

Reproductive biology of three gadiform fish species through the Mediterranean deep-sea range (147-1850 m)*

GUIOMAR ROTLLANT¹, JOAN MORANTA², ENRIC MASSUTÍ³, FRANCISCO SARDÀ¹
and BEATRIZ MORALES-NIN²

¹ Institut de Ciències del Mar (ICM/CSIC), CMIMA, Passeig Marítim de la Barceloneta 37-49, E-08003 Barcelona, Spain.
E-mail: guio@icm.csic.es

² Institut Mediterrani d'Estudis Avançats (CSIC-UIB), Miquel Marqués 21, E-07190 Palma de Mallorca, Spain.

³ IEO-Centre Oceanogràfic de les Balears, Moll de Ponent s/n, P.O. Box 291, 07080 Palma de Mallorca, Spain.

SUMMARY: Knowledge of deep-sea reproductive biology is slight and interpretations of reproductive strategies in deep-sea fishes are controversial. Since the Mediterranean is a fairly stable and constant sea, we might expect a consistent pattern of reproduction of deep-sea species. Three gadiform species with a successive bathymetric and an ecological and economical importance in the Mediterranean fishing industry, *Phycis blennoides*, *Mora moro* and *Lepidion lepidion*, were selected for the present study. These three species of gadiforms are sexually dimorphic and their reproductive population is located at the lower zone of their bathymetric range. Females were always bigger than males. The smallest mature male was observed at 19, 32 and 18 cm TL (total length) and the smallest mature female at 20, 34 and 20 cm TL for *P. blennoides*, *M. moro* and *L. lepidion* respectively. The three species are iteroparous and females could be all-at-once or batch-spawners. An autumn mature season was observed for *P. blennoides*, whereas *M. moro* and *L. lepidion* had mature individuals all year round except in summer. Hence, physical constancy at greater depths is able to lengthen the reproductive season and the deepest species has a quasi-continuous reproductive pattern. Similar reproductive tissues have been found in the three species studied, and they show analogous structure with other deep-sea gadiforms and their shallow-water congeners.

Key words: biology, reproduction, gadiform, deep-sea, Mediterranean.

INTRODUCTION

The reproductive pattern of deep-sea species was considered continuous for many years on the basis of the physico-chemical stability of the deep-sea (Orton, 1920). Nevertheless, research undertaken in the last three decades into the biology of exploited deep-sea fish in Australia (Koslow *et al.*, 1995), New Zealand (Clark, 1995), the North

Atlantic (Atkinson, 1995; Kelly *et al.*, 1996; Coggan *et al.*, 1999; Allain, 2001), the North Sea (Bergstad, 1990), Greenland (Bowering and Brodie, 1995; Albert *et al.*, 2001; Gundersen *et al.*, 2001) and Iceland (Magnússon and Magnússon, 1995; Magnússon, 2001) demonstrates that most of the fish species studied have seasonal spawning. The timing and duration of the spawning peak and the maturity age vary with the different species, the area of distribution of each species and the depth-range of the species in each area.

*Received January 1, 2001. Accepted October 8, 2001.

Seasonal reproduction in deep-sea species would not be controlled by light and temperature, as occurs in many shallow-water species (cf. Helfman *et al.*, 1997), but could be controlled by food availability, through organic matter sinking, deep ocean currents or vertical migrations (Gage and Tyler, 1991; Grassle, 1994; Tyler *et al.*, 1994; Young and Eckelbarger, 1994).

In particular, the Mediterranean Sea is physically fairly constant: isothermal below 200 m (~13 °C), with high salinity, low oxygen and oligotrophy (Hopkins, 1984). Despite this constancy, the reproduction pattern in Mediterranean deep-sea species is still controversial. Morales-Nin *et al.* (1996) observed continuous spawning with a peak in autumn for *Alepocephalus rostratus*, while D'Onghia *et al.* (1999, 2000) and Massutí *et al.* (1995) found either seasonal or continuous spawning in different species of macrourids.

In the present study we selected three gadiform species, *Phycis blennoides* (Brünnich, 1768), *Mora moro* (Risso, 1810) and *Lepidion lepidion* (Risso, 1820), because they show successive bathymetric distribution along the upper, middle and lower slope, and share morphological and ecological characteristics (Gallardo, 1980; Massutí *et al.*, 1996; Stefanescu *et al.*, 1992; Moranta *et al.*, 1998). Moreover, *P. blennoides* is already the object of important fishery exploitation in the Catalan Sea (Massutí *et al.*, 1996). Although *M. moro* and *L. lepidion* are not yet exploited in the Mediterranean because the commercial trawling is mainly restricted to a depth shallower than 700 m, the decline of traditional fisheries on the continental shelf and the improvement of trawling systems towards greater depths might support a potential fishery of these species in the Mediterranean Sea. However, prior to an establishment of a new fishery, it will be necessary to improve biological studies, mainly in reproduction, to avoid over-exploitation as occurred in other deep-sea species (Koslow *et al.*, 2000; Clark, 2001).

There are several papers concerning the bathymetric distribution and biology of the gadiform species in the western Mediterranean (Morales-Nin, 1990, Stefanescu *et al.*, 1992a, 1992b; Massutí *et al.*, 1995; Carrassón *et al.*, 1997; Moranta *et al.*, 1998), but there is a lack of information concerning their reproduction. *P. blennoides* spawning and recruitment were studied in the Ionian Sea (Eastern-Central Mediterranean) and a restricted reproduction season of about 3-4 months in late autumn-early winter was found (Matarrese *et al.*, 1998). Although

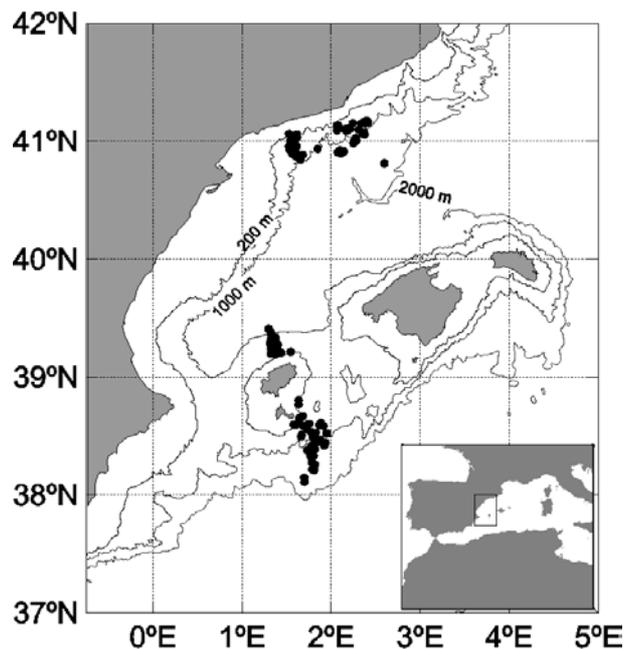


FIG. 1. – Map of the Balearic Sea (western Mediterranean) showing the sampling stations (black dots).

some previous studies have suggested autumn recruitment due to a minor spring spawning peak (Lo Bianco, 1909; Cohen *et al.*, 1990; D'Onghia *et al.*, 1998), the important peak in reproduction in the species occurs in autumn-winter (Matarrese *et al.*, 1998). There are no data for the deeper dwelling species *M. moro* and *L. lepidion*.

