

LIFE HISTORY TRAITS OF THE BLACKSPOTTED SMOOTH-HOUND *MUSTELUS PUNCTULATUS* (CARCHARHINIFORMES: TRIAKIDAE) IN THE ADRIATIC SEA

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We present demographic and reproductive parameters of commercially exploited shark, black-spotted smooth-hound (*Mustelus punctulatus*), based on samples from 117 males and 108 females from the Adriatic Sea. Calculated size and age at maturity were 83.1 cm in total length (TL) and 6.6 years for males and 100.0 cm TL and 12.5 years for females. The oldest observed male and female were 14 and 19 years old, respectively. The Gompertz growth model provided the best fit and predicted a theoretical maximum size (L_{∞}) of 129.3 cm TL and a growth coefficient (k) of 0.15 year⁻¹ for males, and L_{∞} = 141.1 cm TL and k = 0.13 year⁻¹ for females. Obtained life history traits classify smooth-hound as slow-growing species, extremely sensitive to fishing, and highlight the need for the development of management strategy for this vulnerable species.

Key words: age, growth models, reproduction, elasmobranchs, conservation, Mediterranean

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Ovim radom predstavljamo demografske i reproduktivne značajke komercijalno izlovljavanog morskog psa mekušca (*Mustelus punctulatus*), na temelju analize 117 mužjaka i 108 ženki iz Jadranskog mora. Mužjaci postižu spolnu zrelost pri dužini tijela (DT) od 83,1 cm i 6,6 godina, a ženke pri 100,0 cm DT i 12,5 godina. Najstariji mužjak je procijenjen na 14 godina, a najstarija ženka na 19 godina. Gompertzov model najbolje je opisao somatski rast, prema kojem je za mužjake predviđena maksimalna veličina (L_{∞}) od 129,3 cm DT i koeficijent rasta (k) od 0,15 god⁻¹, dok za ženke L_{∞} iznosi 141,1 cm DT, a k = 0,13 god⁻¹. Utvrđene značajke životne strategije određuju mekušca kao spororastuću vrstu izrazito osjetljivu na izlov, pa je stoga potrebno čim prije razviti strategiju upravljanja ovom vrstom morskog psa.

Ključne riječi: starost, modeli rasta, razmnožavanje, hrskavičnjače, zaštita, Sredozemno more

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INTRODUCTION

Elasmobranchs are exploited worldwide, either as the target of specific fisheries or as bycatch in fisheries targeting other more abundant or valuable resources (WALKER, 1998; STEVENS *et al.*, 2000). These K-selected animals have a slow growth rate, late sexual maturity, long life cycle and low reproductive potential, and are hence highly sensitive to exploitation (DULVY & FORREST, 2010).

Although the Mediterranean Sea is considered a biodiversity hot spot for elasmobranchs, it is also the area with the highest proportion of threatened species due to unregulated fishing (BRADAI *et al.*, 2018). Many large predatory sharks in the Mediterranean exhibited some of the most extreme population declines (96–99%, FERRETTI *et al.*, 2008), with serious implications for the entire ecosystem, affecting structure and energetic of marine food webs.

The north-central (NC) Adriatic Sea has the widest continental shelf in the Mediterranean and represents a highly productive region, but also a highly degraded ecosystem, largely due to expanding fishing effort (COLL *et al.*, 2007; COLL *et al.*, 2009; BARAUSSE *et al.*, 2011). Studies on the status of elasmobranch communities in the Adriatic Sea highlight a dramatic decline in elasmobranch landings, loss of large predatory sharks and a shift to a smaller, more productive species (BARAUSSE *et al.*, 2011, 2014; FERRETTI *et al.*, 2013).

Smooth-hounds are medium sized, mesopredatory, demersal sharks, most commonly taken in coastal fisheries, in demersal trawls, longline fisheries and by pelagic fishers using trawls and set nets (JABADO *et al.*, 2021). There are three species of *Mustelus* in the Adriatic Sea (LIPEJ *et al.*, 2004): Smooth-hound, *M. mustelus* (Linnaeus, 1758), blackspotted smooth-hound, *M. punctulatus* (Risso, 1827) and starry smooth-hound, *M. asterias* (Cloquet, 1819), all being classified as 'Vulnerable' on the IUCN's Red List of Threatened Species (JABADO *et al.*, 2021). While *M. asterias* is easily distinguishable, the other two species are morphologically similar, and their landings are typically grouped as "smooth-hounds", without any species-specific data. By analysing the time series data, FERRETTI *et al.* (2013) reported increase in the smooth-hound group (*Mustelus* spp.) catches in the Adriatic following release from predation and competition, and these shark species represented over 60% of the elasmobranchs landings in the Adriatic Sea in early 2000s (BARAUSSE *et al.*, 2014). Recent study, however, showed that the smooth-hounds have overall declined by 80–90% since the beginning of last century (COLLOCA *et al.*, 2017), so that the starry smooth-hound became rare, while there are still large catches of the common and blackspotted smooth-hounds (SERENA *et al.*, 2020). Although smooth-hounds disappeared in a large part of their original distributional range in the Mediterranean in the 1980s and 1990s, viable populations of *M. mustelus* and *M. punctulatus* exist on the extended continental shelves (e.g. north Adriatic, south Tunisia and Libyan coasts, south of Sicily and Malta) and in areas of moderate fishing intensity (e.g. Turkish coast and Libyan waters; COLLOCA *et al.*, 2017).

The blackspotted smooth-hound occurs throughout coastal and continental shelf waters of the Mediterranean Sea with its range extending to the Eastern Central Atlantic. Recent catch data suggested declining trends in the Mediterranean from 2008 to 2012 due to intensive fishing, resulting in a suspected population reduction of 30–49% over the past period of about 50 years (JABADO *et al.*, 2021). It is a poorly inves-

tigated species, and with the exception of some data on foraging and reproductive biology from the central Mediterranean Sea (CAPAPÉ & QUIGNARD, 1977; SAÏDI *et al.*, 2009) and the Adriatic Sea (JARDAS *et al.*, 2007; LIPEJ *et al.*, 2011; GRAČAN & LACKOVIĆ, 2016; GRAČAN *et al.*, 2017; RIGINELLA *et al.*, 2020), there is little demographic information available to guide its management.

