



Abstract—Reproductive parameters of the white anglerfish (*Lophius piscatorius*) in the northwestern Mediterranean Sea were studied in 556 specimens collected monthly aboard commercial fishing vessels that were trawling at depths of 12–836 m. The main spawning season occurred from February through June. The size at maturity was estimated to be 48.8 cm in total length (TL) for males, 59.9 cm TL for females, and 51.3 cm TL for both sexes combined. The white anglerfish has group-synchronous oocyte development and determinate fecundity. It is a total spawner (spawns all its eggs once during a spawning season) and has a batch fecundity ranging from 661,647 to 885,214 oocytes, a relative batch fecundity of 66–128 oocytes per gram of female gutted weight, and a potential fecundity with values from 54,717 to 104,506 oocytes per kilogram of female total weight. This study is the first to provide the reproductive biology of white anglerfish in the northwestern Mediterranean Sea and provide valuable information that can be used to improve the stock assessment and ensure proper management of this species.

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Reproductive strategy of white anglerfish (*Lophius piscatorius*) in Mediterranean waters: implications for management

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The genus *Lophius*, commonly known as anglerfish, monkfish, or goosefish, belong to a family of bathydemersal fishes, which live and feed on the bottom of the seafloor generally below 200 m (Caruso, 1986). It includes 7 species distributed around the world. The white anglerfish (*Lophius piscatorius*) is found in the northeast Atlantic Ocean and the Mediterranean Sea, and the black anglerfish (*Lophius budegassa*) coexists with white anglerfish over most of its range, although the black anglerfish has a more southerly distribution in the Atlantic (Caruso, 1986). The shortspine African angler (*Lophius vaillanti*) is found in the eastern Atlantic (Maartens and Booth, 2005). The devil anglerfish (*Lophius vomerinus*) occupies the southeast Atlantic and the northern and western Indian Ocean (Walmsley et al., 2005). The blackfin goosefish (*Lophius gastrophysus*) inhabits the western Atlantic, and the goosefish (*Lophius americanus*) occurs in the northwest Atlantic (Caruso, 1983). Finally, the yellow goosefish (*Lophius litulon*) is distributed in the northwest Pacific, in the Gulf of Po-Hai, in the Yellow Sea, and in the East China Sea (Yoneda et al., 1997).

We focused on white anglerfish,

which can be found on the continental shelf and slope, inhabiting depths from the shoreline to >1000 m (Afonso-Dias and Hislop, 1996). In the Mediterranean Sea, this species cohabits with black anglerfish, and even though the distributions of both species overlap, no ecological competition exists between them because of a temporal segregation in their daily biorhythms (Colmenero et al., 2010). Both of these species of *Lophius* play an important role in the trophic structure of bathydemersal ecosystems because they represent major predators, along with the European hake (*Merluccius merluccius*) (Díaz et al., 2008). In the community structure of the northwestern Mediterranean Sea, species of anglerfish are considered top predators (Coll et al., 2006; Valls et al., 2014). They are also reported to be important in the deep-sea community (depths from 200 m to the bottom of the ocean) because they are the most abundant species (Labropoulou and Papaconstantinou, 2000; Maiorano et al., 2010).

Despite the fact that the deep sea is the largest ecosystem on the planet, is highly diverse, and has a wealth of resources, it is still mostly unknown and poorly understood in comparison with shallow-water ar-

eas: therefore environmental management in deep waters is difficult (Ramirez-Llodra et al., 2010). In the last few decades, the decline of traditional fisheries on the continental shelf, the increasing demand for food sources, and rapid technological developments have resulted in an increasing exploitation of deep-sea resources (Koslow et al., 2000; Ramirez-Llodra et al., 2011) and in an incremental increase in the global mean depth of fishing (Watson and Morato, 2013).

This rise in deep-sea fishing has affected catches of *Lophius* species, given the growing demand for human consumption of this group of fish that is leading to an increase in worldwide commercial exploitation and targeting of anglerfishes (Fariña et al., 2008). Total catch reported globally for white anglerfish reached more than 26,500 metric tons (t) in 2014 (FAO Global Capture Production database, [website](#)) and total catch of anglerfishes in the northwestern Mediterranean Sea for the same year added up to 660 t (Tudó Vila¹). Landings in our study area were composed primarily of black anglerfish (86%) and generally only a small percentage of white anglerfish (14%) (Tudó Vila¹), but, for landings in Atlantic waters, the opposite is true; white anglerfish (94%) dominate the catch (Dobby et al., 2008). Although the European Commission previously has conducted stock assessments of black anglerfish in the western Mediterranean Sea, there is no corresponding assessment for white anglerfish. The lack of information about the structure of the population of white anglerfish in this region and the lack of knowledge of the basic biology of this species are the main reasons for the absence of any assessment. The actual management regulations applied for black anglerfish generally are those applied to bottom trawling (European Union Council Regulation 1967/2006), with recommendations aimed at reducing the fishing effort of the fleet in order to avoid loss in stock productivity and decreases in landings (Cardinale et al.²).

The small quantity of white anglerfish available from landings in Mediterranean waters makes studies of this species challenging. Studies conducted in the Mediterranean Sea have been scarce, and they have been focused on temporal and spatial distribution of this species (Ungaro et al., 2002; Colmenero et al., 2010), age and growth (Tsimenidis and Ondrias, 1980; Tsimenidis, 1984), feeding ecology (López et al., 2016), morphometrics (Negzaoui-Garali and Ben Salem, 2008), parasites (Colmenero et al., 2015a), and ova characteristics (Colmenero et al., 2015b). Among these studies, only Ungaro et al. (2002) analyzed some of the biological features of this species by using data available from trawl surveys, including data on distribution, abun-

dance, stock demography, and size at maturity. The latter work is valuable but is limited because sampling occurred only in the spring and summer; a whole year of sampling is recommended to obtain more accurate biological information.

A study of reproductive ecology is important for an understanding of population dynamics, and it is critical for assessing the effects of harvesting on fish populations when attempting to develop appropriate management strategies. Recruitment is recognized as a key process for maintaining sustainable populations, and the relationship between the reproductive output of the population and the resulting recruitment is central to understanding how a fish population will respond to constant stressors such as fishing (Chambers and Trippel, 1997). Although knowing more about the relationships between life history strategies and productivity with depth could help managers understand the potential response of a deep-sea species to fishing (Drazen and Haedrich, 2012), it is first necessary to conduct biological studies of fish to gain knowledge of the reproductive system of a species (Koslow et al., 1995). Such studies include gonad morphology (external and cellular description of the ovary and testis), reproductive pattern (hermaphroditism or gonochorism), reproductive behavior, reproductive cycle, spawning season duration, size at maturity, sex ratio, size at sexual transition, and fecundity.