The aims of this study are to describe the reproduction pattern of three gadiform Mediterranean deep-sea species: *Phycis blennoides*, *Mora moro* and *Lepidion lepidion*, in terms of their population structure, seasonal pattern and bathymetric distribution.

MATERIAL AND METHODS

Samples were collected by research vessels from April 1991 to May 1998 and in fishing vessels from April to October 1997 in the Balearic sea around Ibiza Island and off the Catalan coast (approximately 2°E 40°N, Fig. 1) from trawls carried out between 147 and 1850 metres (Table 1). Since deep-sea fishing is very complicated and expensive, samples belonging to different cruises were necessary in order to have a representative number of data, and therefore data were processed together.

A total of 3816 *P. blennoides*, 716 *M. moro* and 2524 *L. lepidion* were caught. On board, total length (TL) and standard length (SL) were measured to the cm below, and weighed to the nearest 1 g (Table 2).

TABLE 1. – Data on the sampling cruises analysed in this study. *Sampling: twice a month.¹Sardà *et al.*, 1994, ²Rucabado *et al.*, 1991.

Cruises	Date	Depth range (m)	Number of hauls	Trawl gear
RETRO I	23-26 April 1991	378-1258	9	OTMS-27.5 ¹
RETRO II	7-10 December 1991	433-1850	10	OTMS-27.5
RETRO III	12-13 March 1992	355-1276	9	OTMS-27.5
ZONAP0592	22-30 May 1992	147-1150	39	OTSB-14 ²
RETRO IV	26-28 July 1992	434-1293	9	OTMS-27.5
BATMAN I	15-19 March 1994	650-1230	25	OTMS-27.5
QUIMERA I	15-30 October 1996	264-1715	32	OTMS-27.5
QUIMERA II	5-12 May 1998	195-1622	14	OTMS-27.5
Fishing vessels*	28 April-21 October 1997	432-684	11	Commercial

TABLE 2. – Sample collection of the three gadiform species studied. I = indeterminate, F = females, M = males.

	Number of fish measured	Number of gonad macroscopic observations			Number of gonad histological observations	
		I	F	M	F	M
<i>Phycis blennoides</i>	3816	213	255	243	38	9
<i>Mora moro</i>	716	35	305	178	22	10
<i>Lepidion lepidion</i>	2524	188	269	131	20	0

Their stage of maturity was determined by macroscopic examination of the gonads following the four-point scale (1: immature, 2: early maturation stage, 3: advanced maturation stage, 4: ripe) and gonads were weighed to the nearest 0.1 g. The sex ratio for each size range was tested using a χ^2 -test (Statistica 4.5) with a probability of $p < 0.05$.

On board, 298 gonads were fixed in 10% formaldehyde for 48 h, rinsed in water and stored in 70% ethanol. For the histological analysis a subsample of 99 specimens (TL > 40 cm for *P. blennoides* and *M. moro*, and TL > 30 cm for *L. lepidion*) was taken on the basis of the fishes' gonadosomatic index (calculated by dividing the sum of the components of the gonads by the body weight and multiplying by 100) and the gonad macroscopic observation. A small piece of tissue from the middle of the right gonad was taken. The pieces of the selected ovaries and testes were dehydrated in an ethanol series and embedded in Historesin (Leica). Sections (3 μ m) were cut by a Reichert-Jung Microtome and stained with hematoxyline-eosine or peridic acid Schiff.

Over 100 oocytes from each reproductive stage of the three species were measured and counted using an OPTIMAS 6.0 analyser at a magnification of x40, x100 or x200 depending on the stage of development of the gonads. Cell density was calculated by Munk's formula (1965) modified by Meer and Anker (1984):

$$\text{Cell density} = 10^6 * m [(t + d - 2f) * w]^{-1} \text{ cells/mm}^2$$

where m is the mean number of cells counted, t is the section thickness, d is the mean diameter of the cells, f is the thickness of the smallest cell fragments counted ($f = 0.1 * d$) and w is the width of the sampled strip.

RESULTS

The samples used in this study for the three gadiform species were distributed successively down the continental slope from 147 m to 1850 m (Fig. 2). The length frequency distributions of the three species studied are shown in Figure 3. *P. blennoides* is the biggest species and shows only one modal group while *M. moro* and *L. lepidion* have two and three modal groups respectively. Females always attained a longer size than males. The smallest

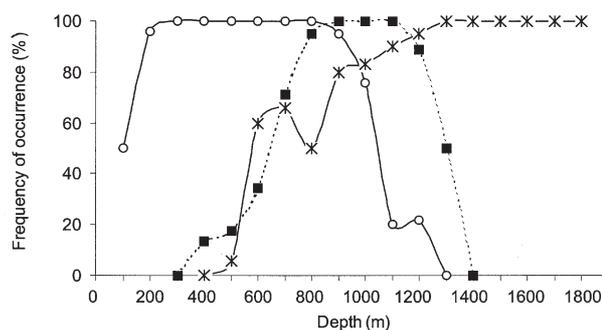


FIG. 2. – Bathymetric distribution of frequency of appearance for *Phycis blennoides* (empty circles) *Mora moro* (full squares) and *Lepidion lepidion* (asterisks).

