of *E. spinax* mature at older ages than males. The oldest immature males were 4 years and the oldest immature females were 8 years. On the other hand, the youngest mature males and females were both 4 years. The two-way ANOVA showed significant differences between sexes and for mature or immature condition (two-way $ANOVA_{sex}$, d.f. = 1,729, $P < 0{\cdot}05$; two-way $ANOVA_{maturity}$, d.f. = 1,729, $P < 0{\cdot}05$).

The age-based maturity ogives produced good fits to the observed data, with high r^2 values, namely 0·996 and 1 for females and males. Females matured at later ages than males, with estimated ages of first maturity of 3·97 years for males and 4·67 years for females (Fig. 6). These differences between sexes were significantly different (maximum likelihood, d.f. = 2,2, $P < 0{\cdot}05$).

TABLE IV. Comparison of coefficients estimated for the different models for total length (L_T) at age and mass (M) at age for male and female *Etmopterus spinax*. The maximum asymptotic size is indicated in mm for the L_T-at-age models (L_∞) and in g for the mass-at-age models (M_∞). The growth coefficient refers to the parameters K (VBGF models), r (logistic model) and g (Gompertz model)

			L_∞–M_∞			Growth coefficients (K, r and g)		
Data set	Sex	Model	Estimate ± S.E.	Lower 95% CI	Upper 95% CI	Estimate ± S.E.	Lower 95% CI	Upper 95% CI
L_T at age	Males	VBGF	579·6 ± 59·4	462·8	696·4	0·09 ± 0·02	0·06	0·12
		VBGF known L_0	465·0 ± 22·3	421·0	509·0	0·14 ± 0·01	0·12	0·17
		Logistic	368·3 ± 8·7	351·1	385·5	0·40 ± 0·02	0·37	0·44
		Gompertz	449·7 ± 8·4	433·2	466·3	0·25 ± 0·02	0·21	0·28
	Females	VBGF	558·4 ± 23·8	511·5	605·3	0·12 ± 0·01	0·10	0·14
		VBGF known L_0	524·2 ± 15·4	494·0	554·4	0·14 ± 0·01	0·12	0·15
		Logistic	413·8 ± 5·1	403·8	423·9	0·41 ± 0·01	0·39	0·43
		Gompertz	414·3 ± 15·7	383·4	445·3	0·26 ± 0·01	0·24	0·28
M at age	Males	VBGF	226·1 ± 24·4	1780·2	2741·6	0·23 ± 0·03	0·18	0·28
		Gompertz	177·2 ± 11·8	1540·7	2003·3	0·37 ± 0·03	0·32	0·43
	Females	VBGF	311·5 ± 14·8	2823·6	3406·3	0·33 ± 0·02	0·28	0·38
		Gompertz	283·2 ± 10·1	2633·1	3030·7	0·45 ± 0·03	0·40	0·51

L_0, L_T at birth.

TABLE V. Values of the coefficient of determination (r^2), the small sample corrected form of Akaike information criterion (A_{IC}) and the Akaike's differences (Δi) for each growth model, both in total length (L_T) and mass (M) and for each sex. In each case, models are listed from best to worst according to the A_{IC}

Data set	Sex	Model	r^2	A_{IC}	Δi
L_T at age	Males	VBGF	0·94	2·52	0·14
		VBGF known L_0	0·93	2·74	0·35
		Logistic	0·94	2·39	0·00
		Gompertz	0·94	2·44	0·06
	Females	VBGF	0·95	3·76	0·60
		VBGF known L_0	0·95	3·83	0·67
		Logistic	0·96	3·16	0·00
		Gompertz	0·96	3·38	0·22
M at age	Males	VBGF	0·93	108·06	0·00
		Gompertz	0·92	110·25	2·19
	Females	VBGF	0·90	770·84	0·00
		Gompertz	0·90	774·50	3·66

Since no significant differences were found between left and right side claspers (ANCOVA, d.f. = 1,663, $P > 0{\cdot}05$), only the left size structure of each specimen was used and plotted against L_T. There is a clear relationship between clasper length and L_T, with an accentuated increase once the specimens attained maturity (Fig. 7). Likewise, no significant differences were found between left and right side uterus of females (ANCOVA, d.f. = 1,671, $P > 0{\cdot}05$). Immature females have relatively narrow uterus independent of L_T, while in mature specimens, the uterus can either appear substantially enlarged in the case of pregnant females with embryos inside the uterus or remain relatively narrow in the case of mature specimens with ripe oocytes in the gonads. Resting specimens have uterus widths somewhat between these conditions (Fig. 7).