All of this information can be applied at the population level to evaluate reproductive potential and to serve as a basis for limits on fishing that aim in order to keep recruitment at sustainable levels (García-Díaz et al., 2006). Because reproductive strategy varies within species, depending on the area of distribution of each species and the depth distribution of each species in each area (Rotllant et al., 2002), there is a need for knowledge about reproduction of deep-sea fish species. Such information is needed particularly in the Mediterranean Sea because the data available for this region are limited (Morales-Nin et al., 1996; D'Onghia et al., 2008; Muñoz et al., 2010; Bustos-Salvador et al., 2015), and, furthermore, target species of fisheries have been the focus of only a few studies (Rotllant et al., 2002; Recasens et al., 2008).

The goal of this study was to describe the reproductive parameters—gonadal morphology, spawning season, size at sexual maturity, oocyte development, and fecundity—of white anglerfish in the northwestern Mediterranean Sea in order to provide valuable information and scientific background to improve stock assessments and effective management for *Lophius* species in Mediterranean waters.

Materials and methods

Sampling and data collection

Between June 2007 and December 2010, 556 white anglerfish, with total lengths (TLs) of 9–120 cm, were

¹ Tudó Vila, P. 2015. Unpubl. data. Directorate of Fishing and Maritime Affairs, Government of Catalonia, Avinguda Diagonal 523-525, 08029 Barcelona, Spain.

² Cardinale, M., D. Damalas, and C. G. Osio (eds.). 2015. Scientific, Technical and Economic Committee for Fisheries (STECF)—Mediterranean Assessments, part 2 (STECF-15-06), 396 p. Publications Office of the European Union, Luxembourg. [Available from [website](#).]

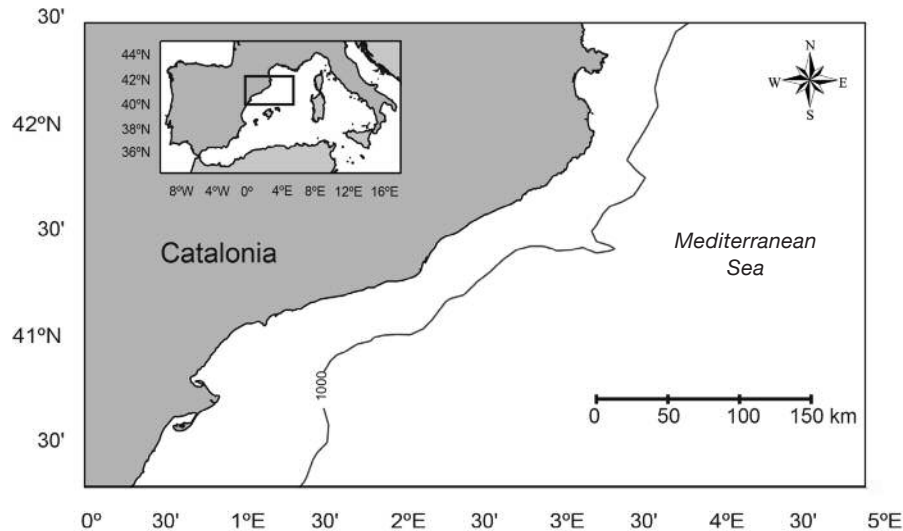


Figure 1

Map of the northwestern Mediterranean Sea showing the study area where white anglerfish (*Lophius piscatorius*) were collected from fishing grounds off the Catalan coast between June 2007 and December 2010.

collected monthly aboard commercial fishing vessels that were trawling at depths of 12–836 m. Fish were sampled from 467 stations located in the fishing grounds off the Catalan coast in the northwestern Mediterranean Sea from 40°5.980'N to 43°39.310'N and from 0°32.922'E to 3°35.718'E (Fig. 1). For each individual, TL was measured to the nearest centimeter, total weight (TW) and gutted weight (GW) were measured to the nearest gram, and gonad weight (GNW) and liver weight (LW) were measured to the nearest 0.01 g. The sex of all fish was determined and assigned macroscopically to a gonadal stage on the basis of a scale of 5 maturity phases proposed by Colmenero et al. (2013): immature (phase I), developing or regenerating (phase II), spawning capable (phase III), actively spawning (phase IV), and regressing (phase V).

Fish that were too small (<20 cm TL) for their sex to be determined or for assignment to a gonadal phase were classified as indeterminate. Macroscopic gonadal stage was validated histologically, according to the most advanced cell within the gonad (West, 1990). Gonads were fixed in 10% buffered formalin solution, dehydrated in ascending solutions of alcohols and embedded in a methacrylate polymer resin, sectioned at a thickness of 4 μ m with a manual microtome Leica Reichert-Jung 2040³ (Leica Microsystems, Wetzlar, Germany), stained with Lee's stain (methylene blue and basic fuchsin), and mounted in a synthetic resin of dibutyl phthalate xylene on microscope slides. Gonads were classified according to their size and color and the presence or absence of specific inclusions (oil droplets,

yolk, postovulatory follicles, or sperm), as well as the type of oocytes (Wallace and Selman, 1981).

Reproductive biology

The spawning season was estimated by analyzing the monthly variation in the percentage of maturity phases and the changes in gonadosomatic index (GSI) and hepatosomatic index (HSI) for mature fish of each sex (Afonso-Dias and Hislop, 1996; Colmenero et al., 2013). Because indeterminate individuals ($n=27$) were not considered, 251 males and 278 females were used to determine both indices, which were calculated according to Yoneda et al. (2001) as

$$GSI = (GNW / GW) \times 100 \quad (1)$$

and

$$HSI = (LW / GW) \times 100. \quad (2)$$

The lengths at which 25%, 50%, and 75% of sampled fish reached sexual maturity were estimated by fitting the proportion of sexually mature males and females (phase III, phase IV, or phase V) and for both sexes combined to the logistic equation (Colmenero et al., 2013):

$$P = 100 / (1 + \exp [a + bTL]), \quad (3)$$

where P = the percentage of mature individuals as a function of size class (measured in TL); and

a and b are specific parameters that can change during the life cycle.

A logarithmic transformation was applied to this equation to calculate the parameters a and b by means of linear regression.

³ Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Oocyte development and fecundity

Oocyte diameters obtained from 21 randomly selected specimens at all phases of maturity were measured to the nearest 0.01 μm with an image analysis program (Image-Pro Plus, vers. 5.0, Media Cybernetics, Inc., Rockville, MD) in combination with an Axioskop 2 Plus microscope (Carl Zeiss Microscopy, LLC, Thornwood, NY), and a ProgRes C14 digital microscope camera (Jenoptik AG, Jena, Germany). Only oocytes sectioned through the nucleus were taken into account. The developmental stages of the oocytes were categorized according to the descriptions in Colmenero et al. (2013) that were adapted from Wallace and Selman (1981). The mean oocyte diameter by developmental stage was determined by calculating the diameter of all oocytes encountered in each subsample, and the range was set with the smallest and largest oocytes found at each developmental oocyte stage.