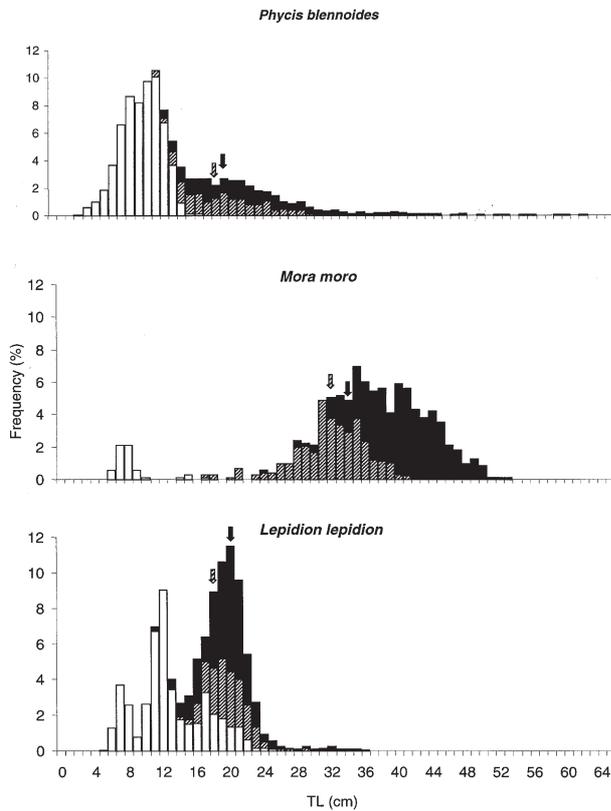


FIG. 3. – *Phycis blennoides*, *Mora moro* and *Lepidion lepidion* length frequency distributions and sex ratios. Open columns = sex indeterminate, hatched columns = males, solid columns = females, hatched arrow = smallest mature male observed and solid arrow = smallest mature female observed.

mature male was observed at 19, 32 and 18 cm TL and the smallest mature female at 20, 34 and 20 cm TL for *P. blennoides*, *M. moro* and *L. lepidion* respectively. The mean size of the three studied species increases with depth (Fig. 4).

P. blennoides females only had mature stages in autumn, while mature males were found from summer to early autumn. Mature females of *M. moro* and *L. lepidion* were found all year round except in summer. *M. moro* mature males were found in autumn and spring and *L. lepidion* mature males in autumn and winter (Fig. 5). The mature individuals were situated at the lower depth of the bathymetric range of *P. blennoides* and at intermediate depth in the case of *L. lepidion*. Mature specimens of *M. moro* were observed in all its depth distribution, but individuals with mature gonads were only observed at the lower range (Fig. 6).

The results of the gonad histological study are very similar, so a common description for the three species could be made. Gonads were internal, longitudinal, paired and laid along the gas bladder. The lengths of both gonads were very similar. No histo-

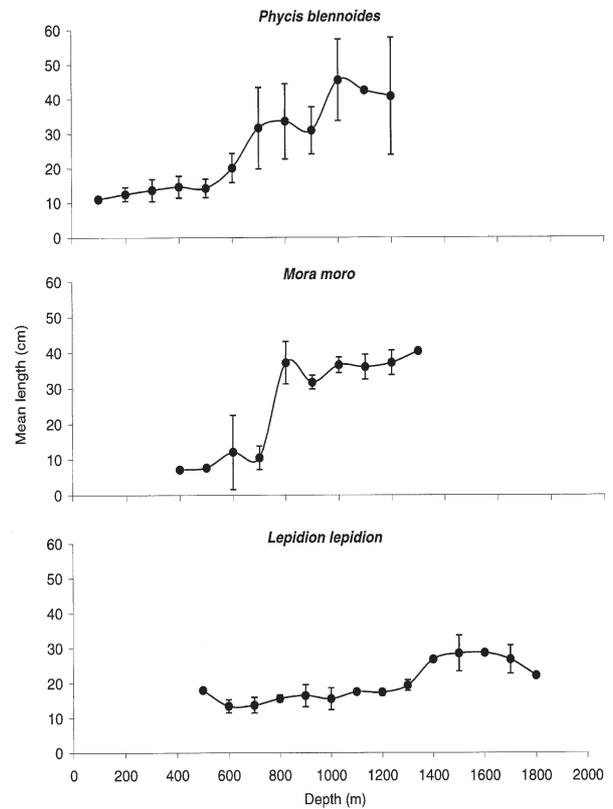


FIG. 4. – Mean length distribution of *Phycis blennoides*, *Mora moro* and *Lepidion lepidion* by depth. Bars represent standard deviation.

logical differences were observed between the left and right gonads or between the anterior and posterior parts of the gonads.

Technical problems made it impossible to study *L. lepidion* testes. *P. blennoides* and *M. moro* had testes with white lobular structure, which grew throughout development. Immature testes showed a rich connective tissue with no reproductive cells visible yet (Fig. 7a). When mature, the testes were well organised in lobes with each lobe surrounded by connective tissue. Each lobe contained several cysts with germ cells at different stages of spermatogenesis (Fig. 7b). One specimen of *P. blennoides* had oocytes in its testis (Fig. 7c).

The histological characteristics of the ovaries enabled us to determinate four maturity stages for the three species of gadiforms:

– Stage I. Immature: the oogonia and oocytes I and II were present. The oocyte I had a large nucleus surrounded by a thin cytoplasm with an intense basophilic substance. This nucleus increased in size and multiple nucleoli appeared generally at its periphery, and then it was named oocyte II.

These ovaries corresponded to slender white-translucent thread.