Age and growth data, as key factors for estimating the population's status and assessing the risks associated with exploitation, are still largely unknown for the smooth-hounds in the Mediterranean Sea. To our knowledge, only one study reported demographic data for *M. mustelus*, based upon samples from Turkish waters (ÖZCAN & BAŞUSTA, 2018). Moreover, reported aging data from different oceanic basins showed large variations in this genus. For example, Von Bertalanffy growth constants among the smooth-hounds range from 0.11 to 0.70 year⁻¹ for males and from 0.06 to 0.40 year⁻¹ for females (FRANCIS, 1981; FRANCIS & FRANCIS, 1992; GOOSEN & SMALE, 1997). Long-standing commercial use, signs of smooth-hound depletion in the Mediterranean basin, and absence of species-specific biological data provide justification for investigation of this species (JABADO *et al.*, 2021). With this study we provide the first data on demographic traits of *M. punctulatus* in the Mediterranean basin, based upon samples from the Adriatic Sea.

MATERIALS AND METHODS

Sample collection and body morphometry

We sampled 225 *M. punctulatus*, collected by on-board observers on commercial bottom trawls undertaking fishing activities in the North-Central (NC) Adriatic Sea (Fig. 1), at depths between 45–84 m. Samples were collected each month throughout the year, from sharks selected by fishermen for sale, with additional samples obtained from several large catches of smaller animals that were to be discarded as bycatch. Specimens were identified following JARDAS (1996) and LIPEJ *et al.* (2004), sexed by visual inspection of pelvic fins, measured for total body length (TL) and clasper length (CL) and weighed (BW).

We dissected sharks, sampled gonads for reproductive information, fixed them in 10% neutral buffered formalin for 48 h, and stored at 4°C in 70% ethanol. Since smaller animals have undifferentiated gonads enveloped in the epigonal organ, we collected gonads from males larger than 50 cm TL (N = 74) and females larger than 55 cm TL (N = 55). For age estimation analyses, we excised three to five vertebrae from beneath the first dorsal fin, fixed them in 10% neutral buffered formalin for 24 h and stored samples in 70% ethanol until processing.

Histomorphometric analysis of gonads

A cross section from the middle of each gonad was dehydrated through a graded ethanol series (70%, 80%, 96% and 100%), exposed to chloroform and embedded in Paraplast embedding media (Sherwood Medical, USA). Blocks were sectioned on a rotating microtome at 6–8 µm, slides were stained with hematoxylin–eosin and viewed through a light microscope with a digital camera AxioCam ERc 5s (Carl Zeiss Microscopy GmbH, Germany). Histomorphometric measures were performed using software Zen 2 (Carl Zeiss Microscopy GmbH, Germany).

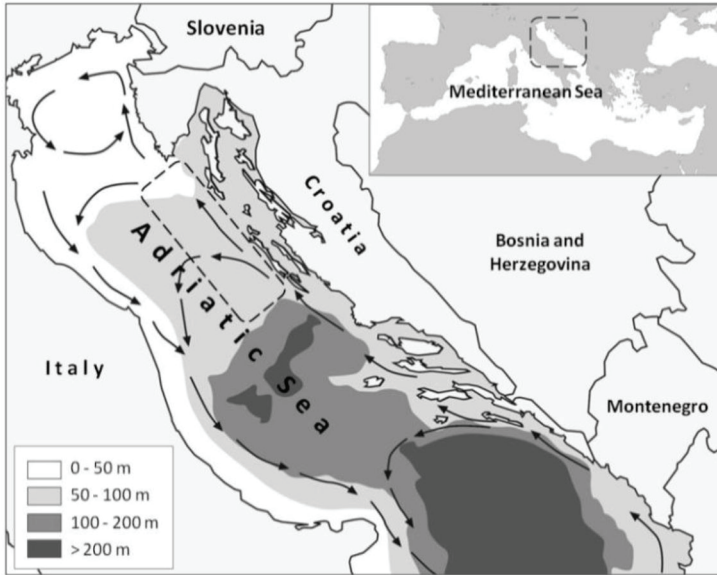


Fig. 1. Map of the Adriatic Sea, with shaded bathymetry and arrows indicating direction of major sea currents. Study area is marked with a dotted rectangle.

Maturity stages of both sexes were divided into three general categories: immature, maturing and mature. Sexual maturity of males was based on macroscopic examination of claspers and microscopic analysis of testes and classification of spermatocysts into seven distinct structural stages (MARUSKA *et al.*, 1996; CONRATH & MUSICK, 2002). Since stages III through VII (stage III, spermatocysts; stage IV, spermatids; stage V, immature sperm; stage VI, mature spermatozoa; stage VII empty spermatocysts) are associated with reproductive readiness (HEUPEL *et al.*, 1999; TRICAS *et al.*, 2000; SULIKOWSKI *et al.*, 2004), we concentrated our analysis on these specific stages.

Females were considered mature if they were gravid or contained oocytes >3 mm in diameter (SAÏDI *et al.*, 2009; FARRELL *et al.*, 2010a; PÉREZ-JIMÉNEZ & SOSA-NISHIZAKI, 2010). When larger eggs were visible in ovaries, they were isolated and macroscopically measured with a digital caliper. Otherwise, the diameter of the five largest observed follicles per single ovary from each specimen were measured on histological slides (without theca layers), with three consecutive measurements of each follicle. The calculated mean size of the five largest follicles within each ovary was regressed against the TL of the females. When pregnant females with developed embryos were collected, we recorded sex, TL and BW for each embryo.

Age and growth dynamics

Vertebrae were soaked in a 10% sodium hypochlorite solution for 20 to 40 min to remove excess connective tissue and haemal arches, washed in tap water for 20–30 min, and air-dried for 24–48 h. One centrum from each specimen was embedded in epoxy resin (Epothin hardener and Epothin Resin, Buehler, USA) and sectioned sagittally through the focus at 0.6–0.7 mm thickness (NATANSON *et al.*, 2006; RIZZO *et al.*, 2006) with a low-speed Isomet Rotary Diamond saw (IsoMet 1000, Buehler, USA).