Fecundity was determined by using the gravimetric method described by Hunter and Goldberg (1980). Because homogeneity in oocyte distribution within ovaries of white anglerfish has already been established (Afonso-Dias and Hislop, 1996), ovarian tissue subsamples of approximately 500 mg were taken randomly from 2 specimens with ovaries in phase III that had neither postovulatory follicles nor atretic oocytes present. Whole tissue subsamples were placed on several slides and covered with cover slips, then photographed with a Canon Powershot SD870 IS digital camera (Canon USA, Melville, NY). Oocytes were counted manually with Image-Pro Plus.

Batch fecundity (BF), the total number of hydrated oocytes produced in a single spawning event by an individual female, of each female was determined by means of this equation:

$$BF = (\text{oocyte number} / \text{sampled GNW}) \times \text{total GNW}, \quad (4)$$

where *BF* is the product of the number of secondary vitellogenic oocytes per unit of weight multiplied by the total ovarian weight (Yoneda et al., 2001). Relative batch fecundity (RBF), the total number of mature eggs released by a female during the spawning batch per gram of female GW, was calculated with the following equation (Pavlov et al., 2009):

$$RBF = BF / GW. \quad (5)$$

Potential fecundity was calculated as the number of vitellogenic oocytes divided by TW in kilograms for each mature female and then averaged (Murua et al., 2003).

Results

Gonad morphology

The gonad of female white anglerfish has 2 ribbon-like ovarian lobes connected to each other at their posterior end. One side of the “ribbon” consists of an ovigerous

membrane from which a single layer of oocyte clusters, which contain oocytes at different developmental stages, projects into the lumen. The other side is non-ovigerous and secretes a gelatinous material during maturation that fills the ovarian lumen, where mature oocytes develop (Fig. 2). During maturation, the gonad increases in size until it fills the abdominal cavity (Fig. 3). Testes are a pair of elongated organs with a bean shape in transverse section. Spermatogenesis takes place in a capsule-like sac called a *cyst*, but it is completed in the lumina of the lobules. The cysts appear to be arranged with a gradient of germ cells of increasing maturation from the cortex to the sperm duct (Fig. 4).

Spawning season

The monthly distribution of maturity phases (Fig. 5) revealed a peak in reproduction during spring, when a major portion of the spawning females and the highest value of GSI (0.77) were found. Spawning capable females (phase III) were caught primarily between April and June, and females in the actively spawning phase (IV) were observed in November, December, and March—the latter month having the maximum occurrence (11%). Females in immature, regressing, and developing or regenerating phases (I, V, and II, respectively) were found year-round, although the highest percentage of immature individuals (49%) was observed in January. The GSI values followed the same pattern shown in these maturity phases: highest during spring, decreasing during summer and autumn, and increasing again during winter. Males in all maturity phases were observed throughout the year, but with a maximum percentage of mature males (66%) in February and March. Immature males were found primarily in July (69%). The mean GSI for females increased as their ovaries developed and peaked in phase IV. For males, the mean GSI increased with testicular development and reached a maximum in phase IV (Table 1). The mean HSI for females and males increased during the summer and autumn months and decreased during winter and spring. On the basis of these observations, a main spawning season was found from February through June and a secondary one occurred in November and December.

Size at sexual maturity

The maturity ogive for males indicates that the length at which 50% of them reached sexual maturity (L_{50}) was 48.4 cm TL (Fig. 6A). Maturity in males occurred at about 37% of their maximum observed TL. The smallest mature male found was 32.5 cm TL, and the largest immature male was 50 cm TL. The maturity ogive for females indicates that L_{50} was 59.9 cm TL (Fig. 6B). Female maturity occurs at about 30% of their maximum observed TL. Like the smallest male, the smallest mature female was 32.5 cm TL. The largest immature female measured 56 cm TL. The maturity ogive for the sexes combined indicates an L_{50} of 51.3

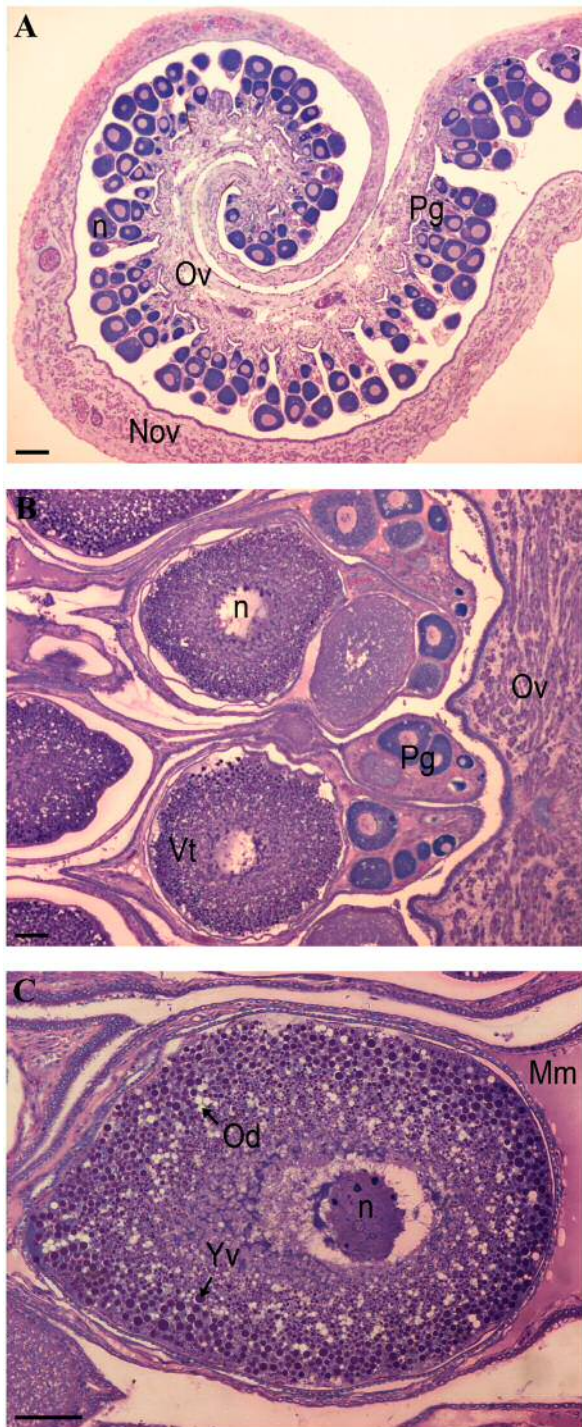


Figure 2

Histological sections from ovaries of female white anglerfish (*Lophius piscatorius*) in 3 phases of maturity: (A) immature, (B) spawning capable, and (C) actively spawning. Ov=ovigerous membrane, Nov=nonovigerous membrane, n=nucleus, Pg=primary growth stage, Vt=vitellogenesis stage, Od=oil droplet, Yv=yolk vesicle, Mm=mucus matrix. Scale bars=100 μ m.

cm TL. The lengths at which 25% and 75% of fish attained maturity were 43.5 and 53.4 cm TL for males, 48.6 and 71.1 cm TL for females, and 44.7 and 58 cm TL for the sexes combined.