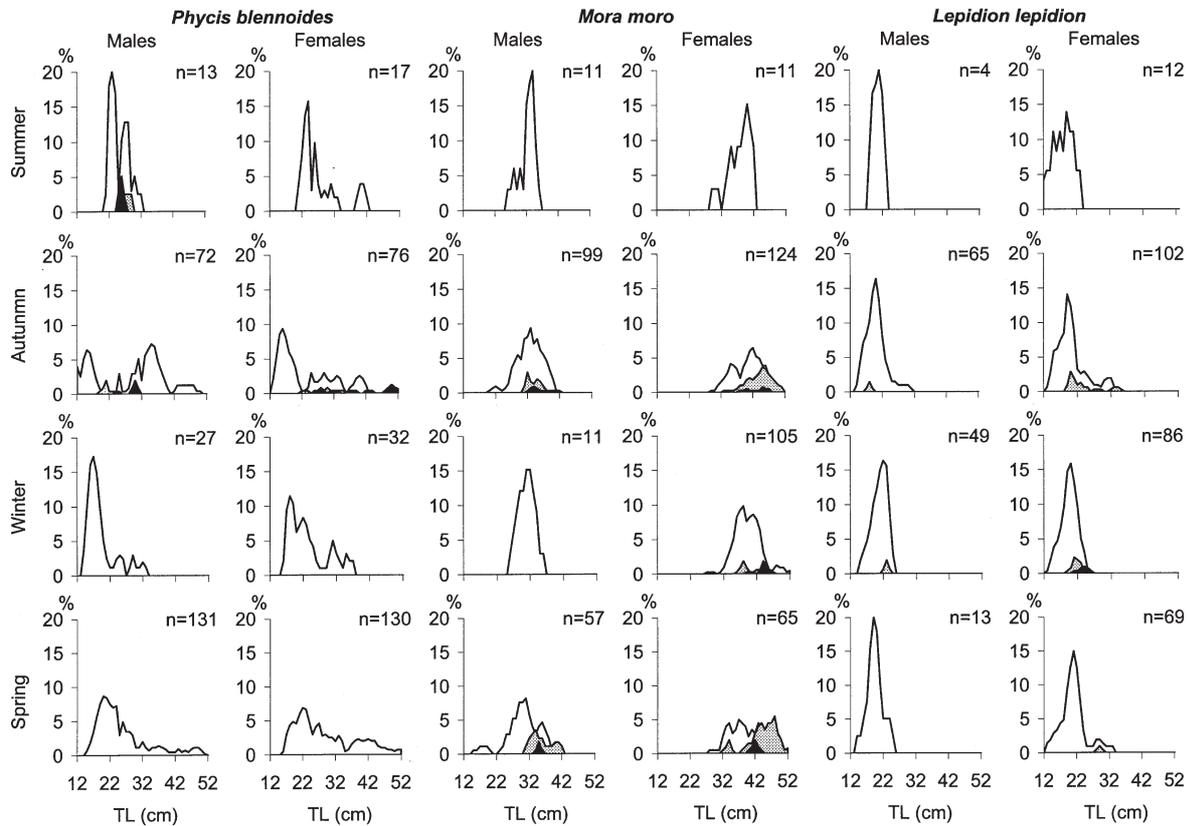


FIG. 5. – Size frequency of males and females and maturity stage in each season by species: *Phycis blennoides*, *Mora moro* and *Lepidion lepidion*. White = immature (stage 1, 2), grey = mature (stage 3) and black = mature (stage 4).

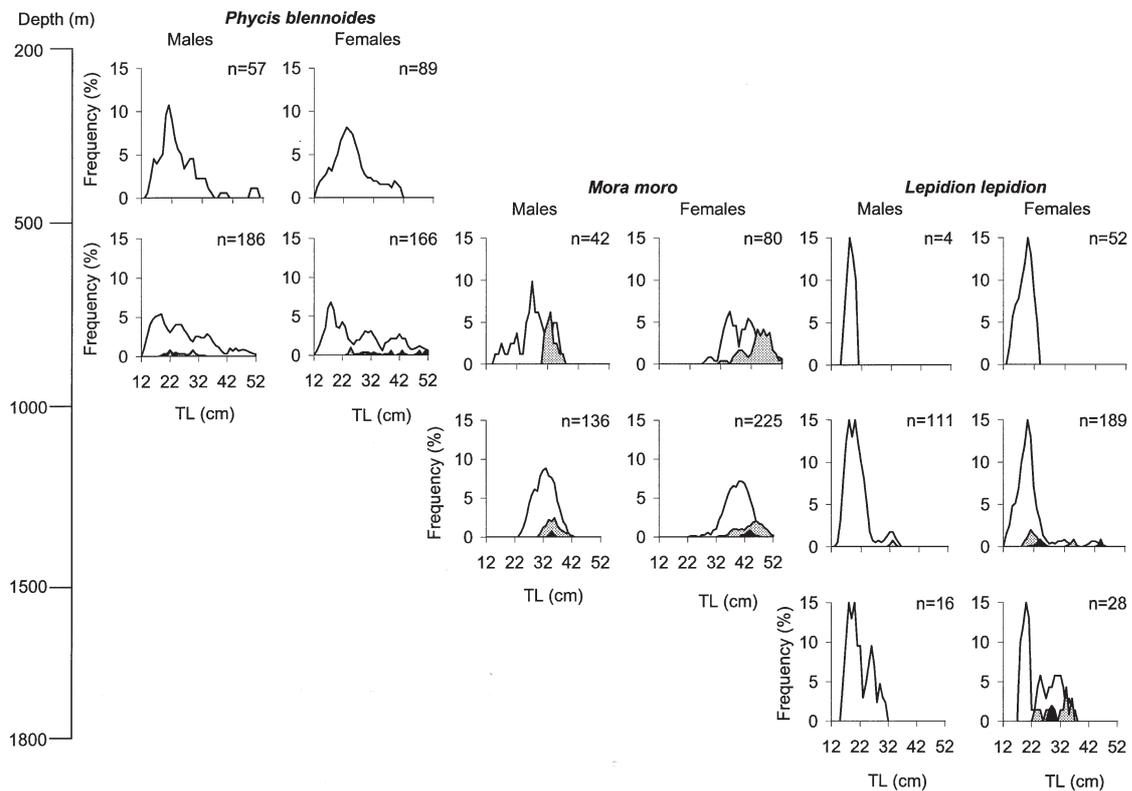


FIG. 6. – Size frequency of males and females and maturity stage by species (*Phycis blennoides*, *Mora moro* and *Lepidion lepidion*) at different depth intervals. White = immature (stage 1, 2), grey = mature (stage 3) and black = mature (stage 4).

