

SCIENTIA MARINA 72(4)

December 2008, 721-732, Barcelona (Spain)

ISSN: 0214-8358

doi: 10.3989/scimar.2008.72n4721

Spawning pattern and batch fecundity of the European hake (*Merluccius merluccius* (Linnaeus, 1758)) in the western Mediterranean

LAURA RECASENS¹, VELIA CHIERICONI² and PAOLA BELCARI²¹ Institut de Ciències del Mar de Barcelona (ICM-CSIC), Passeig Marítim 37-49, 08003 Barcelona, Catalonia, Spain.
E-mail: laura@icm.cat² Dipartimento di Scienze dell'Uomo e dell'Ambiente, Università di Pisa, Via A. Volta, 6, 56126 Pisa, Italy.

SUMMARY: The spawning cycle of the European hake (*Merluccius merluccius*, (Linnaeus, 1758)) was studied in two western Mediterranean areas, the Catalan Sea and the northern Tyrrhenian Sea, including observation of the monthly seasonal variation of the gonad maturity and the gonadosomatic index (GSI). The estimation of the maturity stages by GSI gave similar values in the two study areas: the spawning stage (IV) was easily distinguished from the other maturity stages and its range of variation showed a low overlap with stage III and no overlap with other stages. Although in both study areas active females were present during all the sampled months, the peak of reproductive activity was concentrated from February to May in the northern Tyrrhenian Sea but from August to December in the Catalan Sea, which was subjected to winter cascading events. Batch fecundity gave similar values in the Catalan and northern Tyrrhenian Seas: 204 and 202 eggs per gonad-free female gram, respectively. An asynchronous oocyte development is suggested for *M. merluccius* in the western Mediterranean.

Keywords: *Merluccius merluccius*, cascading events, spawning pattern, fecundity, western Mediterranean.

RESUMEN: PATRÓN REPRODUCTIVO Y FECUNDIDAD DE LA MERLUZA (*MERLUCCIVS MERLUCCIVS* (LINNAEVS, 1758)) EN EL MEDITERRÁNEO OCCIDENTAL. – Se ha estudiado el ciclo reproductivo de la merluza (*Merluccius merluccius*, (Linnaeus, 1758)) en dos áreas del Mediterráneo occidental, el Mar Catalán y el norte del Mar Tirreno, analizando la evolución mensual de la madurez en las gónadas y el índice gonadosomático (GSI). La estimación del estadio de madurez mediante el GSI dio resultados parecidos en ambas áreas de estudio: el estadio de puesta (IV) resultó fácil de distinguir de los otros estadios de madurez y su rango de variación mostró poca superposición con el estadio III y ninguna con los otros estadios. Aunque en ambas áreas de estudio se encontraron hembras activas durante todos los meses muestreados, el pico de actividad reproductiva se concentró entre febrero y mayo en el norte del Mar Tirreno, mientras que en el Mar Catalán es entre agosto y diciembre, esta última área sujeta en invierno a fenómenos de cascadas submarinas. La fecundidad relativa presentó valores similares en los mares Catalán y Tirreno norte: 204 huevos por gramo de hembras sin gónada y 202, respectivamente. Se sugiere un desarrollo ovocitario asíncrono para *M. merluccius* del Mediterráneo occidental.

Palabras clave: *Merluccius merluccius*, patrón reproductivo, cascadas submarinas, fecundidad, Mediterráneo occidental.

INTRODUCTION

The European hake, *Merluccius merluccius* (Linnaeus, 1758), is widely distributed in the eastern North Atlantic Ocean and the Mediterranean Sea (Alheit and Pitcher, 1995). The species inhabits the

shelf and shelf-break zones throughout the western Mediterranean (Oliver and Massutí, 1995).

M. merluccius is a commercially and ecologically important species in the Mediterranean, where catches increased until 1995 and then abruptly declined to less than half from 1995 to 2002 (52000 to

21000 t), being at present similar to the level of the 1980s (FAO, 2005). Nevertheless, it is still the second most important demersal fish species by landings (after blue whiting, *Micromesistius poutassou*) and one of the most important target species of the western Mediterranean trawl fleet (Sánchez *et al.*, 2007). In the Catalan and northern Tyrrhenian seas, recruits and juveniles are caught by bottom trawls, while the adult population, representing a percentage of between 37 and 46% of the total landings (Sartor *et al.*, 2001), is also caught with longlines and gillnets (Aldebert *et al.*, 1993; Sbrana *et al.*, 2007). In both study areas, as in many zones of the Mediterranean, growth overfishing can be assumed (the hake stock shows signals of growth overexploitation) (Aldebert *et al.*, 1993; Aldebert and Recasens, 1996; Lleonart *et al.*, 2003; FAO, 2005).