Oocyte development and fecundity

Oocytes in different developmental stages were found in each maturity phase. They were organized in clusters where a gradient in the size of the oocyte was observed. A group of oocytes differentiated from others as the ovaries developed, indicating that white anglerfish has group-synchronous oocyte development and can be considered to have determinate fecundity (Fig. 7). Ovaries at each maturity phase contained primary oogonia- and perinucleolar-stage oocytes. Chromatin nucleolar were difficult to find and were present only in immature phase. Females at the cortical alveolar stage were not found in our samples. Vitellogenic and hydrated oocytes were located in females capable of spawning. Oocyte diameters at each stage of oocyte development are shown in Table 2.

Batch fecundity ranged from 661,647 to 885,214 oocytes from 2 females that measured 76 and 105 cm TL, 6331 and 16,178 g TW, and 5182 and 13,330 g GW, respectively. Relative batch fecundity ranged from 66 to 128 oocytes/g GW (average of 97 oocytes/g GW [standard deviation, SD 43]). Potential fecundity values moved from 54,717 to 104,506 oocytes/kg TW with a mean of 79,612 oocytes/kg TW (SD 35,206).

Discussion

Relevance of reproductive traits for sustainable management

Fishing activity during spawning seasons may affect population parameters, specifically composition of the size distribution, mortality rate, sexual structure of the population, size at maturity, and changes in the spawning season. These parameters, in turn, can increase the risk of over-exploitation of a stock.

Fishing during spawning periods may result in targeting a specific size class of the population and thus increasing the chance of catching the older (and larger) age classes and making the stock vulnerable to reproductive collapse (van Overzee and Rijnsdorp, 2015). Because spawning is generally limited to specific areas and times (Cushing, 1990), the conservation of resources can be enhanced by limiting fishing activity in a spatiotemporal frame. Furthermore, fishing pressure has been documented to have reduced initial size at maturity—an issue that is a concern particularly for late-maturing species (Stewart et al., 2010). If size of capture is below the size at first maturity, there is a genuine risk of recruitment overfishing. Therefore, knowledge of the spawning season and the size at maturity can help managers establish closed seasons and prevent fishing at this vulnerable time in the life cycle

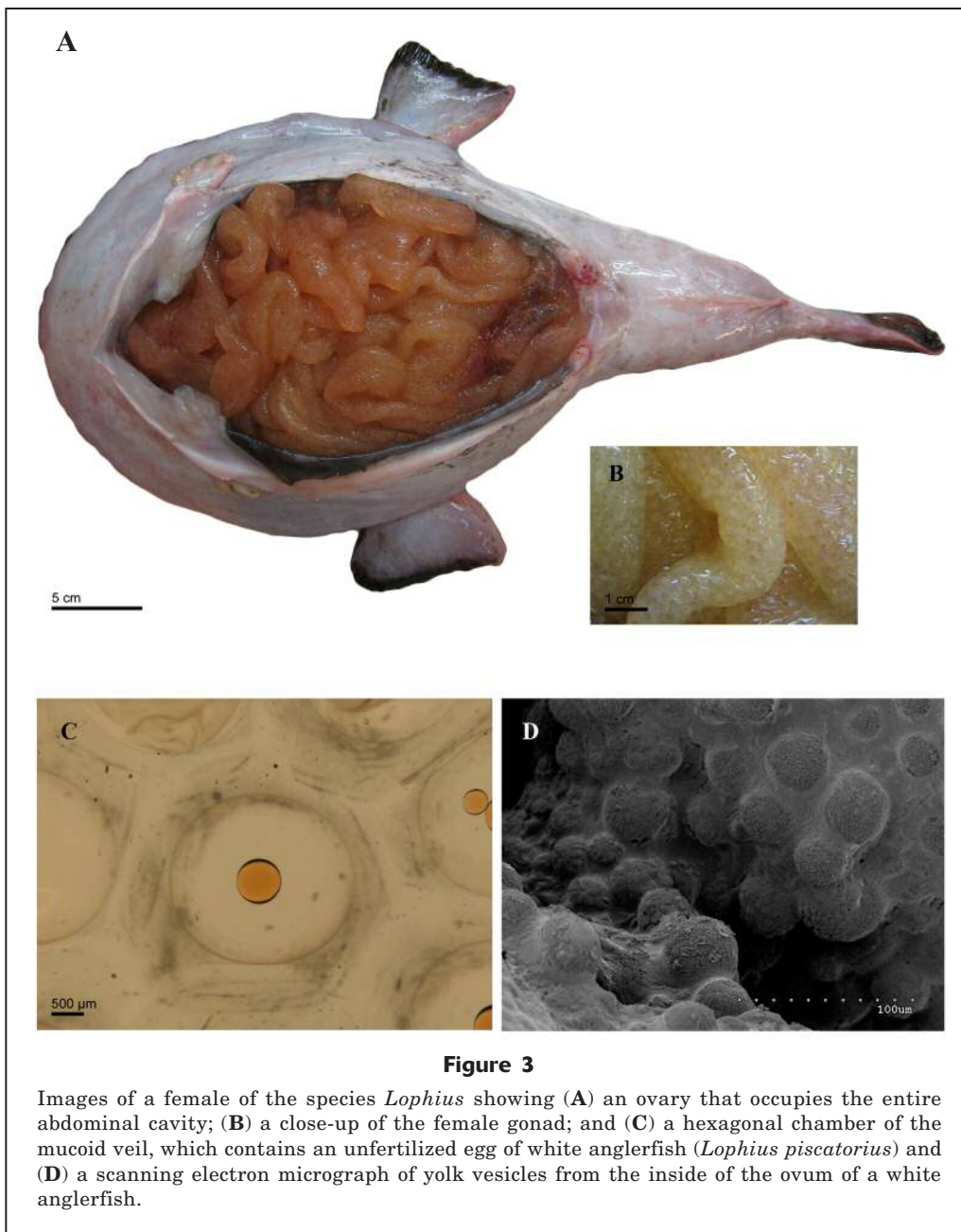


Figure 3

Images of a female of the species *Lophius* showing (A) an ovary that occupies the entire abdominal cavity; (B) a close-up of the female gonad; and (C) a hexagonal chamber of the mucoid veil, which contains an unfertilized egg of white anglerfish (*Lophius piscatorius*) and (D) a scanning electron micrograph of yolk vesicles from the inside of the ovum of a white anglerfish.

of fish species by preserving breeding individuals and establishing a legal minimum size.

The results of our study of white anglerfish in the northwestern Mediterranean Sea indicate that a long spawning period occurs during mid-winter and late spring, from February through June, although a secondary breeding period has been observed in November and December. These results agree with those obtained in studies that were focused on the northeastern Atlantic Ocean, where this species spawns from November through June (Fulton, 1898; Afonso-Dias and Hislop, 1996; Hislop et al., 2001). However, a previous study in the northwestern Mediterranean Sea identified a

spawning season during spring–summer (Ungaro et al., 2002). Discrepancies between the latter study and our work may be explained by the differences in sampling periods.