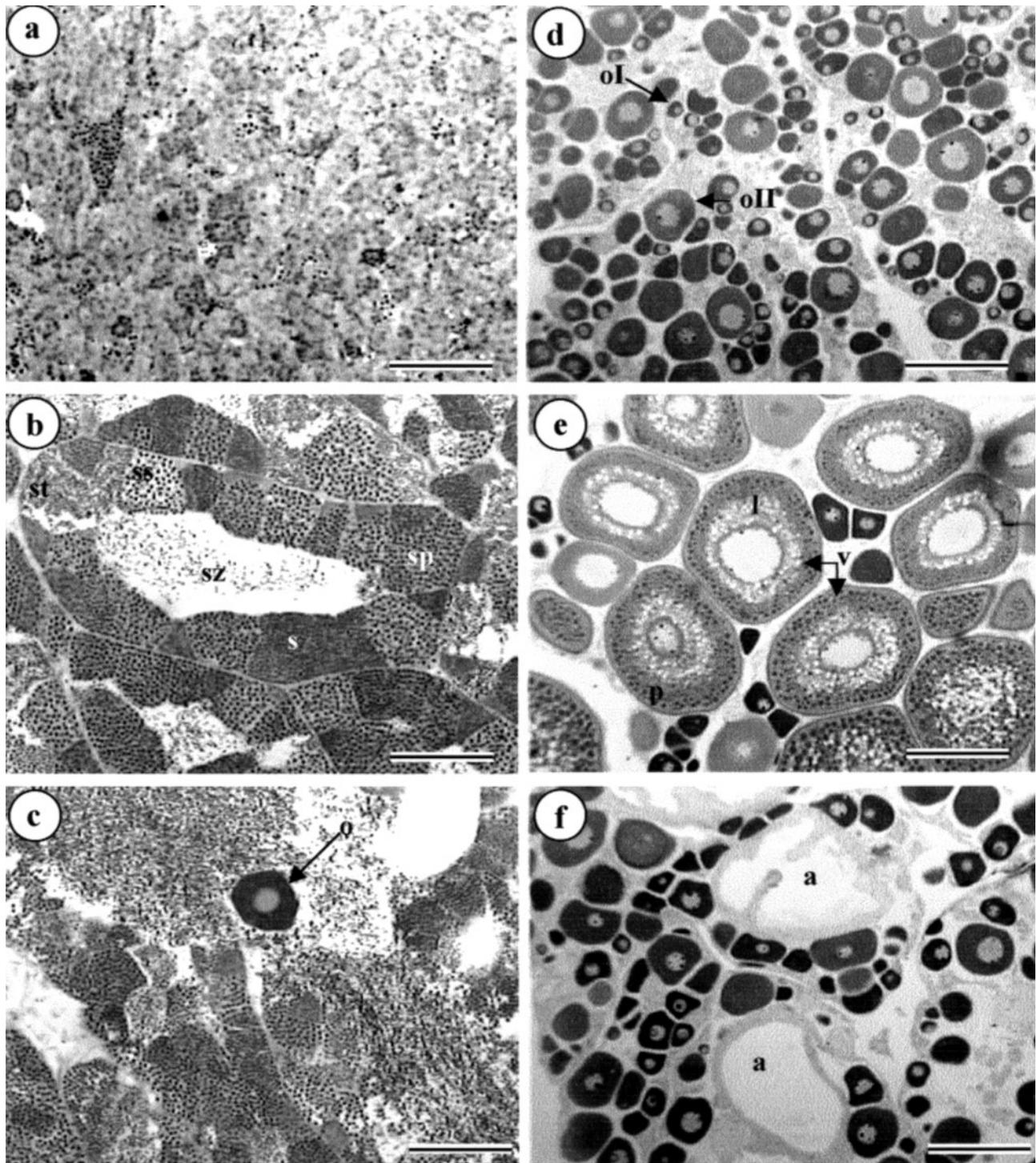


FIG. 7. – Histological sections of gonads: a) Immature male of *Phycis blennoides*, b) Mature male of *Phycis blennoides*, s = spermatogonia, ps = primary spermatocyte, st = spermatids, sz = spermatozoa, c) Intratesticular oocyte (o) in a male of *Phycis blennoides*, d) Immature female (stage II) of *Mora moro*, oI = primary oocyte, oII = secondary oocyte, e) Mature female (stage IV) of *Mora moro*, l = lipid vesicles, p = protein vesicles, v = vitellogenic oocyte, and f) Atresia (a) in stage II ovaries of *Lepidion lepidion*.

– Stage II. Early developing: distinguished by the presence previtellogenic oocytes characterised by a large cytoplasm because of the development of the cytoplasmic organelles. Oocytes I and II were present as well.

The ovaries were a small orange-pink tube.

– Stage III. Late developing: distinguished by the presence of lipid vesicles that constitute the previtellogenic oocyte II. Oocytes I and II and previtellogenic oocytes I were present as well.

The ovaries were a long orange-red tube.

TABLE 3. – Cell characteristics of the ovaries of *Phycis blennoides* (Pb), *Mora moro* (Mmo) and *Lepidion lepidion* (Ll): Density and percentage of the different cell types in each maturity stage.

Species	Stage	Density (cells/mm ²)	Oogonia	Oocyte I	Oocyte II	Previtellogenic oocyte I	Previtellogenic oocyte II	Vitellogenic oocyte	Indeterminates
Pb	I	2.95 x 10 ¹¹	6.52%	3.20%	40.37%				49.91%
	IV	1.10 x 10 ⁹		1.42%	14.17%	10.31%	31.31%	23.58%	19.20%
Mmo	II	2.28 x 10 ¹⁰		2.68%	23.96%	41.57%			31.79%
	III	9.00 x 10 ¹⁰		5.32%	18.09%	37.77%	7.98%		30.85%
	IV	7.67 x 10 ⁹		4.72%	24.53%	26.41%	5.66%	5.97%	32.70%
Ll	II	1.87 x 10 ¹⁰		2.42%	34.54%	25.22%			37.82%

TABLE 4. – Diameter of the ovarian cells (µm) of *Phycis blennoides* (Pb), *Mora moro* (Mmo) and *Lepidion lepidion* (Ll).

Species	Oogonia	Oocyte I	Oocyte II	Previtellic oocyte I	Previtellic oocyte II	Vitellic oocyte
Pb	20.25 ± 3.72	39.47 ± 9.49	45.95 ± 14.69	142.34 ± 18.02	195.36 ± 40.34	305.08 ± 64.43
Mmo		33.19 ± 11.11	51.27 ± 14.75	86.80 ± 24.83	207.54 ± 33.77	249.59 ± 19.31
Ll		24.95 ± 2.12	58.43 ± 21.19	76.41 ± 21.78		

– Stage IV. Gravid: distinguished by the presence of protein yolk granules that constitute the vitellogenic oocytes which occupy most of the ovary. Oocytes I and II, previtellogenic oocytes I and II, and vitellogenic oocytes were present as well.

The characteristics of the ovarian cells for each species are shown in Table 3 and 4. Cell density decreased as the gonads matured. In stage IV of maturity all ovarian cell types occurs but oogonia, and the percentage of previtellogenic oocytes II and vitellogenic oocytes were 4 times greater in *P. blennoides* than in *M. moro*. *L. lepidion* presented the smallest oocytes I and *P. blennoides* the largest vitellogenic oocytes. *P. blennoides* and *M. moro* had immature (Fig. 7d) and well-developed ovaries (Fig. 7e). *L. lepidion* only had females in stage II: high atresia was observed in their ovaries (Fig. 7f). No hydrated oocyte was observed for any species.

DISCUSSION

P. blennoides, the shallowest species studied (maximum frequency of appearance between 200 and 800 m in this study), reached maturity in autumn while the deepest species *M. moro* (800-1200 m) and *L. lepidion* (1000-1800 m) had mature individuals all year round except for summer. Hence, for these species the physical constancy at greater depths in the Mediterranean deep-sea is able to lengthen the reproductive season supporting Orton's hypothesis.

