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Reproductive biology of the Bluntnose sixgill shark *Hexanchus griseus* (Bonnaterre, 1788) (Chondrichthyes: Hexanchidae) from the Mediterranean Sea: a review

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Adult bluntnose sixgill shark (Hexanchus griseus) *males and females from the Mediterranean were over 3000 mm TL and 3940 mm. Size at birth was 556-680 mm TL. Ripe oocytes ranged between 68 and 75 mm TL (mean 71.71±2.6) in diameter and 127-147 g (mean 134±8.4) in weight. The reproductive cycle lasted at least one year, but probably more. The chemical balance of development (dry weight of newborn pup/dry weight of ripe oocyte) was 3. One adult female contained 57 ripe oocytes; a second contained 100.* Hexanchus griseus *is probably able to live and reproduce in the Mediterranean Sea, however, further observations are needed to confirm that a sustainable bluntnose sixgill shark population has been established here, especially off the Maghrebin coast.*

Key words: Chondrichthyes, Hexanchidae, *Hexanchus griseus*, reproductive biology, Mediterranean Sea, Maghrebin shore

INTRODUCTION

The bluntnose sixgill shark *Hexanchus griseus* is widely distributed in temperate and tropical waters. It can be found in the Pacific and Indian Oceans, off the eastern and western Atlantic coasts, and in the Mediterranean Sea (BASS *et al*., 1975). A historical survey of Mediterranean reports since 1892 showed that *H. griseus* has been captured in restricted areas, more commonly in the western than in the eastern basin (CAPAPÉ *et al*., 2003a).

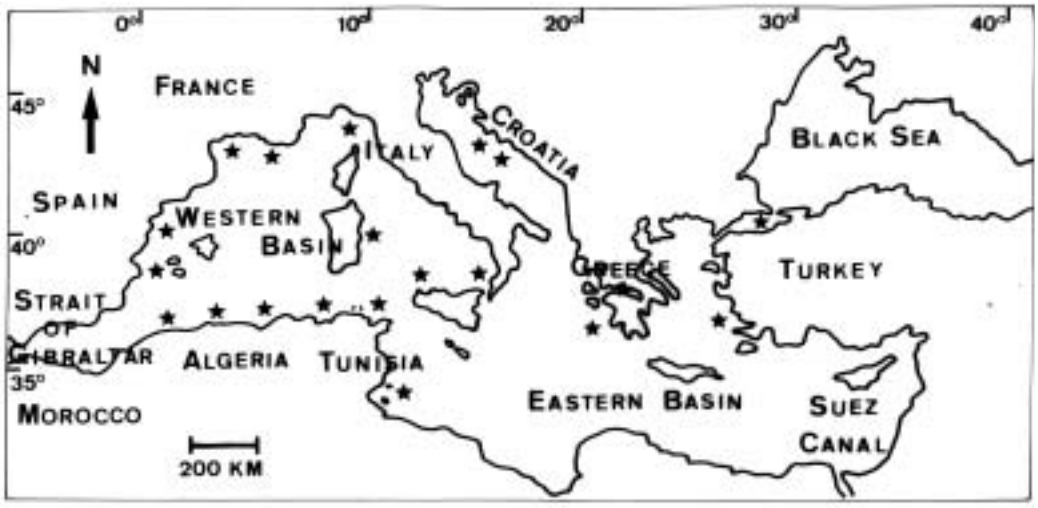

Fig. 1. Mediterranean fishing sites (*) where Hexanchus griseus *in our samples were captured*

The biology of *H. griseus* in the Mediterranean is poorly known and there is little published information that deals with ichthyological treatises (CAPAPÉ *et al*., 2003a). Review of records of specimens collected from the coasts of France, Spain, Italy, Malta, Algeria and Tunisia provide the opportunity to increase our current knowledge on the reproductive biology of the Mediterranean *H. griseus* and compare it with *H. griseus* in other marine areas (VAILLANT, 1901; DESBROSSES, 1938; BIGELOW & SCHROEDER, 1948; EBERT, 1986a,b, 1990, 1996, 2002).

MATERIALS AND METHODS

Our paper is based on a literature review and observations conducted off the Maghrebin shore (the Algerian and Tunisian coasts). It comprises 167 Mediterranean bluntnose sixgill shark records (Fig. 1).