FIG. 6. Age-based maturity ogives for *Etmopterus spinax* [the proportion of mature males (●) and females (○) in each age class, and fitted logistic curves for males (——) and females (- - - -)].

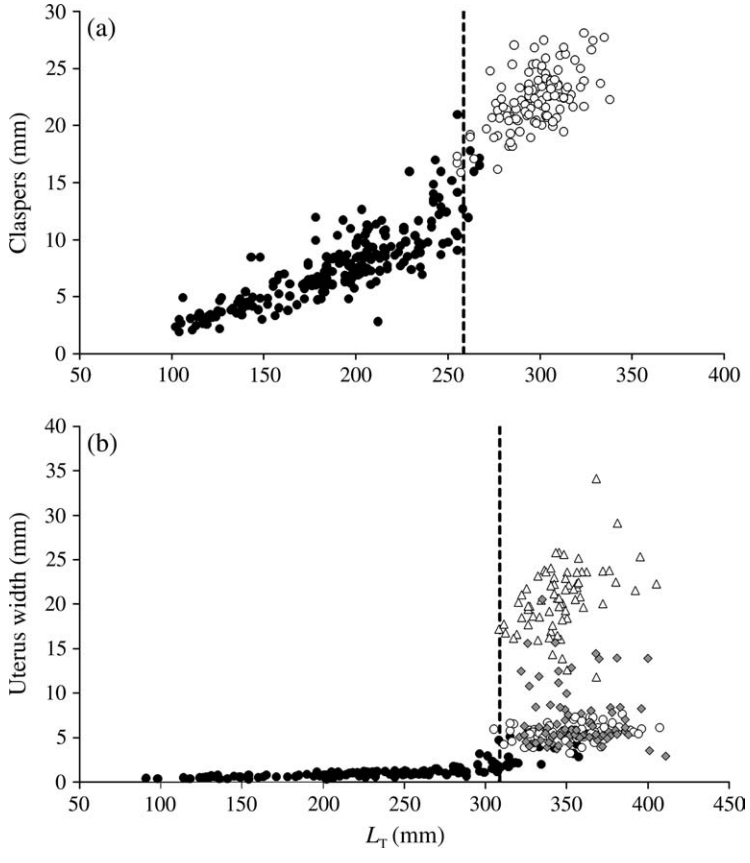

FIG. 7. Relation between total length (L_T) and (a) clasper length in males and (b) uterus width in females of *Etmopterus spinax*. [●, immature specimens (males $n = 217$ and females $n = 133$), ○, mature specimens (males $n = 115$ and females $n = 62$), △, pregnant females ($n = 70$) and ◆, resting females ($n = 78$)]. The L_T at 50% maturity (L_{50}) value estimated by Coelho & Erzini (2005), specifically 253·9 mm for males and 308·6 mm for females is also indicated.

TABLE VI. Total length (L_T) and age mean values (with ranges in parentheses) of mature and immature *Etmopterus spinax*, with the estimated value of age at maturity (A_{50}) with 95% (CI)

		Females	Males
L_T (mm)	Immature	216 (91–362)	190 (102–266)
	Mature	351 (305–411)	297 (242–338)
Age (years)	Immature	2·4 (0–8)	1·9 (0–4)
	Mature	6·2 (4–11)	5·1 (4–8)
A_{50} (years)	Estimate	4·67	3·97
	Lower 95% CI	4·57	3·97
	Upper 95% CI	4·78	3·97
100 $A_{50}/A_{maximum}$%		42·5	49·6

$A_{maximum}$, maximum age (years).