The radius of each sectioned vertebra (VR) was measured with an ocular micrometer on a stereo microscope (Zeiss Stemi 2000-C, Carl Zeiss Microscopy GmbH, Germany) at 2x magnification, from the focus to the distal margin of the corpus calcareum. Total length was plotted against VR to confirm that the vertebral growth is proportional to somatic growth. The relationship between VR and TL was calculated for the sexes separately and compared using ANCOVA in SPSS 17.0.

Growth bands were defined as band pairs of one optically opaque (calcified) and one translucent (less-calcified) band on the corpus calcareum (CAILLIET *et al.*, 2006), while the birthmark was identified as the change in the angle of the corpus calcareum (GOLDMAN, 2004). Sections from each vertebra were viewed unstained under a microscope and growth bands were counted by two independent readers to assign an age to each specimen (R. Gračan, T. Polak). Readers had no prior knowledge of the size, mass, sex or month of capture during aging. When counts differed between readers, a third reading was performed to reach a consensus. We performed a comparison between the readers using paired t-test in SPSS 17.0. The precision between the two readers was tested by the index of average percent error (IAPE; BEAMISH & FOURNIER, 1981), percent reader agreement (PA) between readings and the $PA \pm 1$ year (GOLDMAN, 2004).

To examine the annual periodicity of ring formation we performed marginal increment ratio (MIR) analysis (GOLDMAN, 2004). The MIR was measured on digital images enhanced in Adobe Photoshop, following recommendations from CAMPANA (2014), as the distance from the last opaque band to the edge of the margin and divided by the width of the last complete band pair (CONRATH *et al.*, 2002). Edge type and mean MIR were both compared against season of collection to determine the timing of opaque and translucent growth zone deposition and to confirm the annual nature of band pair formation. We plotted average MIR only from 2 to 5 year-old sharks, since the centrum edge of older sharks is difficult to interpret due to the proximity of the band pairs.

We evaluated the ability of four different models to characterize growth: the three parameter von Bertalanffy growth function (BEVERTON & HOLT, 1957), the three parameter Gompertz growth function (GOMPERTZ, 1825; RICKER, 1979; WEATHERLEY & GILL, 1987; GOLDMAN, 2004), the three parameter exponential growth function and the three parameter logistic growth function (VERHULST, 1845). The mathematical expressions of these models are found in SEABY & HENDERSON (2006), while the parameters (L_{∞} – theoretical asymptotic length; W_{∞} – theoretical asymptotic weight; t_0 – theoretical age at zero length; k – growth coefficient) and their 95% confidence intervals were estimated using a non-linear regression procedure by means of the Growth II software (ver. 2.1.2.51; PISCES Conservation Ltd, United Kingdom). The Weighted Sum of Squares of Residuals (WSSR) and the Akaike Information Criterion (AIC; AKAIKE, 1983; BURNHAM & ANDERSON, 2002) were calculated using the Growth II software and were used for model selection. We also evaluated the biological accuracy of models by comparing the predicted minimum and maximum length and weight values with the observed minimum and maximum length and weight values of sampled individuals (COTTON *et al.*, 2011).

The percentage of mature individuals per length/age class was estimated for males and females separately. Immature and maturing stages were both considered immature for these analyses. The length ($TL_{50\%}$) and age ($A_{50\%}$) were calculated with

the following functions: $P=[1+e^{-(r(L-L_m))}]^{-1}$ for length, $P=[1+e^{-(r(T-T_m))}]^{-1}$ for age, where P is the proportion mature in each size class, r is a parameter controlling the shape of the curve, L_m is the length at 50% maturity and T_m is the age at 50% maturity (KING, 1995).

While the oldest sharks from our sample provided an initial estimate of longevity, we also calculated age at 95% of L_∞ (longevity in years) using the Gompertz growth function (NATANSON *et al.*, 2006).

RESULTS

We collected 108 females ranging from 43.1 to 136.2 cm TL (mean \pm SD = 76.2 \pm 20.4 cm) and 117 males ranging from 44.6 to 126.5 cm TL (76.1 \pm 20.4 cm). Large females (>100 cm TL) were quite rare in the sample (5.8%; Fig. 2). While sampling was conducted throughout the year, catches were not equally distributed: most of the samples (50.5%) were collected during winter months (December-February), with the species being quite rare in the catches between June and September (5.4%; N = 12). Unequal gender distribution was visible in samples collected during spring, when males were more frequent.

Reproductive characteristics

Immature females (N = 79) had threadlike, undeveloped gonads, which were difficult to visually distinguish from the epigonal organ. Maturing females (N = 15) ranged from 78.6 to 98.5 cm TL and contained vitellogenic follicles (1–3 mm in diameter, filled with yolk). Among 14 mature females (TL range: 100.7–136.2 cm), four were gravid and ranged in size from 114.9 cm to 136.2 cm TL. One, caught during October, carried 27 embryos ranging in size from 12.1 to 14.6 cm TL (average TL: 13.5 \pm 0.7 cm TL) as well as previtellogenic follicles, 3–5 mm in diameter, with no yolk platelets. The other three females, collected in December and January, carried between 14 and 25 embryos each (average TL: 20.5 \pm 1.8 cm) and also contained early vitellogenic follicles (6–8 mm in diameter with individual yolk platelets). We calculated an average fecundity of 22.3 \pm 5.7 pups per litter, while the ratio of female to

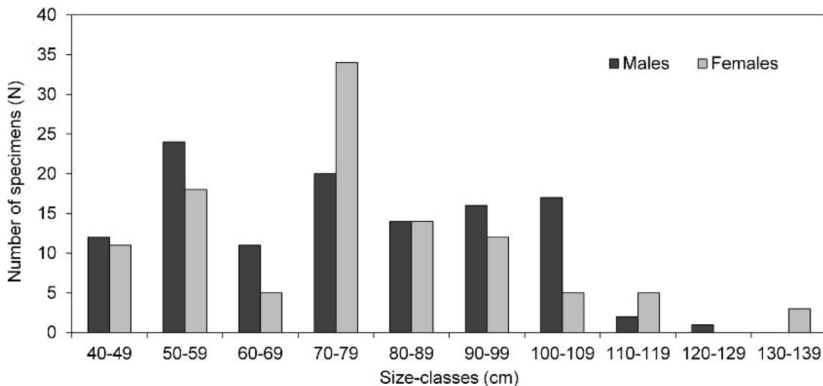


Fig. 2. Length frequency distribution of 225 sampled blackspotted smooth-hounds *Mustelus punctulatus* in the Adriatic Sea.