Fifty-nine specimens were from the northern coast including six caught off France, 32 off Spain, 20 in the Italian Seas and one off Malta. Ten specimens, captured by trawling and longlines between 1976 and 2002, were recorded off the southern Mediterranean coast near Tunisia. Another 98 specimens were captured between 1996 and 2002 by longlines at a depth of 30-700 m off the Algerian coast (Fig. 2). Unfortunately, they were eviscerated by fishermen when landed on the boat deck.

The specimens caught off Sète (France) and the Maghrebin shore were measured to

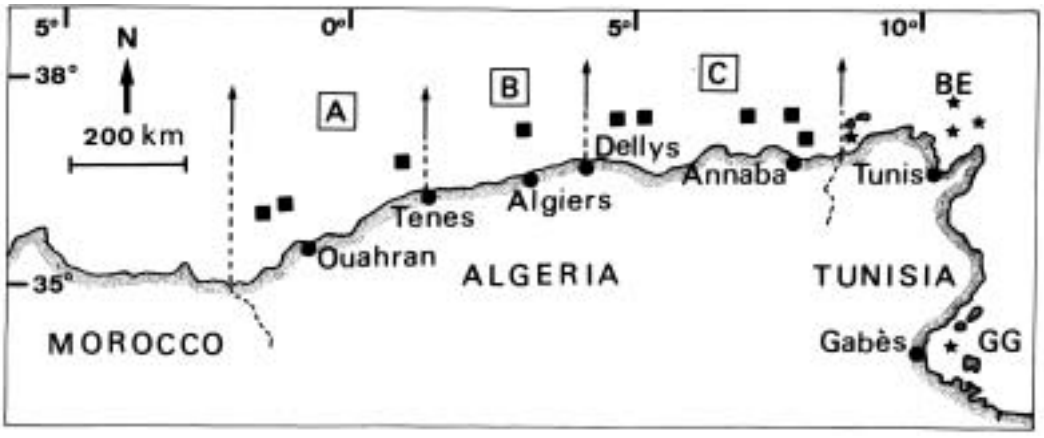

Fig. 2. The Maghrebin shore (redrawn from Capapé et al., 2003), showing where one or more Hexanchus griseus *were captured. Squares - off the Algerian coast; stars - off the Tunisian coast; A - eastern area; B - central area; C - western area; BE - Bank of Esquerquis; GG - Gulf of Gabès*

the nearest millimeter for total length (TL) following BASS *et al.* (1975; STEVENS & LYLE (1989) and weighed to the nearest gram. The clasper (Fig. 3) was measured following COLLENOT (1969).

Morphological structures of bluntnose sixgill shark claspers were compared with those

Fig. 3. Clasper of a Hexanchus griseus *caught off the Algerian coast (photo F. Hemida)*

of closely related species such as the sharpnose sevengill shark *Heptranchias perlo* studied by TANAKA *et al.* (1975), CAPAPÉ (1980) and FRENTZEL-BEYNE & KÖSTER (2002) and the sevengill shark *Notorynchus cepedianus* by EBERT (1986b).

Onset of sexual maturity in males was determined by the relationship between clasper length (CL, mm) and TL following BASS *et al.* (1975) and STEVENS & LYLE (1989) who noted that claspers of juveniles are short and flexible and adult claspers are rigid, elongated and calcified. In addition, aspects of the testes and the genital organs were examined. The size of females at sexual maturity was determined by the condition of the ovaries and the morphology of the reproductive tract. Males and females were classified into two categories, juveniles and adults.

To investigate embryonic development and the role of the female during gestation, a chemical balance of development (CBD) was calculated according to CBD = mean dry weight of newborn pups/ mean dry weight of fertilized eggs or ripe oocytes. Standard values for water content are 50% in ripe oocytes and 75% in new born pups, based on chemical analyses of the small spotted catshark, *Scyliorhinus canicula* by MELLINGER & WRISEZ (1989). CBD is a tentative estimate.

The relationships between eviscerated weight or total weight and total length were studied. The linear regression was expressed in decimal logarithmic coordinates. Correlations were assessed by least-squares regression. Comparisons of curves were made by ANCOVA.