Nevertheless, spawning seasonality, which is associated with environmental conditions and local oceanographic features, varies between species as well as by geographical area. An example of this variability in spawning seasonality can be observed in 2 locations along the Atlantic–Iberian coast: on the Portuguese and western Spanish coasts, spawning of the white anglerfish takes place during winter–spring (Duarte et al., 2001), whereas on the northern Spanish coast (Bay

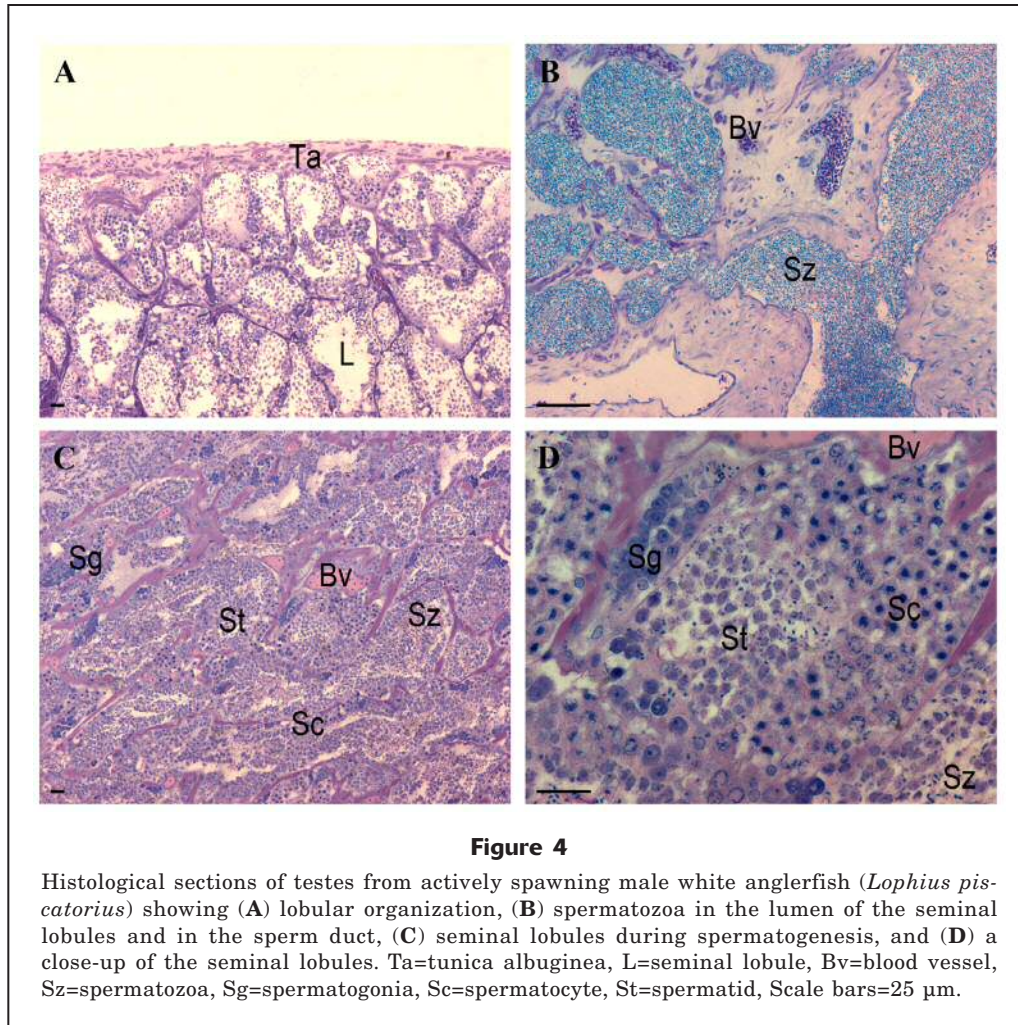


Figure 4

Histological sections of testes from actively spawning male white anglerfish (*Lophius piscatorius*) showing (A) lobular organization, (B) spermatozoa in the lumen of the seminal lobules and in the sperm duct, (C) seminal lobules during spermatogenesis, and (D) a close-up of the seminal lobules. Ta=tunica albuginea, L=seminal lobule, Bv=blood vessel, Sz=spermatozoa, Sg=spermatogonia, Sc=spermatocyte, St=spermatid, Scale bars=25 μ m.

of Biscay), spawning occurs during summer (Quincoces et al.⁴). In fact, spawning activity for one of its congeners, the black anglerfish, in the northwestern Mediterranean seems to occur from November through March and a secondary spawning occurs in August and September (Colmenero et al., 2013). Although a little overlap exists between spawning seasons of both of these *Lophius* species in Mediterranean waters, the main period is markedly different, and that difference lessens competition among these species.

Usually, species of *Lophius* have long spawning periods ranging between 4 and 6 months. Black anglerfish off the Spanish-Atlantic coasts spawn from November through February (Duarte et al., 2001), and in the Bay of Biscay the peak spawning period is from May through July (Quincoces et al.⁵). The goosefish off the