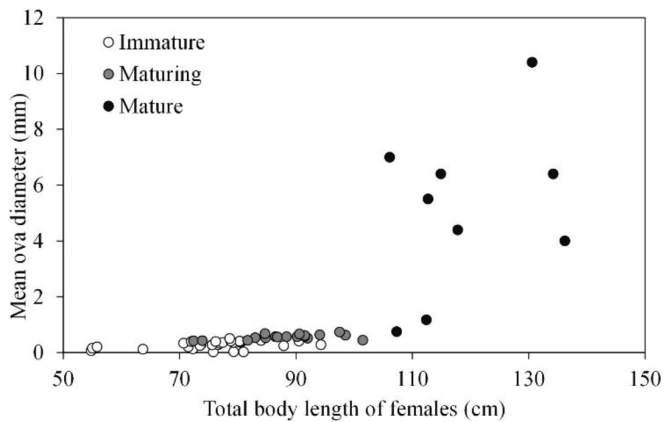


Fig. 3. Relationship between mean diameter of the five largest ovarian follicles and the total body length for female blackspotted smooth-hounds *Mustelus punctulatus* in the Adriatic Sea.

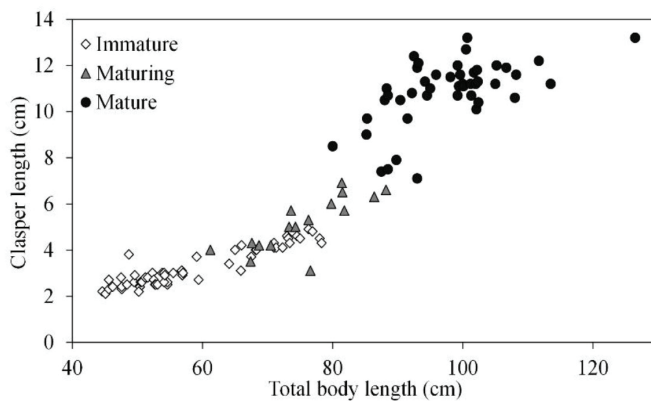


Fig. 4. The relationship between clasper length, maturity and total body length for male blackspotted smooth-hounds *Mustelus punctulatus* in the Adriatic Sea.

male embryos was 1:1.3. The average diameter of the five largest ovarian follicles was positively correlated with TL in females (Fig. 3; Spearman $r_s = 0.825$, $P < 0.001$, $N = 55$). Measured ova of mature females were largest during March (>10 mm) while maximum mean oocyte diameter was the smallest in June (≈ 2 mm).

Juvenile males had small and flexible claspers and undeveloped testes ($N = 56$), while maturing males (61.2 cm to 88.2 cm TL, $N = 16$) had relatively larger claspers (CL range: 3.1 cm to 6.9 cm) and propagating spermatocysts. Mature males (TL range: 80.0 to 126.5 cm, $N = 45$) had fully calcified claspers between 7.1 cm and 13.2 cm (Fig. 4), with spermatocysts in the late stages of spermatogenesis (Stages III-VI). While some of the smallest animals contained only undifferentiated tissue in gonads, most of the animals had visible spermatocysts undergoing different stages of spermatogenesis.

Demographic characteristics

Of the original 225 samples, 201 animals were aged while vertebrae from 24 sharks were unreadable. There were no significant differences in the relationship between vertebral radius and TL between sexes (ANCOVA $F = 0.187$, $P = 0.666$, $N = 187$; Fig. 5), hence, the data for both sexes were combined.

Our results showed that narrow translucent bands were present at the centrum edge during January and February, while broad opaque bands were largest during September and October. The largest decrease in increment was in samples collected in March. Since the seasonal pattern in incremental growth through the remaining months was not large enough to indicate a double band formation (NATANSON *et al.*, 1995), bands were assumed to form once a year. Due to the unbalanced monthly distribution of samples, further statistical analysis was not performed.

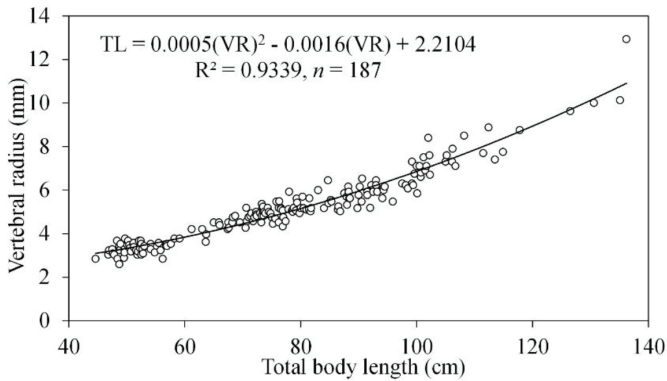


Fig. 5. Relationship between vertebral radius (VR) and total body length (TL) for combined male and female blackspotted smooth-hounds *Mustelus punctulatus* in the Adriatic Sea.

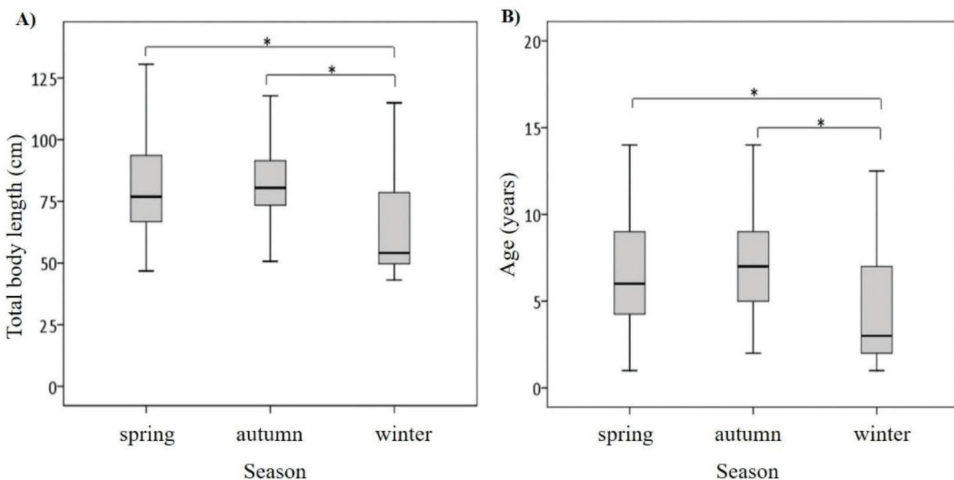


Fig. 6. Box-and-Whisker Plot comparison of A) total body length distribution and B) estimated age distribution by seasons for blackspotted smooth-hounds *Mustelus punctulatus* in the Adriatic Sea. The center line represents the median, while the boxes are lower and upper quartiles. *Significant statistical difference between the two groups.