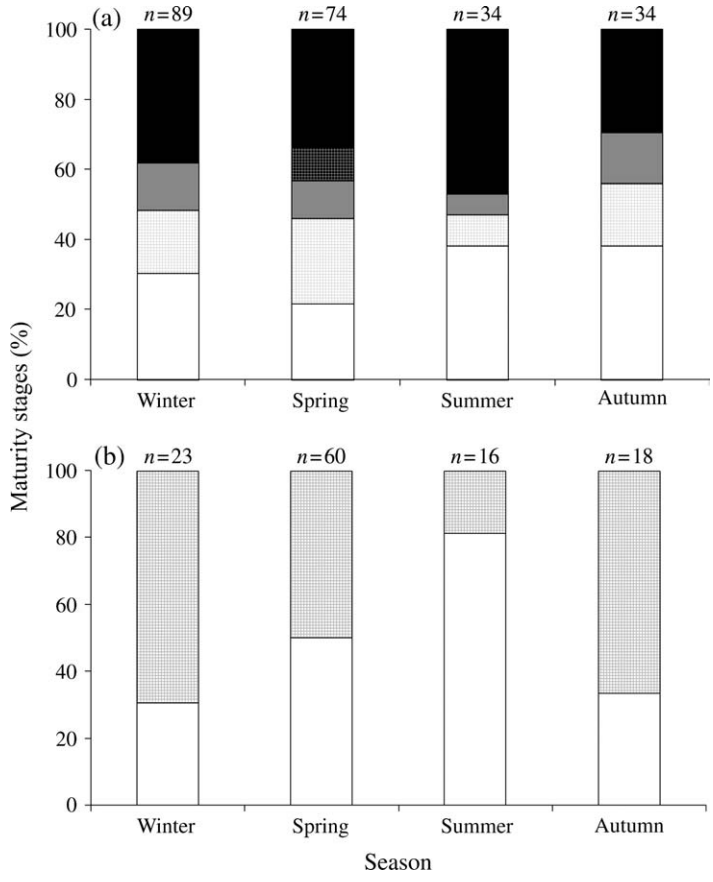

FIG. 8. Seasonal variation of the percentage of occurrence of the different mature stages in (a) female and (b) male *Etmopterus spinax* (□, stage 3, ▒, stage 4, □, stage 5, □, stage 6 and ■, stage 7). n = sample size.

Fifty per cent of the females and the males in this population are mature, respectively, at 42·5 and 49·6% of the maximum observed ages (Table VI).

REPRODUCTIVE CYCLE

The annual variation of the percentage of occurrence of the different maturity stages showed that most of the mature females stages, namely mature females with ripe oocytes (stage 3), pregnant females (stages 4 and 5) and resting females (stage 7) occurred throughout the year. Late-term pregnant females (stage 6) were only caught during June. For males, both mature stages (stages 3 and 4) also occurred throughout the year, although the percentages varied a little, with mature but not active males (stage 3) occurring in higher percentages during the summer months (Fig. 8).

In general, the I_G values for mature females with ripe oocytes were slightly higher during the summer and lower during the rest of the year, even though no statistical differences were detected (ANOVA, d.f. = 10,56, $P > 0{\cdot}05$) (Fig. 9).

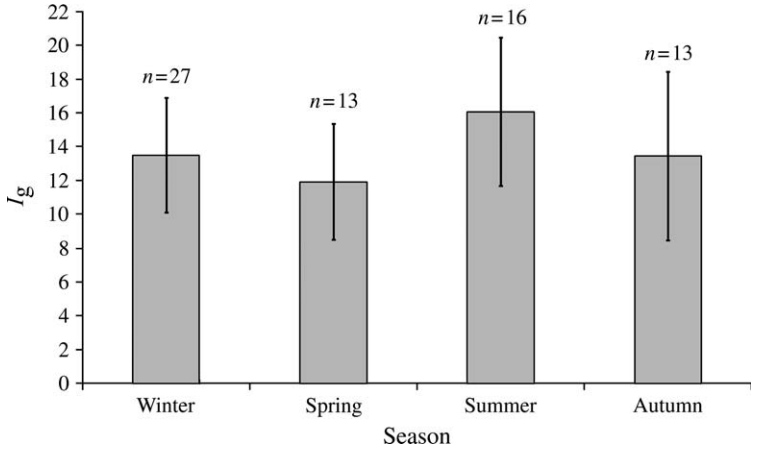

FIG. 9. Seasonal variation of the mean ± S.D. gonado-somatic index (I_G) for mature females with ripe oocytes (stage 3) *Etmopterus spinax*. n = sample size.