The maturing period observed for *P. blennoides* confirms the spawning period proposed for this species in the Mediterranean from January to March (Svetovidov, 1986; Cohen *et al.*, 1990; Massutí *et al.*, 1996). In the Ionian Sea, mature females were caught from November to January and mature males between August and March (Matarresse *et al.*, 1998). In the western Mediterranean the mature males appear a longer period of time from May to November, while mature females were only seen in autumn. Gordon and Duncan (1985) suggested that spawning of *M. moro* in the Rockall Trough is in June or July, while Cohen (1986) indicated that *M. moro* in the Mediterranean is probably a winter or early spring spawner. No reproduction data about *L. lepidion* have been found in the literature. In the Rockall Trough *Lepidion eques* had a seasonal reproductive cycle with spawning in April and May (Gordon *et al.*, 1979).

In the Mediterranean, other gadiform species living in the upper-middle slope can present a continuous reproductive pattern as in *Nezumia sclerorhynchus* (D'Onghia *et al.*, 1996, 1999, 2000), *N. aequalis* (Massutí *et al.*, 1995) and *Hymenocephalus italicus* (Massutí *et al.*, 1995; D'Onghia *et al.*, 1996), a quasi-continuous strategy with a reproductive peak as in *Coelorhynchus coelorhynchus* (Massutí *et al.*, 1995; D'Onghia *et al.*, 1996, 1999), or a seasonal pattern as in *Trachyrhynchus trachyrhynchus* (D'Onghia, 1996). The lower slope macrourid studied, *Coelorhynchus labiatus*, has an autumn-winter spawning (Massutí *et al.*, 1995). The

other deep-sea species studied in the area, *A. rostratus*, with a depth distribution in the lower middle slope, has a high reproductive activity all year round with a peak in autumn (Morales-Nin *et al.*, 1996). The overview about reproductive biology of deep-sea fishes in the Mediterranean cited above and the reproductive studies performed all over the world in deep-sea gadiform species (Bergstad, 1990; Clark, 1995; Koslow *et al.*, 1995; Albert *et al.*, 2001; Allain, 2001; Gundersen *et al.*, 2001; Magnússon, 2001) demonstrate that in this zoological group spawning varies with the different species and their area of distribution. Hence, it is not possible to identify a reproductive tendency for these species. Following Tyler *et al.* (1994) and Grassle (1994), the reproductive strategy should be related to changes in feeding. Recently, high concentrations of suspended particles have been related to reproductive processes and the spatial distribution of deep-water benthic shrimps (Puig *et al.*, 2001). Nevertheless, no seasonal changes in the diet composition of *P. blennoides* have been noted (Macpherson, 1978).

The three studied species, *P. blennoides*, *M. moro* and *L. lepidion* are dimorphic in size (females larger than males) with sex ratios weighted in favour of females. This can be explained because many slope-dwelling fish females become mature when they are reaching their maximum total length and somatic growth slows down (Gordon *et al.*, 1995). *M. moro* and *L. lepidion* have several modal peaks of length. The first mature specimen had a total length corresponding to the beginning of the last peak, as in *Coryphaenoides rupestris* (Merrett and Haedrich, 1997). Also in the case of *P. blennoides*, the length frequency distribution clearly separates the juveniles from the adults indicating a seasonal recruitment, but this is a common feature of many deep-sea fish and invertebrates (Gordon *et al.*, 1995).

This is the first morphological study of the gonads of *P. blennoides*, *M. moro* and *L. lepidion*. The histological results of the reproductive systems of these three species of gadiforms seem to indicate that they are very similar. Cystic spermatogenesis was observed in *P. blennoides* and *M. moro*, as previously in the North Atlantic specimens of *C. rupestris* (Alekseyeva *et al.*, 1992). Testicular aplasia had been described in *Merluccius hubbsi* (Louge and Christiansen, 1992). In the present study immature testes also had a large amount of connective tissue, as shown in the cod aplasia. Some intratesticular oocytes were observed in *P. blennoides*. Many fishes go through a prematura-

tional sex change, differentiating but not maturing first as females, with some individuals later changing to males (Shapiro, 1992).

In deep-sea gadiforms, the histological characteristics of the ovaries have only been described in *C. rupestris* (Alekseyeva *et al.*, 1992; Kelly *et al.*, 1996), *Macrourus berglax* (Eliassen and Falk-Petersen, 1985; Murua and Motos, 2000), and partially in *Nezumia stelgidolepis* (Hoff *et al.*, 2000). The fourth stages of development described here for *P. blennoides*, *M. moro* and *L. lepidion* are homologous at the first stages described in the above mentioned species. However, oil drop coalescence and hydrated oocytes seem to escape our sampling since the mature oocytes measured in the present study were around 300 µm and hydrated oocytes in these macrourids were bigger than 1.6 mm.

Gravid females (stage IV) had only 24% of vitellogenic oocytes for *P. blennoides* and 6% for *M. moro*, revealing that oocytes did not exhibit synchronous development. Whether these species are all-at-once or batch-spawners as described in other deep-sea gadiforms (Eliassen and Falk-Petersen, 1985; Alekseyeva *et al.*, 1992; Kelly *et al.*, 1996; Murua and Motos, 2000; Allain, 2001) is hard to conclude since the samples belong to different stocks and different years due to their difficulty of extraction.

In conclusion, the shallowest studied species, *P. blennoides*, shows a seasonal pattern and females seem to be all-at-once spawners while the deepest species, *M. moro* and *L. lepidion*, living in a stable and oligotrophic medium, show a quasi-continuous reproductive pattern and their females seem to be batch-spawners. Hence, for these species the physical constancy at greater depths is able to lengthen the reproductive season in the Mediterranean deep-sea. The deep-sea adaptations include ecological and ethological issues, but the main similarities observed between the morphology of their gonads and the gonads of their shallow-water congeners suggest Grassle's hypothesis (1994) that phylogenetic constraints affect reproduction more than deep-sea adaptations.

ACKNOWLEDGEMENTS

This paper is a result of the Spanish CICYT Projects RETRO (MAR90-757), ZONAP (PB90-O166) and BATMAN (AMB93/0283) and the European Commission project EU FAIR (CT 95-0655). The

authors would like to thank Drs. P. Abelló, M. Ballesteros, A. Bozzano, J.E. Cartes, J.B. Company, L. Dantart, D. Lloris, F. Maynou, P. Torres, J. Rucabado, C. Ruíz-Altaba and C. Stefanescu for their help during sampling cruises, the Captains and crews of R/V “García del Cid”, F/V “La Blava” and F/V “Bonamar”, Ms. E. García and S. Palenzuela for their technical support, Dr. R.I. Ochoa and R. Torres for their histological support, and F. Maynou for providing Figure 1.