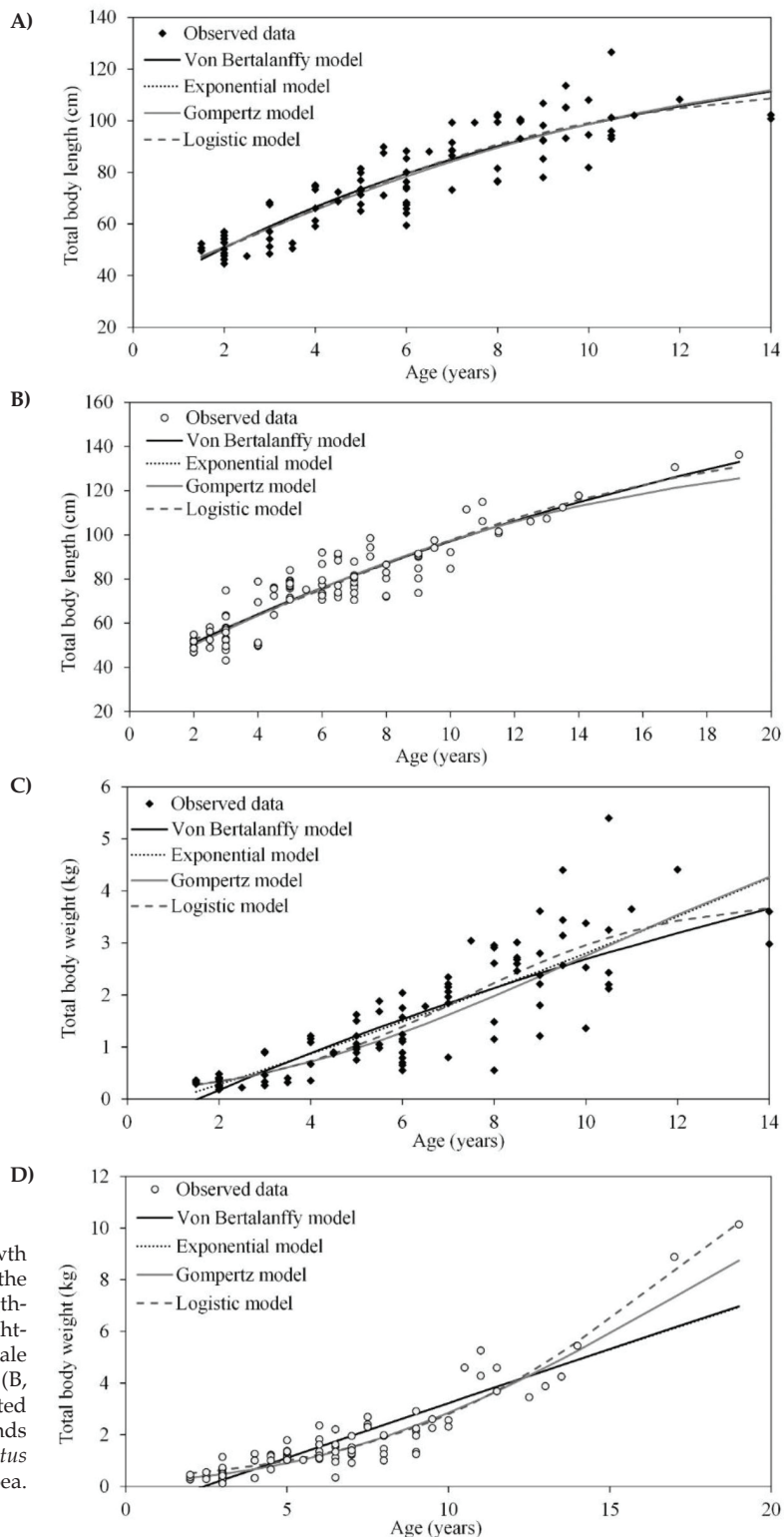


Fig. 7. Growth functions fitted to the observed length-at-age and weight-at-age data for male (A, C) and female (B, D) blackspotted smooth-hounds *Mustelus punctulatus* in the Adriatic Sea.

A paired t-test demonstrated no significant difference in age determination between two readers ($t = -1.372$, $P > 0.10$), with a high level of precision (IAPE = 2.20%, PA = 64.9%, PA \pm 1 year = 86.3%). Estimated ages ranged from 2 to 19 years, with the oldest male aged 14 and the oldest female at 19 years. The estimated age structure showed that 54.2% of studied animals ranged from 2 to 7 years. We did not record the young of the year (age 0+) and age 1+ animals. Within mature animals (29.4% of the sample), the youngest male was aged 7 years while the youngest female was 11 years old. When estimated age distribution was compared among seasons, it was visible that older and larger animals were dominant in the area during spring and autumn, while younger and smaller sharks were more frequent in the sample throughout the winter (Fig. 6).

Among the four models fitted to length-at-age and weight-at-age data, the logistic model provided the best statistical fit (smallest WSSR and AIC values) for length-at-age and weight-at-age data for males and weight-at-age data for females. However, this model produced lower L_{∞} values than observed and conversely yielded the highest k values for both sexes. Thus, the logistic model did not provide biologically realistic results (Fig. 7). The Gompertz model, on the other hand, provided the biologically most sounded estimates of the minimum and maximum length and weight values, a second best statistical fit for length-at-age data for males and weight-at-age data for females, and was consistent between length-at-age and weight-at-age values (Tab. 1). This model predicted a L_{∞} of 129.3 cm TL and a k of 0.15 year⁻¹ for males, and L_{∞} = 141.1 cm TL and k = 0.13 year⁻¹ for females.