A clear pattern in I_G values was observed in the different maturity stages of both males and females (Fig. 10). In females, this index is very low while specimens are immature (stages 1 and 2) and increases to the highest value in stage 3. In pregnant females (stages 4–6), I_G falls again to values similar to those of immature specimens, indicating that this species has an alternate reproductive

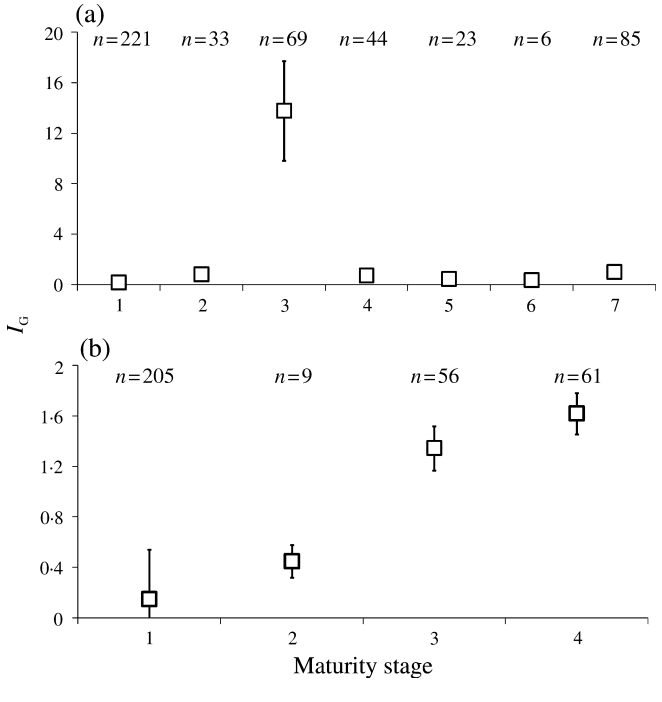

FIG. 10. Changes in the mean ± S.D. the gonado-somatic index (I_G) with maturity stage for both (a) female and (b) male *Etmopterus spinax*. n = the sample size.

cycle, with the ovarian and the uterine phases occurring separately. In this type of reproductive strategy, while females are pregnant the oocytes remain immature and the gonads do not develop, remaining relatively small. In stage 7 females, there is a slight increase of the I_G, reaching values similar to stage 2, probably due to the fact that in some specimens the oocytes are already starting to develop in order to start a new ovarian cycle. Significant differences were found between the I_G values of the different maturity stages (Kruskal–Wallis, d.f. = 6, $P < 0{\cdot}05$). The pair-wise Dunn tests showed that significant differences occurred between stage 3 and all others (Dunn, $P < 0{\cdot}05$ in all cases) and between stage 1 and all others except stage 6 (Dunn, $P < 0{\cdot}05$ in all cases). No differences were detected between the other possible pair-wise combinations (Dunn, $P > 0{\cdot}05$ in all cases). In males, there is an increase of I_G with the evolution of the maturity stages, with the highest differences observed when specimens reach maturity (between stages 2 and 3). Significant differences were found (Kruskal–Wallis, d.f. = 3, $P < 0{\cdot}05$), and according to the pair-wise multiple comparison test, there are significant differences between stage 1 and all other stages (Dunn, $P < 0{\cdot}05$ in all cases) but not between the other pair-wise possible combinations (Dunn, $P > 0{\cdot}05$ in all cases).

A clear pattern of I_H was also observed with changes in maturity stages in both males and females (Fig. 11). In females, this index increases until they reach stage 3 and then, during pregnancy (stages 4–6), it decreases probably due to the high energy demand during these stages. In the resting phase (stage 7), the I_H increases again, probably due to a start of energy accumulation for the next reproductive cycle. The variations in I_H were significant (Kruskal–Wallis, d.f. = 6, $P < 0{\cdot}05$), with the pair-wise tests showing differences between