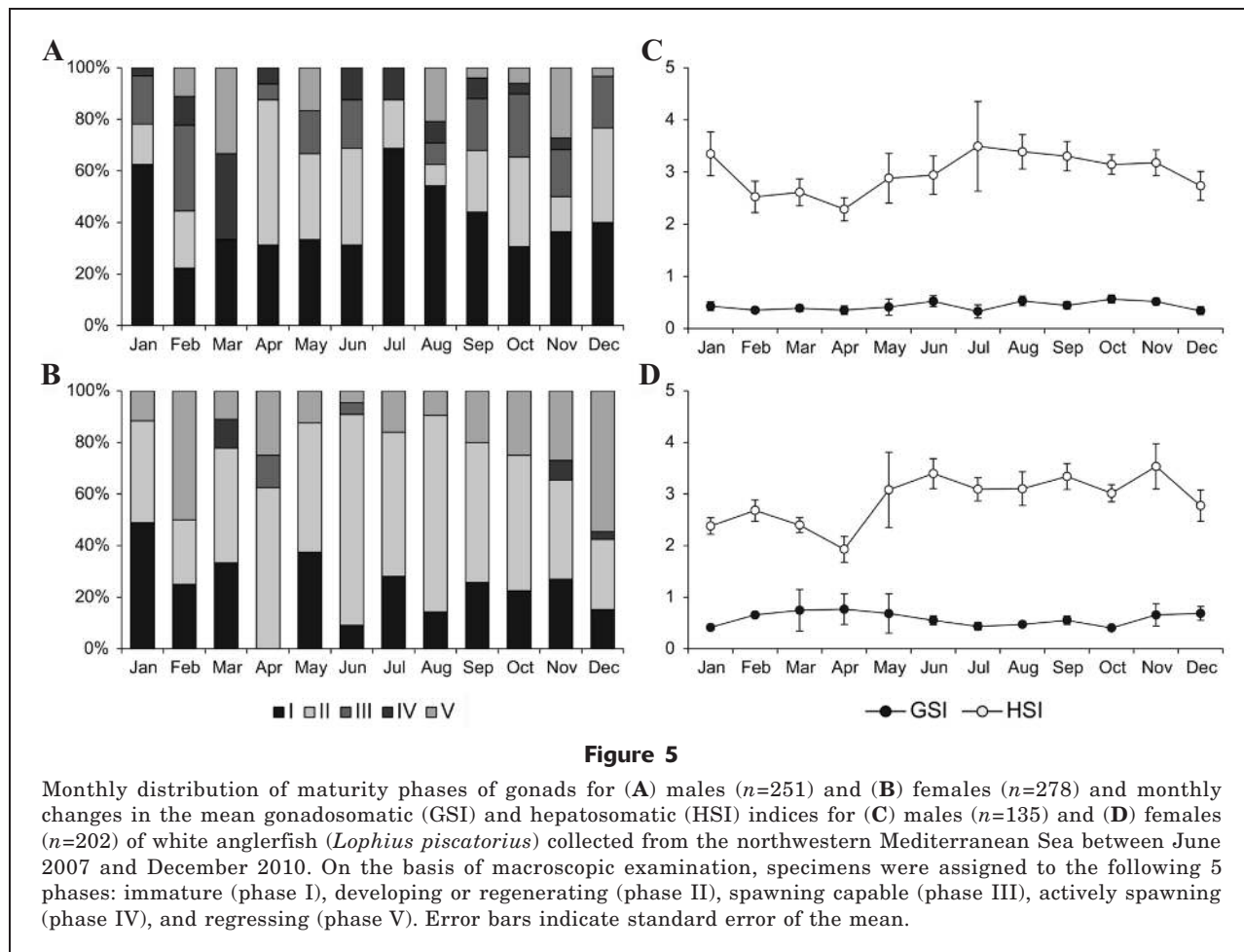
East Coast of the United States has its reproductive period from May through June (Armstrong et al., 1992), spawning for the blackfin goosefish off the Brazilian coasts takes place during spring and summer (Valentim et al., 2007), and the yellow goosefish spawns between February and May in the East China Sea and the Yellow Sea (Yoneda et al., 2001). The devil anglerfish off the coast of South Africa has a well-defined summer breeding season (Griffiths and Hecht, 1986), and individuals of this species off the coast of Namibia spawn throughout the year with a slight increase between autumn and spring (Maartens and Booth, 2005).

Most deep-sea fish species reach sexual maturity at sizes larger than those of species that inhabit the continental shelf reach maturity, and, in some cases, males mature at smaller sizes than females (Rotllant et al., 2002; Pajuelo et al., 2008). A similar pattern was observed for white anglerfish—one in which females mature sexually at larger sizes (59.9 cm TL) than those recorded for males (48.4 cm TL). This pattern has also

⁴ Quincoces, I., M. Santurtún, and P. Lucio. 1998. Biological aspects of white anglerfish (*Lophius piscatorius*) in the Bay of Biscay (ICES Division VIIIa, b, d), in 1996–1997. ICES Council Meeting (C.M.) Documents 1998/O:48, 29 p.

⁵ Quincoces, I., P. Lucio, and M. Santurtún. 1998. Biology of black anglerfish *Lophius budegassa* in the Bay of Biscay

waters, during 1996–1997. ICES Council Meeting (C.M.) Documents 1998/O:47, 28 p.



been found for white anglerfish in other areas (Ofstad and Laurenson⁶) and for other species of anglerfish. Female black anglerfish, for example, mature at 48.2 cm TL, whereas males attain first maturity at 33.4 cm TL (Colmenero et al., 2013), and female devil anglerfish reach sexual maturity at 58.2 cm TL, whereas males of this species mature at 39.9 cm TL (Maartens and Booth, 2005). For the goosefish, L_{50} for females and males was estimated at 48.5 and 36.9 cm TL, respectively (Armstrong et al., 1992), and female yellow goosefish mature at 56.7 cm TL and males of this species mature at 36.2 cm (Yoneda et al., 2001). This dissimilarity in size at maturity is usually associated with a trade-off between life history traits, where early maturity involves a larger size but a slower growth (Stearns and Koella, 1986; Charnov, 2008).

Reproductive strategy

The reproductive strategy of white anglerfish is one of discontinuous oogenesis with synchronous development

of vitellogenic oocytes and is, therefore, this species is considered a total spawner (Afonso-Dias and Hislop, 1996). The oocytes ovulate at once, and the eggs are released in either a unique event or over a short period of time, as part of a single episode during the spawning season (Murua and Saborido-Rey, 2003; Pavlov et al., 2009). This pattern of oocyte development and spawning patterns is also found in other species of *Lophius* (Leslie and Grant, 1990; Armstrong et al., 1992; Colmenero et al., 2013). Yoneda et al. (2001) suggested that yellow goosefish may have the potential to spawn more than once a year, on the basis of the observation of a captive specimen that released several infertile egg masses. However, this spawning behavior cannot be considered normal.

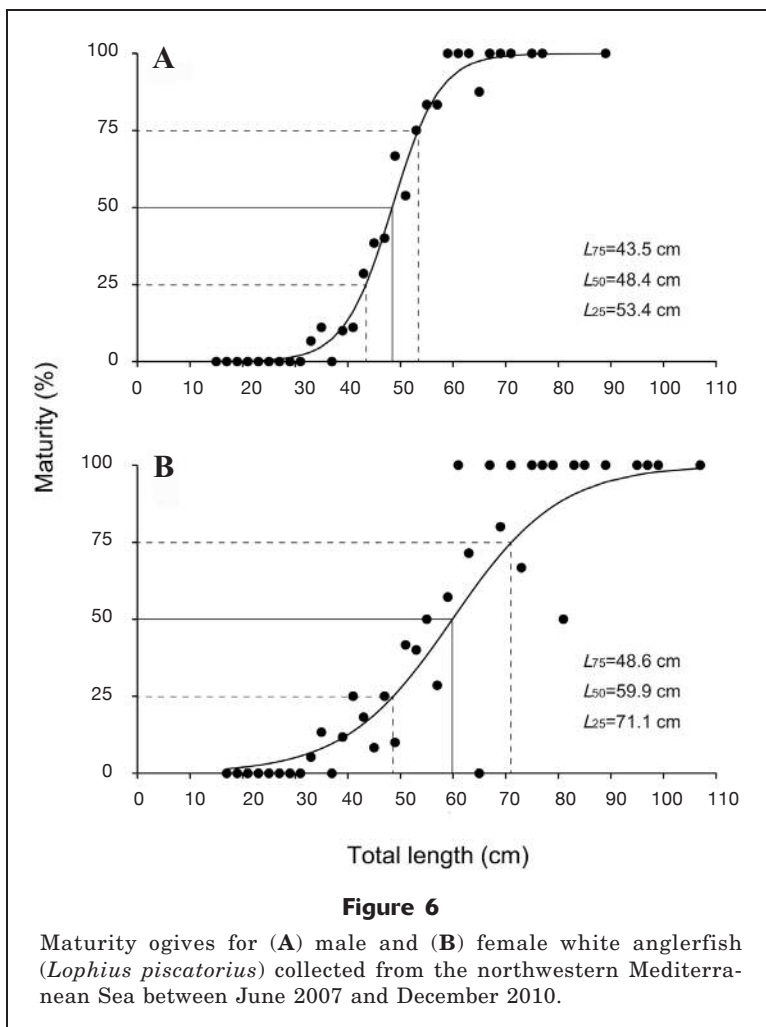
Female anglerfish spawn their eggs in a mucoid veil that floats near the surface. The veil consists of individual chambers that contain 1–3 eggs and has an opening that provides water circulation. In our study, we recognized in some chambers the presence of 2 eggs sharing the same chamber. Although this way of releasing eggs is not common among fish species, some Scorpaeniformes, such as the shortfin turkeyfish (*Dendrochirus brachypterus*) (Fishelson, 1978) or the short-