All four models showed differences in growth between sexes (Fig. 7). Both sexes showed similar growth for the first four years (<70 cm TL), while afterward, females showed a lower growth coefficient and a larger maximum size in comparison to males. Sexual maturity followed the same pattern: males matured at a smaller size and younger age than females. Length at 50% maturity (L_{50}) was estimated at 83.1 cm TL for males and 100.0 cm TL for females, while age at 50% maturity (A_{50}) was estimated at 6.6 years for males and 12.5 years for females (Fig. 8). Maximum observed age was 14 years for males and 19 years for females, whilst calculated longevity estimate (age at 95% of L_{∞}), based on Gompertz model, was 22 years for males and 26 years for females.

DISCUSSION

The length range of the specimens in the present study (43.1–136.2 cm TL) was similar to that reported previously from the Adriatic Sea (69.5 to 111.3 cm, JARDAS *et al.*, 2007; 50–135 cm TL, LIPEJ *et al.*, 2011), while SAÏDI *et al.* (2009) had smaller sharks (25–122 cm TL) from the central Mediterranean. Lack of the smallest (<43 cm TL) and youngest (0+ and 1+ year) animals in our study indicates that either nursery grounds for neonates and age 1+ sharks are outside the study area, probably somewhere in nearshore waters, or our gear was not effective at sampling this size class. The estimated length at birth in the present paper (30–35 cm TL) coincides with the findings from *Mustelus* spp. studies elsewhere in the Mediterranean, in which newborn pups range in size from 25 to 40 cm TL (CAPAPÉ & QUIGNARD, 1977; CAPAPÉ *et al.*, 1996; SAÏDI *et al.*, 2008; SAÏDI *et al.*, 2009).

Due to the small number of mature females and absence of samples during the summer months, some reproductive characteristics remain unanswered. Previous

Tab. 1. Estimated parameters and model selection criterion for the four growth models of length-at-age and weight-at-age data for male and female blackspotted smooth-hounds *Mustelus punctulatus* in the Adriatic Sea. Numbers in parentheses are 95% confidence intervals (CI) for parameter estimates. WSSR, weighted sum of squared residuals; AIC, Akaike Information Criterion for each model fit

| | Growth models | Estimated parameters | | | | Model diagnostics | |
|-------------|-------------------|-------------------------------|-------------------------------|---------------------------------------|-------|-------------------|-------|
| | | L_{∞} (cm) (95% CI) | W_{∞} (kg) (95% CI) | k (year ⁻¹) (95% CI) | t_0 | WSSR | AIC |
| Males | <i>Age-length</i> | | | | | | |
| | von Bertalanffy | 136.39 (2.18) | | 0.10 (2.187) | -2.53 | 7103.2 | 884.0 |
| | Gompertz | 129.29 (1.07) | | 0.15 (0.31) | | 7051.7 | 883.2 |
| | Exponential | 136.39 (2.19) | | 0.10 (0.004) | | 7103.9 | 884.0 |
| | Logistic | 114.52 (0.78) | | 0.26 (0.004) | | 6884.7 | 880.9 |
| | <i>Age-weight</i> | | | | | | |
| | von Bertalanffy | | 9.03 (11.84) | 0.04 (0.066) | 1.53 | 37.6 | 365.0 |
| | Gompertz | | 7.66 (1.26) | 0.14 (0.10) | | 37.4 | 364.4 |
| Exponential | | 12.68 (36.82) | 0.02 (0.058) | | 36.7 | 362.6 | |
| Logistic | | 3.86 (0.74) | 0.44 (0.11) | | 34.1 | 355.3 | |
| Females | <i>Age-length</i> | | | | | | |
| | von Bertalanffy | 208.37 (6.86) | | 0.04 (0.002) | -4.49 | 5923.6 | 892.0 |
| | Gompertz | 141.10 (1.07) | | 0.13 (0.233) | | 6169.3 | 896.2 |
| | Exponential | 208.37 (6.86) | | 0.04 (0.002) | | 5923.6 | 892.0 |
| | Logistic | 146.81 (1.56) | | 0.16 (0.002) | | 6197.0 | 896.6 |
| | <i>Age-weight</i> | | | | | | |
| | von Bertalanffy | | 18.89 (21.95) | 0.003 (0.03) | 2.43 | 52.0 | 409.5 |
| | Gompertz | | 12.08 (1.33) | 0.11 (0.067) | | 38.3 | 377.7 |
| Exponential | | 20.02 (24.59) | 0.004 (0.03) | | 53.0 | 410.9 | |
| Logistic | | 16.31 (5.34) | 0.23 (0.03) | | 25.5 | 336.2 | |

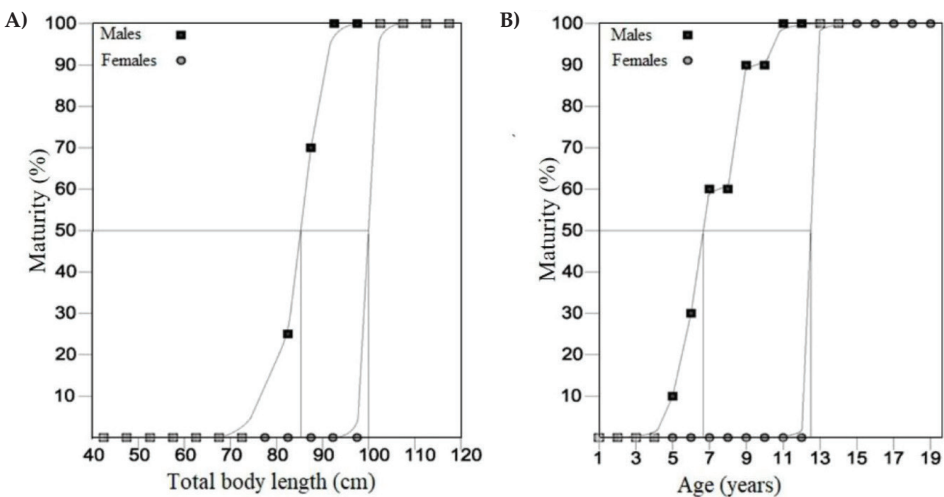


Fig. 8. Relationship between the proportion of sexually mature specimens and A) total body length and B) age for male (black squares) and female (grey circles) blackspotted smooth-hounds *Mustelus punctulatus* in the Adriatic Sea.

records of reproductive events for *Mustelus* in the Mediterranean suggest the timing of parturition between April and June, a 12-month oocyte development period and an 11–12 month gestation period (CAPAPÉ & QUIGNARD, 1977; CAPAPÉ *et al.*, 1996; SAÏDI *et al.*, 2008; SAÏDI *et al.*, 2009; RIGINELLA *et al.*, 2020). Developmental stages of recorded embryos along with the observed trend of oocyte growth and differences in age distribution among seasons provide evidence that similar reproductive cycle occurs also in the study area of the Adriatic Sea.