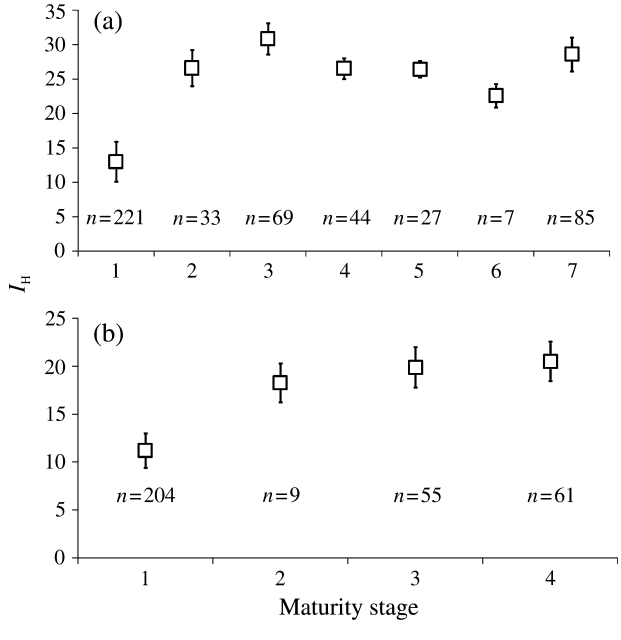

FIG. 11. Changes in the mean ± S.D. the hepato-somatic index (I_H) for (a) female and (b) male *Etmopterus spinax*. n = sample size.

stage 1 and all other stages except stage 6 (Dunn, $P < 0{\cdot}05$ in all cases), but not for the other possible pairs (Dunn, $P > 0{\cdot}05$, in all cases). In males, there is a progressive increase of the I_H with change in the maturity stage, with the differences more accentuated between stages 1 and 2 and more progressive for the other stages. Significant differences were found (Kruskal–Wallis, d.f. = 3, $P < 0{\cdot}05$) between stages 1 and all others (Dunn, $P < 0{\cdot}05$ in all cases) but not between all other possible pairs (Dunn, $P > 0{\cdot}05$ in all cases).

FECUNDITY

The ovarian fecundity in mature (stage 3) females varied from five to 21 ripe oocytes, while the uterine fecundity in mid-term pregnant females (stage 5) was lower and varied from one to 16 embryos (Table VII). Only six pregnant females in final pregnancy (stage 6) were caught, carrying from one to nine completely formed embryos.

A linear relationship between the ovarian fecundity (number of ripe oocytes) and the female L_T was observed (ANOVA, d.f. = 1,81, $P < 0{\cdot}05$), meaning that the fecundity in this species increases with increasing L_T of the females (Fig. 12).

DISCUSSION

Etmopterus spinax has a wide distribution, occurring throughout most of the eastern side of the Atlantic Ocean and the Mediterranean Sea. Lacking any commercial value and commonly discarded in trawl and longline fisheries, it has been poorly studied.

Catches of this species can be very high in the commercial deep water fisheries operating in the study area, and although caught specimens are mostly discarded, they are usually returned to sea either dead or with severe injuries that probably affect their survival. Specimens caught with trawls tend to arrive dead on board, while specimens caught with longlines are often still alive, but with injuries caused by the hooks and by the sudden changes in pressure and temperature. By-catch reduction strategies such as the one proposed by Coelho *et al.* (2003) for longlines might be the only possibility to prevent excessive fishing-related mortality on this and other similar deep-water squalid species.

Although this study included a relatively large sample in number with a wide size range, the maximum sizes caught were considerably smaller that the maximum sizes described by Compagno *et al.* (2005). Specifically, the largest

TABLE VII. Mean ± S.D. and ranges of ovarian and uterine fecundity of *Etmopterus spinax*

	Ovarian (stage 3)	Uterine (stage 5)
Mean ± S.D. fecundity	9·94 ± 2·61	7·59 ± 3·31
Range	5–21	1–16
$n_{specimens}$	83	34
$n_{oocytes\ or\ embryos}$	825	258

$n_{specimen}$, numbers of specimen; $n_{oocytes,\ or\ embryos}$, number of ripe oocytes or mid-term embryos.