⁶ Ofstad, L. H., and C. Laurenson. 2007. Biology of anglerfish *Lophius piscatorius* in Faroese waters. ICES Council Meeting (C.M.) Documents 2007/K:07, 16 p.

Table 1

Gonadosomatic (GSI) and hepatosomatic (HSI) indices at each maturity phase for male and female white anglerfish (*Lophius piscatorius*) collected from the northwestern Mediterranean Sea between June 2007 and December 2010. SE=standard error.

Sex	Maturity phase	GSI range	Mean GSI (SE)	HSI range	Mean HSI (SE)	n
Male	I	0.01–0.41	0.10 (0.01)	1.04–4.65	2.37 (0.07)	106
	II	0.06–1.07	0.25 (0.03)	0.27–5.11	2.67 (0.14)	54
	III	0.21–1.30	0.61 (0.05)	1.92–6.72	3.20 (0.18)	35
	IV	0.30–1.70	0.70 (0.09)	0.40–5.39	3.34 (0.28)	17
	V	0.19–1.11	0.50 (0.06)	2.04–5.10	3.35 (0.22)	17
Female	I	0.01–0.86	0.23 (0.02)	0.92–5.33	2.37 (0.11)	66
	II	0.04–1.22	0.40 (0.02)	0.42–7.79	2.87 (0.10)	133
	III	0.61–1.65	1.13 (0.52)	2.15–5.83	3.99 (1.85)	2
	IV	1.59–3.86	2.81 (0.52)	2.68–8.50	5.80 (1.20)	4
	V	0.18–2.44	0.66 (0.06)	0.36–8.59	3.03 (0.17)	60



spine thornyhead (*Sebastolobus alascanus*) (Erickson and Pikitch, 1993), also spawn buoyant gelatinous egg masses. It has been proposed that the advantages of releasing eggs in these veils facilitate their dispersal; the egg veil floats near the surface and is subject to the actions of wind, currents, and waves. The veil also serves as protection for eggs against predation because of the presence of obnoxious or toxic substances in the veils (Armstrong et al., 1992). Moreover, the veil may help with the fertilization of eggs. When males are present and the egg ribbon is laid, the ribbon keeps the eggs together and prevents their dispersion through the water. The males then eject milt near the veil to guarantee fertilization of all the eggs (Dahlgren, 1928). Armstrong et al. (1992) suggested that sperm reach oocyte chambers through the pores that connect the chambers when the ribbon is extruded from the female and starts to absorb water.

Another feature of the reproduction of the white anglerfish to highlight is its type of spermatogenesis, which is known to be semicyclic. Spermatogenesis starts inside the cysts that contain germinal cells in different stages of development from spermatogonia to spermatids, but it is not completed within the cyst. During spermatogenesis, the cyst breaks and spermatids are released from the cyst into the lumen of the lobule, where they become spermatozoa. This kind of spermatogenesis has been described previously in the family Lophiidae only in the blackmouth angler (*Lophiomus setigerus*) (Yoneda et al., 1998) and in black anglerfish

Table 2

Oocyte diameters, ranges and means with standard errors (SEs), and histological characteristics of ovarian follicles in white anglerfish (*Lophius piscatorius*), collected from the northwestern Mediterranean Sea between June 2007 and December 2010. SE=standard error, at each stage of oocyte development.

Stages of oocyte development	Mean oocyte diameter (μm) (SE)	Oocyte diameter (μm) range	Histological characteristics
Primary growth stage	82.79 (2.34)	12–203	Nucleus contains a large nucleolus and some peripheral nucleoli. Yolk granules are not present in the cytoplasm.
Cortical alveolar stage	256.10 (3.08)	207–316	Cortical alveolar vesicles and oil droplets appear in the cytoplasm. Yolk granules are not yet present in the cytoplasm. Nucleus is central within the yolk
Vitellogenesis	729.31 (17.58)	324–876	Yolk granules appear between cortical alveolar vesicles. As vitellogenesis advances, yolk granules fill the cytoplasm until they are in contact with the nucleus, which remains in a central position.
Migratory nucleus	939.31 (7.77)	902–1008	Yolk granules and oil droplets start to fuse. Nucleus migrates to one pole of the oocyte.
Hydration	1672.50 (4.77)	1523–1750	Yolk granules form a single mass. Nucleus is not present in the cytoplasm.

(Colmenero et al., 2013). This specialized spermatogenesis also has been found in other deep-sea species of Neoceratiidae (Jespersen, 1984) and of Macruridae (Fernandez-Arcaya et al., 2013), in the shore clingfish (*Lepadogaster lepadogaster*) (Mattei and Mattei, 1978), in species of Blennidae (Lahnsteiner and Patzner, 1990), in a species of *Ophidion* (Mattei et al., 1993), in the dusky jawfish (*Opistognathus whitehursti*) (Manni and Rasotto, 1997), and in species of *Scorpaena* (Muñoz et al., 2002; Sàbat et al., 2009), which also release their eggs in gelatinous substances.