Sexual dimorphism in growth has previously been observed for *M. punctulatus* in the Mediterranean (CAPAPÉ & QUIGNARD, 1977; CAPAPÉ *et al.*, 1996; SAÏDI *et al.*, 2009) and for other species in the genus *Mustelus* (SMALE & COMPAGNO, 1997; YAMAGUCHI *et al.*, 1997; CONRATH & MUSICK, 2002; ODDONE *et al.*, 2005; SAÏDI *et al.*, 2008). Although males and females from the present paper showed similar body lengths and weights, we recorded differences in size- and age-at-maturity, growth coefficients and longevity. These differences in biological traits emphasize the need for growth rates to be analysed separately for sexes (CAILLIET *et al.*, 1983).

The length at 50% maturity for *M. punctulatus* in the present study ($TL_{50\%} = 83.1$ cm for males and 100.0 cm for females) is similar to that found from the Gulf of Gabès (Tunisia) where $TL_{50\%}$ was 81.4 cm for males and 95.6 cm for females (SAÏDI *et al.*, 2009), and with study on *M. mediterraneus* (considered to be synonymous to *M. punctulatus*; COMPAGNO, 1984) from Senegalese waters (males 83 cm TL, females 91 cm TL, CAPAPÉ *et al.*, 1996), while slightly higher values (91.3 cm for males and 109.9 for females) are reported for sharks sampled in the north-western Adriatic (RIGINELLA *et al.*, 2020). These variations may be related to differences in methodology, since maturity was mainly assessed by visual, macroscopic examination of reproductive organs and tracts, while the present study combined both microscopic and macroscopic approaches. However, results from a study carried out more than 40 years ago in Tunisian waters indicate larger size sharks, with maximum observed length of 182 cm TL for males and 191 cm TL for females, and size-at-maturity of 90 cm TL for males and between 100 and 120 cm TL for females (CAPAPÉ & QUIGNARD, 1977). Although it is possible that species identification before the development of genetic and standardized morphological tools is questionable, and some variations in size values may be contributed to the life-history plasticity of the species, these results may also indicate that current populations are responding to overfishing, by shifting in length composition to smaller sizes. Since elasmobranchs are particularly vulnerable to overexploitation due to their K-selected life-history traits, changes in species abundance may easily alter their size structure and population parameters (STEVENS *et al.*, 2000).

Previous studies have demonstrated that the age of *Mustelus* spp. can be successfully determined by enumerating calcified concentric layers (band pairs) in the vertebral centra (GOLDMAN, 2004). Bands formed during summer are opaque and calcified, whereas those formed during winter are translucent and less calcified (CAILLIET *et al.*, 1983). Our results of MIR suggested an annual pattern in band formation, which agrees with previous studies. However, due to the low sample size in summer, complete verification of the annual banding pattern was not possible and should be made in future studies.

Evaluating the use of multiple growth models is important in describing the growth of a species (CAILLIET *et al.*, 2006). Previous age and growth studies have esti-

Tab. 2. Comparison of estimated parameters for different growth models used for *Mustelus* spp. stocks. L_{∞} , theoretical asymptotic length; k , growth coefficient; t_0 , theoretical age at zero length (literature sources: 1 – MOULTON *et al.* (1992); 2 – FARRELL *et al.* (2010b); 3 – CONRATH *et al.* (2002); 4 – FRANCIS & FRANCIS (1992); 5 – TANAKA & MIZUE (1979); 6 – YAMAGUCHI *et al.* (1996); 7 – GOOSEN & SMALE (1997); 8 – Present study)

| Species | Locality | Males | | | Females | | | Literature source |
|------------------------|----------------------------|-------------------|---------------------------|-------|-------------------|---------------------------|--------|-------------------|
| | | L_{∞} (cm) | k (year ⁻¹) | t_0 | L_{∞} (cm) | k (year ⁻¹) | t_0 | |
| <i>M. antarcticus</i> | Southern Australian waters | 155.9 | 0.16 | -1.94 | 233.6 | 0.09 | -2.05 | 1 ^a |
| <i>M. asterias</i> | Northwest Atlantic | 103.7 | 0.20 | | 123.5 | 0.15 | | 2 ^b |
| <i>M. canis</i> | Northeast Atlantic | 105.2 | 0.44 | -1.52 | 123.6 | 0.29 | -1.94 | 3 ^a |
| <i>M. lenticulatus</i> | New Zealand, Pacific Ocean | 161.1 | 0.11 | -1.91 | 87.0 | 0.40 | 0.68 | 4 ^a |
| <i>M. manazo</i> | East China Sea | 71.4 | 0.70 | -0.73 | 88.6 | 0.38 | -1.113 | 5 ^a |
| <i>M. manazo</i> | Tokyo Bay, Pacific Ocean | 124.1 | 0.12 | -2.59 | 134.1 | 0.11 | -2.55 | 6 ^a |
| <i>M. mustelus</i> | Indian Ocean, South Africa | 145.1 | 0.12 | -2.14 | 204.9 | 0.06 | -3.55 | 7 ^a |
| <i>M. punctulatus</i> | Adriatic Sea | 129.3 | 0.15 | | 141.1 | 0.13 | | 8 ^b |

^a – Three parametric von Bertalanffy growth model.