RESULTS

Onset of sexual maturity in males

The following observations were made on males captured off France, Tunisia and Algeria. During the juvenile stage, the males had short flexible claspers and the testes and genital duct were membranous and undeveloped. At the beginning of maturation, the claspers became elongated and rigid and the testes increased in size. In adults, the clasper sheath was very developed and a mucus substance was elaborated at the clasper tip, which transferred into a pocket or expansion of the clasper. The

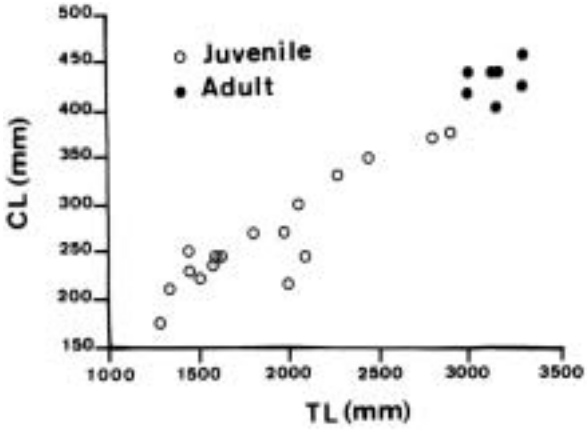

Fig. 4. Clasper-length (CL) vs total length (TL) in Hexanchus griseus *from the Mediterranean Sea*

mucus contained spermatozoa. The testes were developed, and spermatocysts were visible. The genital duct was conspicuously developed and the *ductus deferens* (*sensu* HAMLETT *et al*., 1999) was clearly twisted. The clasper length vs total length is plotted in Fig. 4. Together with the above observations, we suggest that males reached adulthood at 3000 mm TL. Forty-four specimens were juveniles and seven were adults.

Onset of sexual maturity in females

Juvenile females had whitish ovaries with microscopic oocytes and inconspicuous oviducal glands. The smallest juvenile was a newborn pup. Females entering the maturation stage had translucent oocytes and a differentiated genital duct. They were 3000-3500 mm TL. The smallest adult female was caught in Tunisian waters. It was less than 3000 mm and contained developing oocytes. A second female was 3940 mm TL and contained ripe oocytes. All females over 4000 mm TL were adult. Of the 117 observed females, 95 were adult and 2 were juvenile.

Size and mass at birth

Eight small free-swimming specimens, five off Spain and three off France, ranged 556-680 mm TL (CAPAPÉ *et al*., 2003a). Two specimens caught off Sète (France), 625 and 603 mm TL and 860 and 785 g (CAPAPÉ *et al*., 2000b), had unhealed scars on the ventral surface and a residual vitellin vesicle; they probably were neonates. Of the 35 specimens from Spain, one caught off Marbella was 556 mm TL (LOZANO REY, 1928) and another caught off Barcelona was 560 mm TL (BARRULL & MATE, 2000). Their sizes suggest they also were neonates.

Weight-total length relationships

For specimens from the Algerian coast, eviscerated weight vs total length (Fig. 5) was log EW = 2.98 log TL - 5.25, r = 0.99 for males (n = 9) and log EW = 3.137 log TL - 5.879, r = 0.98 for females (n = 20). There were no significant differences in intercept or slope between the sexes ($p>0.05$).

Total weight (TW) vs total length for males and females (n = 29) from the Mediterranean coast was log TW = 3.13 log TL - 8.61, r = 0.95 (CAPAPÉ *et al*., 2003a).

The heaviest specimen recorded in the Mediterranean was a male, 4000 mm TL, caught off Izmir, Turkey, which weighed 1000 kg (MATER *et al*., 2000). According to CAPAPÉ *et al*. (2003a), this weight suggests an overestimation because larger specimens of 5000 mm TL,