Fecundity

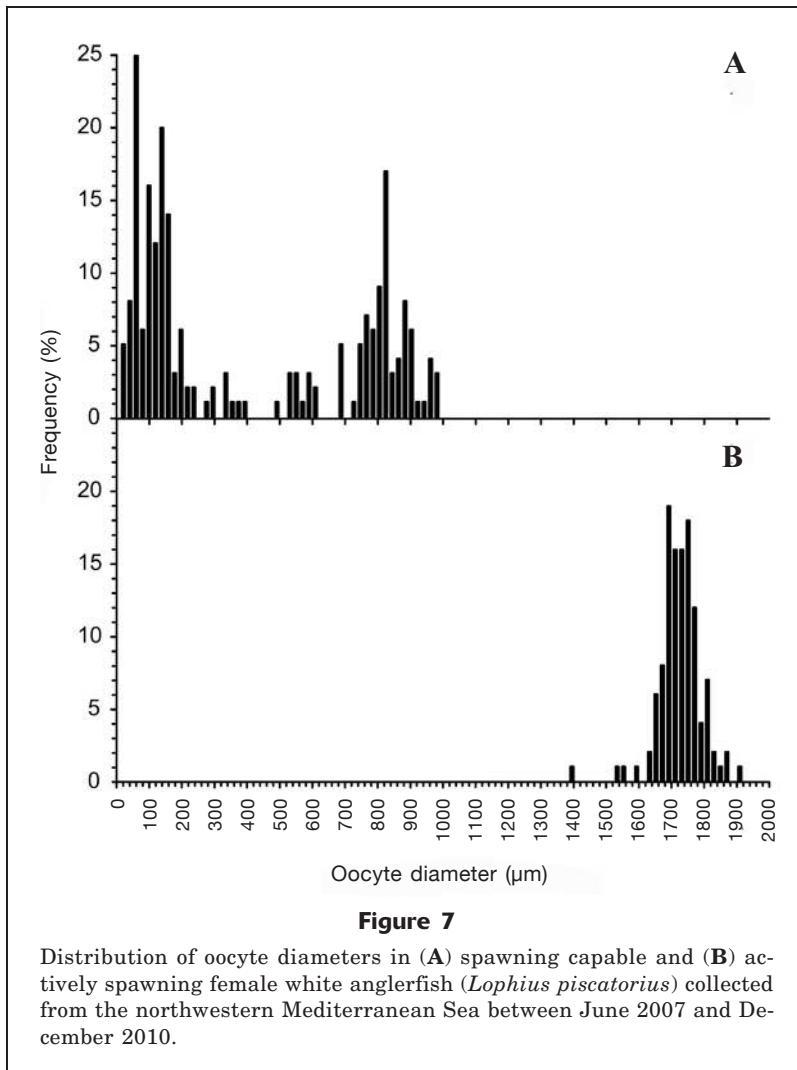
Because of their particular reproduction behavior, which includes a high parental investment in the offspring, white anglerfish are likely to spawn once a year, and the population dynamics of this species are expected to be highly sensitive to external biological and ecosystem factors (ICES⁷). Spawning occurs in deep waters because mature white anglerfish have been described by Hislop et al. (2001) as migrating to deeper water before spawning. The same behavior is seen in yellow goosefish: adult fish migrate to deeper waters in response to seasonal changes in water temperature and gonadal maturation (Yoneda et al., 2002).

These vertical migrations into deeper waters where commercial fishing and scientific surveys cannot reach could be the reason that very few mature females were captured during our study—a trend that is common in other studies of *Lophius* species (Ofstad and Laurenson⁶). Clearly, this low number of mature females will affect the estimation of such reproductive parameters as fecundity.

Generally, deep-sea species have low fecundity and large egg sizes (Gage and Tyler, 1991; Herring, 2002). The white anglerfish has determinate fecundity with values between 661,647 to 885,214 oocytes—levels that are high in comparison with other deep-sea species that inhabit the same depth strata but that are similar to the mean potential fecundity of its Mediterranean congeneric, the black anglerfish (Colmenero et al., 2013). Fecundity values vary among populations as a result of adaptations to local environmental conditions, and they are related to abiotic factors, such as temperature and salinity (Nissling and Dahlman, 2010; Thorsen et al., 2010), and to biotic factors, such as food supply, population density, allocation of energy to reproduction, and fish size (Treasurer, 1981; Merrett, 1994; Nash et al., 2000).

In this study, we were not able to determine correlations between fecundity and these factors because only 2 actively spawning females were collected. Eggs of white anglerfish have been reported to have a mean diameter of 2.72 mm (SD 0.08) (Colmenero et al., 2015b), a size that is considered large for pelagic eggs, which typically range from 0.5 to 5.5 mm in diameter (Ahlstrom and Moser, 1980). Larger eggs have more

⁷ ICES (International Council for the Exploration of the Sea). 2012. Report of the working group on the assessment of southern shelf stocks of hake, monk and megrim (WGHMM), 10–16 May 2012, ICES Headquarters, Copenhagen, Denmark. ICES CM 2012/ACOM:11, 617 p.



yolk, which increases the potential for larval survival (Duarte and Alcaraz, 1989). The only information available about egg diameters for other species of *Lophius* is for yellow goosfish, which occupy a bathymetric range that is similar to that occupied by white anglerfish and have a similar egg size (Yoneda et al., 2001). In contrast, the black anglerfish has an egg diameter of 1.88 mm (SD 0.12), a size that is nearly 1.5 times smaller than the diameters reported for the white anglerfish and yellow goosfish, and inhabits shallower waters than those inhabited by the other 2 species (Colmenero et al., 2015b). A comparative study of egg sizes in deep-sea species found that egg size increased significantly with depth (Fernandez-Arcaya⁸). Egg size is important to offspring survival in many organisms, and large eggs survive better than small ones in environments

⁸ Fernandez-Arcaya, U. 2015. Personal commun. Departamento de Recursos Marinos Renovables, Institut de Ciències del Mar, Passeig Marítim de la Barceloneta, 37-49, 08003 Barcelona, Spain.

where dissolved oxygen is low (Hendry and Day, 2003).

General remarks

In this study, we estimated the spawning season, size at sexual maturity, and fecundity of white anglerfish. Considering the parameter values that we obtained, we can conclude that this species is one that employs a *K* reproductive strategy. In general, this strategy is defined by a large body size, longevity, late maturation, and low fecundity (Pianka, 1970, 1974). A wide range of deep-sea demersal fish species generally display life history characteristics consistent with *K*-selection (Adams, 1980; Gage and Tyler, 1991). These traits make deep-sea fish stocks highly vulnerable to fishing and capable of little resilience to over-exploitation, increasing the urgency for the conservation and management of this group of animals (Koslow et al., 2000; Morato et al., 2006; Norse et al., 2012).

Theoretically, the *K*-strategy for deep-sea fish species should imply a low fecundity; however, some species, such as the North Pacific armorhead (*Pseudopentaceros wheeleri*), wreckfish (*Polyprion americanus*), and splendid alfonso (*Beryx splendens*), have high fecundities (Sedberry et al., 1996; Lehodey et al., 1997; Humphreys, 2000). White anglerfish and species of *Lophius* in general also should be included in this group because of their high fecundity (Afonso-Dias and Hislop,

1996; Colmenero et al., 2013). This variability in reproductive strategy is the result of adaptation to environmental changes, such as temperature, bathymetric pressure, light, and food availability (Herring, 2002; Brown-Peterson et al., 2011). Likely, the high fecundity and the low economic value of the white anglerfish, at least until the last decades of the 20th century, has allowed the stock to be sustainable within acceptable limits. With the recent expansion of anglerfish fisheries, sustainability is in question, and our study is the first step toward an informed assessment of this deep-sea resource and its management with an ecosystem perspective.

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