REFERENCES

- Albert, O.T., E.M. Nilssen, A. Stene, A.C. Gundersen and K.H. Nedreaas. – 2001. Maturity classes and spawning behavior of Greenland halibut (*Reinhardtius hippoglossoides*). *Fish. Res.*, 51: 217-228.
- Alekseyeva, F.Y., Y.I. Alekseyev and A.N. Zakharov. – 1992. Vitellogenesis, nature of spawning, fecundity, and gonad maturity stages of the roundnose grenadier, *Coryphaenoides rupestris*, in the North Atlantic. *J. Ichthyol.*, 33: 32-45.
- Allain, V. – 2001. Reproductive strategies of three deep-water benthopelagic fishes from the northeast Atlantic Ocean. *Fish. Res.*, 51: 165-176.
- Atkinson, D. B. – 1995. The biology and fishery of roundnose grenadier (*Coryphaenoides rupestris* Gunnerus, 1765) in the north west Atlantic. In: Hopper, A. G. (ed.), *Deep-water fisheries of the north Atlantic oceanic slope*, pp. 51-111. Netherlands: Kluwer Academic Publishers.
- Bergstad, O.A. – 1990. Distribution, population structure, growth and reproduction of roundnose grenadier *Coryphaenoides rupestris* (Pisces: Macrouridae) in the deep waters of the Skagerrak. *Mar. Biol.*, 107: 25-39.
- Bowering, W. R. and W.B. Brodie. – 1995. Greenland halibut (*Reinhardtius hippoglossoides*). A review of the dynamics of its distribution and fisheries off eastern Canada and Greenland. In: A.G. Hopper, (ed.), *Deep-water fisheries of the north Atlantic oceanic slope*, pp. 114-160. Netherlands: Kluwer Academic Publishers.
- Carrasón, M., J. Matallanas and M. Casadevall. – 1997. Feeding strategies of deep-water morids on the western Mediterranean slope. *Deep-sea Res.*, 44(9-10): 1685-1699.
- Clark, M. – 1995. Experience with the management of orange roughy (*Hoplostethus atlanticus*) in New Zealand, and the effects of commercial fishing on stocks over the period 1980-1993. In: Hopper, A. G. (ed.), *Deep-water fisheries of the north Atlantic oceanic slope*, pp. 251-266. Netherlands: Kluwer Academic Publishers.
- Clark, M. – 2001. Are deepwater fisheries sustainable? - the example of the orange roughy (*Hoplostethus atlanticus*) in New Zealand. *Fish. Res.*, 51: 123-135.
- Cohen, D. M. – 1986. Family Moridae. In: P. J. P. Whitehead, M.L. Bauchot, J.C. Hureau, J. Nielsen and E. Tortonese (eds.), *Fishes of the north-eastern Atlantic and the Mediterranean*, pp. 713-723. Bungalow: UNESCO
- Cohen, D. M., T. Inada, T. Iwamoto and N. Scialabra. – 1990. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cod, hake, grenadiers, and other gadiform fishes known to date. *FAO Fisheries Synopsis*, 10: 1-442.
- Coggan, R.A., J.D.M. Gordon and N.R. Merrett. – 1999. Aspects of the biology of *Nezumia aequalis* from the continental slope west of the British Isles. *J. Fish Biol.*, 54: 152-170.
- D’Onghia, G., A. Tursi, P. Maiorano, A. Matarrese and M. Panza. – 1998. Demersal fish assemblages from the bathyal grounds of the Ionian Sea (middle-eastern Mediterranean). *Ital. J. Zool.*, 65, suppl.: 287-292.
- D’Onghia, G., M. Basanisi, A. Matarrese and F. Megli. – 1999. Reproductive strategies in macrourid fish: seasonality or not? *Mar. Ecol. Prog. Ser.*, 184: 189-196.
- D’Onghia, G., M. Basanisi and A. Tursi. – 2000. Population structure, age and growth of macrourid fish from the upper slope of the Eastern-Central Mediterranean. *J. Fish Biol.*, 56: 1217-1238.
- Eliassen, J. E. and I.B. Falk-Petersen. – 1985. Reproductive biology of the roughhead grenadier (*Macrourus berglax* Lacepède) (Pisces, Gadiformes) from the continental slope of northern Norway. *Sarsia*, 70: 59-67.
- Gage, J. D. and P.A. Tyler. – 1991. *A natural history of organisms at the deep-sea floor*. Cambridge: Cambridge University Press.
- Gallardo, M. – 1980. *Características biológicas de Phycis blennoides (Brünnich, 1968) con especial referencia a algunas modificaciones debidas al efecto de la explotación pesquera*. PhD. Thesis. Univ. de Barcelona.
- Gordon, J.D.M. – 1979. Seasonal reproduction in deep-sea fish. In: E. Naylor and R.G. Hartnoll (eds.), *Cyclic phenomena in marine plants and animals*, pp. 223-229. Oxford, Pergamon Press.
- Gordon, J. D. M. and J.A.R. Duncan. – 1985. The biology of fish of the family Moridae in the deep-water of the Rockall trough. *J. mar. biol. Ass. U.K.*, 65: 475-485.
- Gordon, J. D. M., N.R. Merrett and R.L. Haedrich. – 1995. Environmental and biological aspects of slope dwelling fishes of the north Atlantic. In: A.G. Hopper, (ed.), *Deep water fisheries of the North Atlantic Oceanic Slope*, pp. 1-26. Dordrecht: Kluwer Academic Publishers.
- Grassle, J. F. – 1994. Ecological Patterns in the deep-sea benthos: How are they related to reproduction, larval biology, and recruitment? In: C.M. Young and K.J. Eckelbarger (eds.), *Reproduction, larval biology, and recruitment of the deep-sea benthos*, pp. 306-314. New York.
- Gundersen, A.C., J.E. Ronnerberg and J. Boje. – 2001. Fecundity of Greenland halibut (*Reinhardtius hippoglossoides* Walbaum) in East Greenland waters. *Fish. Res.*, 51: 229-236.
- Helfman, G. S., B.B. Collette and D.E. Facey. – 1997. *The diversity of fishes*, Malden: Blackwell Science.
- Hoff, G.R., T.W. Buckley, J.C. Drazen and K.M. Duncan. – 2000. Biology and ecology of *Nezumia liolepis* and *N. stelgidolepis* from the west coast of North America. *J. Fish Biol.*, 57: 662-680.
- Hopkins, T. S. – 1984. Physics of the Sea. In: R. Margalef (ed.), *Western Mediterranean*, pp. 100-125. Barcelona: Pergamon Press.
- Kelly, C.J., P.L. Connolly and J.J. Bracken. – 1996. Life histories and reproduction. Maturity, oocyte dynamics and fecundity of the roundnose grenadier from the Rockall Trough. *J. Fish Biol.*, 49(Supplement): 5-17.
- Koslow, J.A., J. Bell, P. Virtue and D.C. Smith. – 1995. Fecundity and its variability in orange roughy: effects of population density, condition, egg size, and senescence. *J. Fish Biol.*, 47: 1063-1080.
- Koslow, J.A., G.W. Boehlert, J.D.M. Gordon, R.L. Haedrich, P. Lorance and N. Parin. – 2000. Continental slope and deep-sea fisheries: implications for a fragile ecosystem. *ICES J. Mar. Sci.*, 57: 548-557.
- Lo Bianco, S.E. – 1909. Notizie biologiche riguardanti specialmente il periodo di maturità sessuale degli animali del Golfo di Napoli. *Mitt Zool Stat Neapel*, 19: 1-513.
- Louge, E.B. and H.E. Christiansen. – 1992. Aplasia testicular en merluza *Merluccius hubbsi*. *Atlántica, Río Grande*, 4: 121-127.
- Macpherson, E. – 1978. Régimen alimentario de *Phycis blennoides* (Brünnich) y *Antonogadus megalokinodon* (Kolombatovic) (Pisces:Gadidae) en el Mediterráneo Occidental. *Invest. Pesq.*, 42: 455-466.
- Magnússon, J.V. – 2001. Distribution and some other biological parameters of two morid species *Lepidion eques* (Günther, 1887) and *Antimora rostrata* (Günther, 1878) in Icelandic waters. *Fish. Res.*, 51: 267-281.
- Magnússon, J.V. and J. Magnússon. – 1995. The distribution, relative abundance, and biology of the deep-sea fishes of the Icelandic slope and Reykjanes ridge. In: A.G. Hopper (ed.), *Deep-water fisheries of the north Atlantic oceanic slope*, pp. 161-199. Netherlands: Kluwer Academic Publishers.
- Massutí, E., B. Morales-Nin and C. Stefanescu. – 1995. Distribution and biology of five grenadier fish (Pisces: Macrouridae) from the upper and middle slope of the northwestern Mediterranean. *Deep-Sea Res.*, 42(3): 307-330.
- Massutí, E., B. Morales-Nin and D. Lloris. – 1996. Bathymetric distribution and recruitment patterns of *Phycis blennoides* (Pisces:

- Gadidae) from the slope of the northwestern Mediterranean. *Sci. Mar.*, 60(4): 481-488.
- Matarrese, A., G. D'Onghia, M. Basanisi and F. Mastrototaro. – 1998. Spawning and recruitment of *Phycis blennoides* (Phycidae) from the north-western Ionian Sea (Middle-eastern Mediterranean). *Ital. J. Zool.*, 65: 203-209.
- Meer, H. J. van der and G. Ch. Anker. – 1984. Retinal resolving power and sensitivity of the phototopic system in seven Haplochromine species (Teleostei, Cichlidae). *Netherlands J. Zool.*, 34: 197-209.
- Merrett, N. R. and R.L. Haedrich. – 1997. *Deep-sea demersal fish and fisheries*, London: Chapman & Hall.
- Morales-Nin, B. – 1990. A first attempt at determining growth patterns of some Mediterranean deep-sea fishes. *Sci. Mar.*, 54(3): 241-248.
- Morales-Nin, B., E. Massutí and C. Stefanescu. – 1996. Distribution and biology of *Alepocephalus rostratus* from the Mediterranean Sea. *J. Fish Biol.*, 48: 1097-1112.
- Moranta, J., C. Stefanescu, E. Massutí, B. Morales-Nin and D. Lloris. – 1998. Fish community structure and depth-related trends on the continental slope of the Balearic Islands (Algerian basin, western Mediterranean). *Mar. Ecol. Prog. Ser.*, 171: 247-259.
- Munk, O. – 1965. *Omosodium lowei* Gunther, 1887. A bathypelagic deep-sea fish with an almost pure-cone retina. *Vidensk Meddr dansk naturh Foren*, 128: 341-355.
- Murua, H. and L. Motos. – 2000. Reproductive biology of rough-head grenadier (*Macrourus berglax* Lacepède, 1801) (Pisces, Macrouridae), in Northwest Atlantic waters. *Sarsia*, 85: 393-402.
- Orton, J.H. – 1920. Sea temperature, breeding and distribution in marine animals. *J. Mar. Biol. Ass. U.K.*, 12: 339-366.
- Puig, P., J.B. Company, F. Sardà and A. Palanques. – 2001. Responses of deep-water shrimp populations to intermediate nepheloid layer detachments on the Northwestern Mediterranean continental margin. *Deep-Sea Res. I*, 48: 1-13.
- Shapiro, D.Y. – 1992. Plasticity of gonadal development and protandry in fishes. *J. Exp. Zool.*, 261: 194-203.
- Stefanescu, C., J. Rucabado and D. Lloris. – 1992a. Deep-living demersal fishes in the Catalan Sea (western Mediterranean) below a depth of 1000 m. *J. nat. Hist.*, 26: 197-213.
- Stefanescu, C., J. Rucabado and D. Lloris. – 1992b. Depth-size trends in western Mediterranean demersal deep-sea fishes. *Mar. Ecol. Prog. Ser.*, 81: 205-213.
- Svetovidov, A.N. – 1986. Family Gadidae. In: P.J.P. Whitehead, M.L. Bauchot, J.C. Hureau, J. Nielsen and E. Tortonese (eds.). *Fishes of the North-eastern Atlantic and Mediterranean*, Vol. 1. 680-710 pp. UNESCO, Bungay.
- Tyler, P.A., L.S. Campos-Creasey and L.A. Giles. – 1994. Environmental control of quasi-continuous and seasonal reproduction in deep-sea benthic invertebrates. In: C.M. Young and K.J. Eckelbarger (eds.). *Reproduction, larval biology, and recruitment of the deep-sea benthos*, pp. 158-178. New York: Columbia University.
- Young, C.M. and K.J. Eckelbarger. – 1994. *Reproduction, larval biology, and recruitment of the deep-sea benthos*. New York: Columbia University, Columbia University.

Scient. ed.: P. Oliver