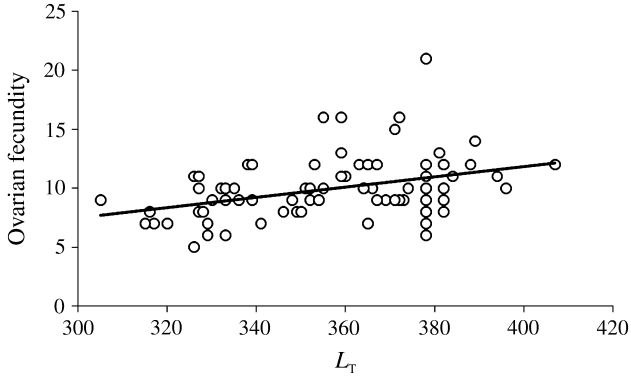

FIG. 12. Relationship between total length (L_T) and the ovarian fecundity (number of ripe oocytes in mature stage 3 females), in *Etmopterus spinax*. The curve was fitted by: $y = 0{\cdot}434x - 5{\cdot}525$ ($n = 83$, $r^2 = 0{\cdot}153$).

females and males in this study with, respectively, 411 and 338 mm L_T were much smaller than the maximum size of 600 mm L_T (rare >450 mm) reported by Compagno *et al.* (2005). Given that during this study, a wide variety of depths and habitats were surveyed, using different commercial and scientific survey fishing gears in different seasons of the year, the lack of larger specimens in the sample probably reflects a lack of specimens in the study area and not a shortcoming of the sampling strategy.

Prior to examination of growth bands, spine growth should be investigated by measuring spine morphometrics (Clarke & Irvine, 2006), and this was accomplished in this study when significant relationships were found between specimen L_T and several spine morphometrics. In addition, relationships between specimen L_T and M_S were also investigated and again, positive and significant relationships were found, thus confirming the relationship between spine and specimen growth.

Given that preliminary investigations showed that the first dorsal spine is often more damaged than the second, age was estimated based only on the inner dentine layer of the second dorsal spine. Irvine *et al.* (2006*a*) estimated ages of *Etmopterus baxteri* Garrick based on both the inner dentine layer and on the exterior bands of the spines and hypothesized that the inner dentine bands may underestimate age of the older specimens. Therefore, future work on *E. spinax* should also investigate the exterior enamel of the spines (Irvine *et al.*, 2006*b*). Even though *E. spinax* is a small-sized species, it has a relatively slow growth rate. Only two other studies are known that have determined growth rates for *Etmopterus* species, specifically Irvine *et al.* (2006*a*) for *E. baxteri* and Coelho & Erzini (2007) for *Etmopterus pusillus* (Lowe) and on both cases, slow growth rates were also detected.

Age validation is an essential aspect of age and growth studies (Cailliet *et al.*, 1986, 2006; Cailliet, 1990; Campana, 2001). In the present study, age was validated by the marginal increment analysis, which is one of the most commonly used techniques (Simpfendorfer, 1993; Conrath *et al.*, 2002; Carlson & Baremore, 2005; Neer & Thompson, 2005*a*). Even though Campana (2001) stated that the marginal increment analysis is not one of the most accurate for age validation,

it was considered that the techniques recommended by Campana (2001) over this analysis are very difficult to apply to *E. spinax*. Such techniques include the release of tagged fish of known age, which implies that the species must be bred in captivity, bomb radiocarbon validation, which implies that at least some specimens must have been born before the 1960s when the ^{14}C in the world oceans increased significantly, or tagging fishes with oxytetracycline, which would be very difficult to undertake. At this point, only one study is known to have validated age on squalid spines based on bomb radiocarbon (Campana *et al.*, 2006). Campana (2001), however, stated that the marginal increment analysis could be used successfully if some suppositions were guaranteed, specifically (1) measuring blindly the structures, without knowledge of the date of capture, (2) observing at least two complete band-forming cycles, (3) making an objective interpretation of the results, ideally with the resource of statistics and (4) analysing few (ideally one) age groups at a time. Given that in the present study, three of these suppositions were respected, with the only shortcoming being that only one, instead of two complete cycles were analysed, it was considered that the age validation procedure used is valid and demonstrates that in this species one pair of bands (one opaque and one translucent) is probably being formed each year. As pointed out by Williams & Bedford (1974), however, the width increments will be dependent on the plane of cutting. Even though care was taken to have a standardized plane of cutting for all the spines, it must be assumed that some error might have occurred due to small differences in the plane of cutting.