Due to its commercial importance, some recent biological studies on this species related to fish and larval distribution, growth, feeding and recruitment have been carried out in the Mediterranean Sea (Bozzano *et al.*, 1997; Morales-Nin *et al.*, 1998; Belcari *et al.*, 2001; Sartini *et al.*, 2002; Maynou *et al.*, 2003; Olivar *et al.*, 2003; Belcari *et al.*, 2004, 2006). The life cycle has been investigated in some areas of the western Mediterranean such as the Gulf of Lions (Recasens *et al.*, 1998) and Santa Pola bay (García-Rodríguez and Esteban, 1995) and studies of some reproductive aspects have been studied in the northern Tyrrhenian Sea (Sbrana and Belcari, 1993; Biagi *et al.*, 1995; Nannini *et al.*, 2001). In Atlantic waters, *M. merluccius* is classified as an asynchronous, indeterminate and batch-spawning species (Murua and Saborido, 2003; Murua and Motos, 2006). A complete study of the reproductive biology of this species in the Mediterranean using a macroscopic and microscopic approach (histology) is still lacking.

The aim of the present work is to study the histological structure of the ovary and the spawning cycle of Mediterranean hake populations, identifying the spawning peaks, and determining females length at first maturity and fecundity parameters. It thus contributes to our knowledge of the general spawning pattern of Mediterranean hake, its variability within the study area and the reproductive potential of this species.

MATERIALS AND METHODS

Adult sampling was carried out in two different areas of the western Mediterranean with a similar lati-

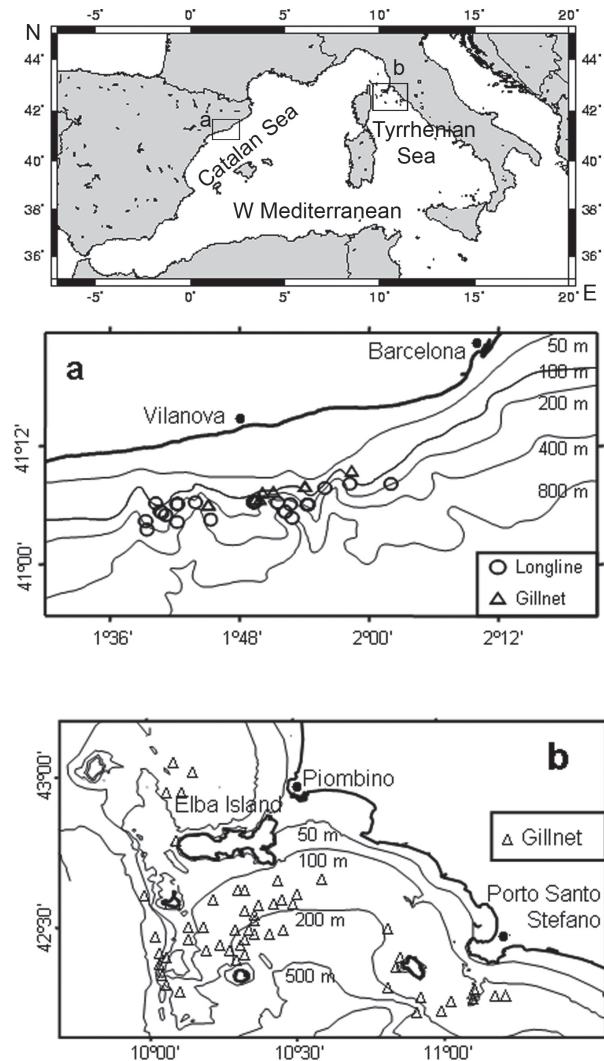


FIG. 1. – Geographical sampling location in western Mediterranean. a) Catalan Sea (O, Longline; Δ, Gillnet); b) northern Tyrrhenian Sea (Δ, Gillnet).