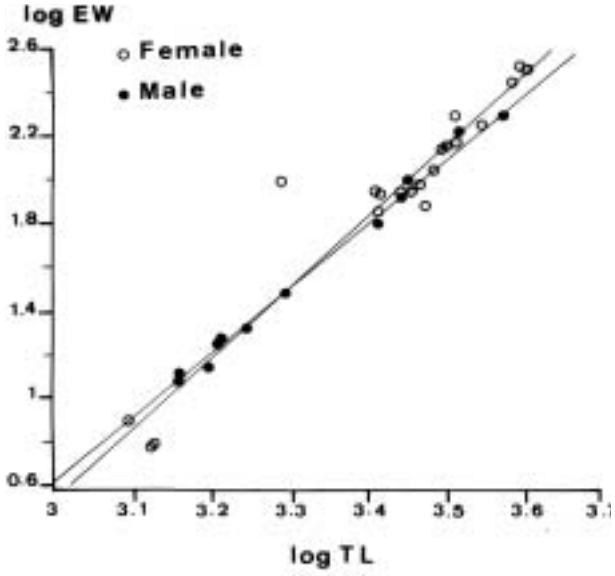

Fig. 5. Eviscerated weight (EW) vs total length (TL) expressed in logarithmic co-ordinates for female and male Hexanchus griseus *from the Algerian coast*

recorded off Naples and Sardinia, did not exceed 600 kg. These two specimens are the largest *H. griseus* recorded to date.

Female reproduction and fecundity

Three females with developing or ripe oocytes were captured in Tunisian waters. One, caught off the northern coast, was 4650 mm TL and contained 57 fully yolked oocytes. Two females were caught in the Gulf of Gabès: one (>3000 mm TL) contained many developing oocytes but the exact number could not be determined since some probably spilled out during capture and handling; the second (3940 mm TL) contained 100 fully yolked oocytes which were neither measured nor weighed.

Two of the females were caught in April and probably were about to ovulate. Neonates were captured off France and Spain in November and April. Therefore, the reproductive cycle seems to last at least one year.

Chemical balance of development

Of the 57 yellow yolked oocytes counted in a female caught in Tunisian waters (4650 mm TL), 14 were measured and weighed. Their diameters ranged 68-75 mm TL (mean 71.71±2.6) and weights 127-147 g (mean 134±8.4). The smallest free-swimming female specimens caught off France weighed 860 and 785 g (mean 822.5±53.03). Therefore, the CBD was 3.

DISCUSSION

CAPAPÉ *et al*. (2003a) showed that *H. griseus* was relatively abundant in the Mediterranean Sea, and that the species is more abundant in the western basin than in the eastern. They suggested the abundance may be due to the development of fisheries in the area, especially along the Maghrebin shore, that began in 1996, about the same time as the beginning of research on elasmobranch species off Algeria (HEMIDA, 1998; HEMIDA & LABIDI, 2001; HEMIDA & CAPAPÉ, 2002, 2003; HEMIDA *et al*., 2002a,b; 2003b) and Tunisia (BRADAÏ, 2000; BRADAÏ *et al*., 2000; BRADAÏ & CAPAPÉ, 2001; CAPAPÉ *et al*., 2001a, 2003a,b; ENNAJAR *et al*., 2002).

With regard to onset of sexual maturity, EBERT (1986a) recorded 4210 mm TL for a female from the northeastern Pacific. In southern African waters, EBERT (2002) noted that "determination of maturity for females was problematic, but most were fully mature by at least 4200 mm TL". Females were adult above 4500 mm TL in the Bay of Biscay (DESBROSSES, 1938), in the western Atlantic (BIGELOW & SCHROEDER, 1948) and off the Bahamas where SPRINGER & WALLER (1969) recorded an immature male at 3480 mm TL. EBERT (1986b) recorded the capture of a mature male measuring 3250 mm TL and 211 kg in the northern Gulf of Mexico. He noted, "development of its claspers and clasper sac was similar to that of the sevengill shark". EBERT (2002) reported that males mature at about 3100 mm TL in South African waters. Our observations suggest that *H. griseus* matures at a smaller size in the Mediterranean than elsewhere, in agreement with MORENO (1995), although the largest recorded specimens of *H. griseus* were from the Mediterranean (CAPAPÉ *et al*., 2003a). Female bluntnose sixgill shark matured at a larger size than males in all areas, similar to other hexanchids such as sevengill sharks (*Heptranchias perlo*) off northern Tunisia (CAPAPÉ, 1980) and in the central eastern Atlantic (FRENTZEL-BEYME & KÖSTER, 2002) and *Notorynchus cepedianus* off California (EBERT, 1986a,b, 2002) and southern Africa (EBERT, 1996).