^b – Gompertz growth model.

mated a wide range of values of k for genus *Mustelus*, from 0.1 to 0.695 year⁻¹ for males and from 0.06 to 0.42 year⁻¹ for females (TANAKA & MIZUE, 1979; YUDIN & CAILLIET, 1990; FRANCIS & FRANCIS, 1992; MOULTON *et al.*, 1992; YAMAGUCHI *et al.*, 1996; GOOSEN & SMALE, 1997; CONRATH *et al.*, 2002). When compared to other species from the genus, *M. punctulatus* is among the larger, slower-growing (Tab. 2), later-maturing and longer-lived species (Tab. 3). However, it must be taken into consideration that the use of different growth models, reader accuracy, reading precision and limitations in sample size may have a significant effect on the calculated growth coefficients (CAILLIET *et al.*, 2006). Previous studies often used only the von Bertalanffy model in ageing studies, whereas new recommendations emphasize the use of multiple models and point out constraints of the von Bertalanffy model (CAILLIET *et al.*, 2006). It is possible that the use of inadequate growth models in previous papers may have contributed to differences in reported values for the growth coefficient (Tab. 2). Among the four growth models employed in the present study, the Gompertz model was the most appropriate for describing growth in *M. punctulatus* in the Adriatic Sea. Models like Gompertz suppose acceleration and deceleration in the growth rate, and assume that younger individuals exhibit faster growth while matures have higher energy demands and invest more in reproduction, migration and feeding (ARAYA & CUBILLOS, 2006).

Longevity in the present paper was estimated to be 14 and 22 years for males and females, respectively, which is generally older than estimates obtained for smaller species like *M. asterias* (13–18 years, FARRELL *et al.*, 2010b) and *M. canis* (10–16 years,

Tab. 3. Comparison of life history traits for some species in genus *Mustelus* (literature sources: 1 – MOULTON *et al.* (1992); 2 – FARRELL *et al.* (2010a, b); 3 – YUDIN & CAILLIET (1990); 4 – CONRATH & MUSICK (2002); 5 – CONRATH *et al.* (2002); 6 – FRANCIS & Ó MAOLAGÁIN (2000); 7 – GOOSEN & SMALE (1997); 8 – SMALE & COMPAGNO (1997); 9 – RIGINELLA *et al.* (2020); 10 – ÖZCAN & BAŞUSTA (2018); 11 – RIGBY *et al.* (2016) ; 12 – Present study)

| Species | Locality | Males | | | Females | | | Literature source |
|------------------------|-----------------------------------|-----------------------|-------------------------|----------------------------|-----------------------|-------------------------|----------------------------|-------------------|
| | | Size-at-maturity (cm) | Age-at-maturity (years) | Observed longevity (years) | Size-at-maturity (cm) | Age-at-maturity (years) | Observed longevity (years) | |
| <i>M. antarcticus</i> | Southern Australian waters | 95 | 4-5 | 15 | 110 | 4-6 | 16 | 1 |
| <i>M. asterias</i> | Northeast Atlantic Ocean | 78 | 4-5 | 13 | 87 | 6 | 13 | 2 |
| <i>M. californicus</i> | Central California, Pacific Ocean | 61 | 1-2 | 6 | 70 | 2-3 | 9 | 3 |
| <i>M. canis</i> | Northwest Atlantic Ocean | 86 | 2-3 | 10 | 102 | 4-5 | 16 | 4, 5 |
| <i>M. henlei</i> | Central California, Pacific Ocean | 59 | 3 | 7 | 57 | 2-3 | 13 | 3 |
| <i>M. lenticulatus</i> | New Zealand, Pacific Ocean | 85 | 5-6 | >8 | 100 | 7-8 | 12.1 | 6 |
| <i>M. mustelus</i> | South Africa, Indian Ocean | 95-110 | 6-9 | 17 | 125-140 | 12-15 | 24 | 7, 8 |
| <i>M. mustelus</i> | Adriatic Sea | 108.1 | | | 121.2 | | | 9 |
| <i>M. mustelus</i> | Gulf of Iskenderun, Mediterranean | 92 | 7 | | 109 | 8 | | 10 |
| <i>M. walkeri</i> | New Zealand | 67-80 | 7-9 | 9 | 83-101 | 10-14 | 16 | 11 |
| <i>M. punctulatus</i> | Adriatic Sea | 91.3 | | | 109.9 | | | 9 |
| <i>M. punctulatus</i> | Adriatic Sea | 83.1 | 6.6 | 14 | 100.0 | 12.5 | 19 | 12 |

CONRATH *et al.*, 2002), but fits well with reported longevity for slightly larger species like *M. mustelus*, which has an estimated maximum lifespan of 17 years for males and 24 years for females (GOOSEN & SMALE, 1997; Tab. 3).

Mustelus spp. dominated in the landings of elasmobranchs in the north Adriatic (BARAUSSE *et al.*, 2014) and this genus was so far presented as rather resilient to harvesting pressures (WALKER, 1992; FRANCIS & SHALLARD, 1999). However, obtained life history traits combined with reported long-term landings of immatures and the scarcity of large mature females in the northern Adriatic Sea (BARAUSSE *et al.*, 2014), suggest that current fishery practice for *M. punctulatus* in the Adriatic Sea may be unsustainable. Smooth-hounds exhibited serious decline in the Mediterranean and their IUCN status as Vulnerable (JABADO *et al.*, 2021) highlight the need for urgent conservation management measures for remaining populations.

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SUMMARY

Life history traits of the Blackspotted smooth-hound *Mustelus punctulatus* (Carcharhiniformes: Triakidae) in the Adriatic Sea

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We estimate demographic and reproductive parameters of the threatened and commercially exploited blackspotted smooth-hound (*Mustelus punctulatus*), based on samples from 117 males (44.6–126.5 cm total length, TL) and 108 females (43.1–136.2 cm TL) from the Adriatic Sea. Calculated size and age at 50% maturity were 83.1 cm TL and 6.6 years for males and 100.0 cm TL and 12.5 years for females. The oldest observed male and female were 14 and 19 years old, respectively. We employed four different growth models to the observed length-at-age and weight-at-age data in order to analyse their ability to fit size-at-age data. Considering the statistical criteria and biological accuracy, the Gompertz model provided the best fit and predicted a theoretical maximum size (L_{∞}) of 129.3 cm TL and a growth coefficient (k) of 0.15 year⁻¹ for males, and $L_{\infty} = 141.1$ cm TL and $k = 0.13$ year⁻¹ for females. These life history traits combined with reported long-term landings of immatures and the scarcity of large mature females imply that current fishery practice in the Adriatic Sea may not be sustainable and highlight the need for urgent development of management strategy for this vulnerable species.