tude: the Catalan and northern Tyrrhenian seas (Fig. 1a,b). In the Catalan Sea, the sampling was carried out on a monthly basis between November 1997 and December 1998 at the port of Vilanova (Table 1a). Specimens were gathered at the port from longline and gillnet boats catching adult hake between 100 and 300 m depth (Fig. 1a). The total number of females sampled was 635, ranging from 24 to 74.5 cm TL (total length). In the northern Tyrrhenian Sea, the sampling was carried out between February 1998 and December 1999 at the ports of Marina di Campo (Elba Island) and Porto Santo Stefano (Table 1b). Specimens were obtained on board gillnet boats targeting hake between 100 and 300 m depth (Fig. 1b) and at ports sampling commercial landings of trawlers. The total number of females sampled was 2729, ranging from 13.5 to 91 cm TL. For each specimen the following parameters were taken:

TABLE 1. – Sampling data on *M. merluccius* females in the Catalan Sea and northern Tyrrhenian Sea.

	Catalan Sea		Northern Tyrrhenian Sea		
	No. females	Length range (cm)	No. females	Length range (cm)	
November 97	20	41.5-69			
December 97	39	34-66			
January 98	21	35-60			
February 98	42	31-66.5	February 98	226	24.5-85
March 98	53	35.5-59.5	March 98	99	27-73.5
April 98	62	41.5-60.5	April 98	116	25-63.5
May 98	73	35.5-51	May 98	347	19.5-73
June 98	56	34.5-48	June 98	44	18-65
July 98	35	30.5-50			
August 98	69	24-54.5			
September 98	15	37-44.5			
October 98	65	35-60			
November 98	58	29-74.5	November 98	132	27-72.5
December 98	27	32.5-51.5	December 98	167	21.5-77
			January 99	96	25.5-64
			February 99	171	13.5-80.5
			March 99	319	28.5-91
			April 99	72	20-72.5
			May 99	122	21-81.5
			June 99	105	20.5-55
			July 99	158	24-67
			August 99	224	23.5-76.5
			September 99	89	25.5-62.5
			October 99	111	24.5-68.5
			November 99	55	26-62.5
			December 99	76	31-75

total length to the lowest half cm, total weight (TW) to 0.1 g, and gonad weight (0.01 g). Macroscopic and microscopic maturity stages were determined according to the Sarano scale (1986), which defines eight stages for hake: I, virgin; II, maturing; III, prespawning; IV, ripe; II+, partial postspawning; V and VI, postspawning; and VII, resting. For fecundity studies ovary-free weight defined as total weight minus gonad weight was also obtained.

Histology

A total of 1574 female gonads, 635 from the Catalan Sea and 939 from the northern Tyrrhenian Sea, were removed, weighed and fixed in buffered 10% formalin. From these, 743 ovaries chosen by length-stratified sampling taking 10 individuals minimum per 2 cm length class (254 for the Catalan Sea and 489 for the northern Tyrrhenian Sea) were selected for histology.

The histological analysis was performed to verify the macroscopic classification, to confirm the partial spawning and to ensure that spawning had not yet started. For each ovary, after dissection and preservation, three subsamples were taken from different parts (anterior, middle and posterior) and exposed to dehydration and inclusion in paraffin. The thickness of the section was about 10 µm. The sections were

coloured by treatment with Carazzi's Hemalum and eosine contrast (Hunter and Macewicz, 1985). The ovarian stages, up to 8, were defined according to the developmental stage of the most advanced oocyte inside the ovary (Sarano, 1986).

Spawning cycle

The spawning cycle of the species was studied. Adult females were used (520 and 1278 in the Catalan and in the northern Tyrrhenian Sea, respectively). Juvenile females were not considered. The monthly evolution of the gonad maturity stages and the gonadosomatic index (GSI, calculated as a percentage of gonad weight in relation to total fish weight) were used to determine the spawning peaks. To ensure the adequate use of GSI the independence of this index in relation to fish size was verified. The isometric relation between gonad weight and fish mass was also verified.