In the Bay of Biscay, VAILLANT (1901) reported that TL ranged 680-736 mm for near-term embryos in a gravid female. DESBROSSES (1938) reported that size at birth is less than 720 mm TL and recorded three near-term fetuses, ranging 650-680 mm TL. EBERT (1986a) noted that near-term embryos off the coast of California ranged 680-736 mm TL. EBERT (2002) recorded newborns in southern African waters ranging 610-930 mm TL and added that the smallest free-swimming specimen was 610 mm TL. DESBROSSES (1938) recorded large variations in size at birth within an area, however, he collected both bluntnose sixgill

shark (*H. griseus*) and bigeyed sixgill shark (*H. nakamurai*) in his sample and it was probably the second species that was illustrated in his article. BIGELOW & SCHROEDER (1948) reported free-swimming specimens of 429-720 mm TL from the northwestern Atlantic but the near-term embryo of 429 mm TL is probably a bigeyed sixgill shark, whose TL at birth is about 430 mm (COMPAGNO, 1984). The gravid females reported by DESBROSSES (1938) ranged 4500-4650 mm TL and were *H. griseus*. The maximum TL reached by *H. nakamurai* is 1800 mm COMPAGNO (1984).

A literature review shows that *H. griseus* can reproduce once (RISSO, 1810; CANESTRINI, 1861 *in* TORTONESE, 1956) or twice (NINNI, 1912) per year. Mediterranean neonates were caught throughout the year (CAPAPÉ *et al*., 2003a). The two adult females with fully yolked oocytes were caught in April, probably at the time of ovulation. No embryos were found in the uteri. No vitellogenetic activity was reported in gravid females bearing embryos in different stages of development (EBERT, 1986b), suggesting that vitellogenic activity does not proceed together with embryonic development in *H. griseus*, but this hypothesis requires confirmation by further observations. A similar pattern was not clearly observed in sevengills (CAPAPÉ, 1980; EBERT, 1986b, 1989, 1996, 2002; FRENTZEL-BEYNE & KÖSTER, 2002). It appears that the reproductive cycle in hexanchids is rather long and exceeds one year. According to EBERT (1986b), for example, in *N. cepedianus*, "after first parturition adult females would give birth every 18 to 24 months". This is a possible hypothesis for *H. griseus* as well.

The CBD of 3 showed that *H. griseus* is not a pure lecithotrophic species according to the definition of WOURMS (1977, 1981) and that the female's role is not negligible during gestation. In pure lecithotrophic species such as squatinids, the CBD is low (0.5-0.8; CAPAPÉ *et al*., 1990, 2002). The CBD of *H. griseus* is higher than the CBD (1.0) of the blackchin guitarfish *Rhinobatos cemiculus* from Tunisian waters (CAPAPÉ & ZAOUALI, 1994) and the torpedinids *Torpedo torpedo* and *T. marmorata* from the coast of Senegal (CAPAPÉ *et al*., 2000a, 2001b), which are not strictly lecithotrophic (*sensu* WOURMS, 1977, 1981). In contrast, the CBD reaches high values in strictly matrotrophic species. The CBD of *C. limbatus* (69) is the highest value ever observed in an elasmobranch species (unpubl. data) and is close to that of the sympatric species *C. brevipinna* (65.8; CAPAPÉ *et al*., 2003b) and higher than that of Mediterranean *D. violacea*, (47; HEMIDA *et al*., 2003), the butterfly ray *Gymnura altavela* from Tunisian waters (30.6; CAPAPÉ *et al*., 1992), and the bull ray *Pteromylaeus bovinus* from the coast of Senegal (31.12; SECK *et al*., 2002).