Even though the von Bertalanffy growth curve is the most widely used approach to model the growth of fishes (Katsanevakis, 2006), several authors have shown that alternative models have provided better fits to L_T-at-age data of some elasmobranch species. In this study, and even though the VBGF produced good fits, additional growth models were used for comparative purposes. It was concluded that for both sexes, the best fit was achieved by the logistic equation, followed by the Gompertz model, then the VBGF and finally the VBGF with known size at birth. Alternative growth models have been applied in elasmobranchs to both rays (Neer & Thompson, 2005*a*; McFarlane & King, 2006) and sharks (Carlson & Baremore, 2005; Neer & Thompson, 2005*b*). Growth model selection was based on A_{IC} criterion (Shono, 2000) as suggested by Katsanevakis (2006), and the Akaike differences (Δi) used to assess the extent of the contribution of the alternative models. All size-at-age based models, both for males and females produced values of $\Delta i < 2$, meaning that every model tested in this study can explain and support the data and be used for subsequent population dynamics and fisheries models.

The changes in the I_G in stage 3 females throughout the year suggested that it takes 1 year for females to develop the oocytes in the gonads until fertilization occurs in the summer. Although numbers are low, the higher proportion of active males in some winter months suggests that mating could occur at this time, before the oocytes are totally mature, with females storing the sperm. If the ovarian and the uterine cycles do not occur at the same time in pregnant females, meaning that while females are pregnant the oocytes in the gonads remain immature and do not develop for the next cycle, and that resting females (with immature oocytes) were found throughout the year, then this

species may reproduce only once every 2 to 3 years. At this stage, and given the relatively low numbers available for this analysis, this is only an hypothesis and further studies will be necessary to confirm it. If this cycle is verified, then it will have significant implications for management and conservation. Other deep-water squalid sharks have been described to have long gestation periods, such as the cases of *Squalus megalops* (Macleay) (Braccini *et al.*, 2006) that may have a 2 year cycle and the case of *Centrophorus cf. uyato* (McLaughlin & Morrissey, 2005) that may have a 3 year cycle.

Etmopterus spinax in Portuguese waters matures relatively late in its life cycle. Coelho & Erzini (2005) presented results regarding size at maturity for this species and this information is now complemented with age at maturity estimates. Cortés (2000) examined 164 species of sharks and concluded that on average, maturity occurs at *c.* 75% of the maximum size and *c.* 50% of the maximum age and the values obtained during this study are very close to these values. Females of this species seem to mature at significantly larger sizes and older ages than males. Sexual dimorphism in terms of size at maturity is common in elasmobranchs and specifically for the *Etmopterus* genus, with females usually maturing later and at larger sizes than males (Jakobsdottir, 2001; Irvine *et al.*, 2006*a*).

This species is an aplacental viviparous shark with a relatively low fecundity. The differences observed between the ovarian and the uterine fecundities may be explained by two hypotheses: (1) that part of the ripe oocytes present in stage 3 females never develop into embryos or (2) that since this is an aplacental species, without an umbilical cord connecting the mother to the embryos, it is possible that the stress produced during the fishing process leads to the release of some of the embryos in the uterus of pregnant females. During the sampling process aboard the fishing boats, and while the specimens were deposited in boxes for later processing, it was common to observe mid-term embryos in the catch. This observation supports the second hypothesis, indicating that there is indeed a loss of embryos by pregnant females during the fishing process. Therefore, fecundity in this species should be estimated by the ovarian fecundity and not by uterine fecundity since the latter may tend to underestimate this variable.

In this species, a significant linear relationship was observed between the female L_T and the number of ripe oocytes in the gonads. Morphologically, this relationship makes sense given that in viviparous species the number of oocytes in the gonads, and after fertilization, the number of embryos in the uterus, are limited by the size of the abdominal cavity, which increases with increasing specimen size. Other species of deep-water viviparous sharks where such relationships were found include *Centroscymnus owstoni* Garman and *Centroscymnus coelolepis* (Yano & Tanaka, 1988) and *Centroscyllium fabricii* (Reinhardt) (Yano, 1995).

In conclusion, this study suggests that *E. spinax* in the north-east Atlantic Ocean has a vulnerable life cycle, a situation previously described for several other deepwater squalid sharks. In the north-east Atlantic Ocean, several deep water fisheries are in operation and there are no prospects of a decrease of effort or a reduction of the discards in the near future, meaning that presently, this species may already be threatened and facing severe declines in this area.

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