In elasmobranch species that produce heavier eggs, the female's role during gestation is usually reduced. However in squatinids and centrophorids, gestation is longer than one year (MELLINGER, 1989, 2002; CAPAPÉ *et al*., 1990; GUALLART & VINCENT, 2001). This could confirm a long gestation period in hexanchids, especially the bluntnose sixgill, in agreement with EBERT (1986a,b, 2002). In strictly lecithotrophic species, the female protects only embryonic development, providing inorganic nutrients to the embryos (MELLINGER, 1989; HAMLETT *et al*., 1998a,b). This was observed in squatinids (CAPAPÉ *et al*., 1990, 2002) and centrophorids (RANZI, 1932, 1934; GUALLART & VICENT, 2001). In matrotrophic elasmobranchs, the contribution of female-derived organic molecules is very important (WOURMS, 1981; HAMLETT & WOURMS, 1984; HAMLETT *et al.* 1985a,b,c,d,e, 1993a,b, 2002; HAMLETT, 1987, 1989; FISHELSON & BARANES, 1998). These species produce an egg mass that is clearly less than the mass of fully developed embryos. Matrotrophy is characteristic of dasyatids, rhinopterids and gymnurids (WOURMS, 1977, 1981; MELLINGER, 1989; CAPAPÉ *et al*., 1992; SECK *et al*., 2002). *H. griseus* may be a transition between lecithotrophic and matrotrophic species and considered a semi-lecithotrophic species.

In the Bay of Biscay, VAILLANT (1901) numbered 108 near-term embryos in a female of 4800 mm TL. BOLIVAR (1907) found 47 fetuses in a female of 4800 mm TL. Off California, a female of 4210 mm TL contained 51 near-term

embryos (EBERT, 1986a). One of the two females caught in Tunisian waters had 57 fully yolked oocytes; the other had 100. There is insufficient data to state if ovarian fecundity is related to female TL. EBERT (1986b) noted: "Therefore, the actual number of young carried by this specimens was uncertain. The tendency of near-term females to abort their young upon capture account for the wide discrepancy reported by SPRINGER & WALLER (1969) for sixgill shark fecundity". *N. cepedianus* had 82-96 eggs per female and EBERT (1986b) found 82 near-term embryos in a gravid female. Litter sizes were high in the sixgill and, like other hexanchid species, can be considered a relatively prolific elasmobranch. Litters were lower than in the whale shark *Rhyncodon typus* where JOUNG *et al.* (1996) reported on 300 fully developed embryos in a "megamamma supreme".

Records regarding the Mediterranean reveal a non-negligible density population of sixgill sharks (CAPAPÉ *et al*., 2003a). Stock decrease seems to be a possible hypothesis (DELATTRE & MAIGRET, 1986). The species is relatively prolific but size at maturity is reached at a large TL and the lengthy reproductive cycle considerably reduces recruitment. The wide distribution suggests large migrations of *H. griseus*. It is relatively common in the eastern tropical Atlantic (FISCHER *et al*., 1981) and its abundance off the Maghrebin shore may be due to migrations through the Strait of Gibraltar.

With regard to some elasmobranch and teleost species, QUIGNARD & TOMASINI (2000) noted: "The discovery of a large number of other species outside of their usual area of distribution may be due to an increase of traditional prospection, or to the use of newer techniques which allow the exploration of otherwise unaccessible habitat". This agrees with GOLANI (1996), GOLANI & SONIN (1996) and HEMIDA *et al.* (2002b, 2003a) and must not be ignored.

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Reprodukcija psa volonje šestoškrgaša *Hexanchus griseus* (Bonnaterre, 1788) (Chondrichthyes: Hexanchidae) u Mediteranu: pregled

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SAŽETAK

Ukupna duljina (*TL*) odraslih mužjaka psa volonje šestoškrgaša u Mediteranu iznosila je preko 3500 mm, dok je duljina ženki iznosila 3940 mm. Ukupna duljina (*TL*) novorođenih primjeraka kretala se između 556 i 680 mm. Promjer zrelih oocita kretao se između 68-75 mm, ukupna duljina (*TL*) iznosila je (71.71±2.6), dok je težina varirala od 127 do 147 g. (134±8.4). Reproduktivni ciklus je trajao minmalno godinu dana, a vjerojatno i dulje. Izračunata kemijska ravnoteža između srednje suhe težine oocita i novorođenih (*CBD*) iznosila je 3. Dvije odrasle ženke imale su 57 i 100 zrelih oocita. Podaci prikazani u ovom radu ukazuju na to da je *Hexanchus griseus* vjerojatno sposoban živjeti i razmnožavati se u Mediteranu. Međutim, neophodna su daljnja promatranja prije nego se konačno potvrdi da dostatna populacija psa šestoškrgaša volonje naseljava ovo područje, posebno priobalje Magreba.

Ključne riječi: Chondrichthyes, Hexanchidae, *Hexanchus griseus*, reprodukcija, Mediteran, obala Magreba