Length at first maturity

Length at first maturity was defined as the length at which 50% of the specimens had already matured at least once, and was estimated considering females in stages higher than stage II. The maturity was determined macroscopically. In the Catalan Sea the fe-

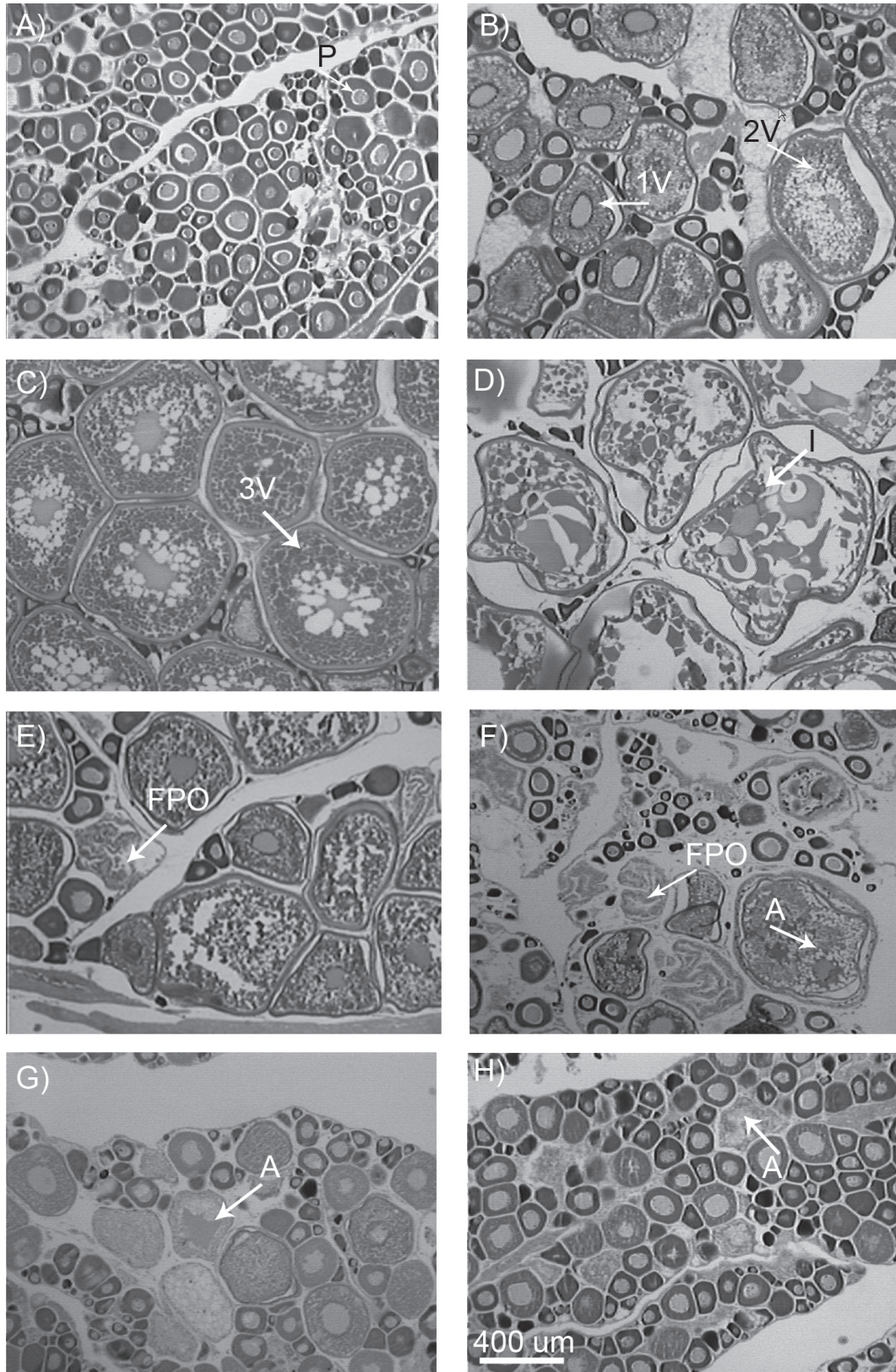


FIG. 2. – Histological sections of ovaries of *Merluccius merluccius* in different maturity stages. A) stage I, immature; B) stage II, in maturation; C) stage III, prespawning; D) stage IV, spawning; E) stage II+, partial postspawning; F) stage V, total postspawning; G) stage VI, regression; H) stage VII, resting (P = previtellogenic oocytes; 1V, 2V, 3V = 1st, 2nd, 3rd vitellogenic stages; I = Hydrated oocytes; FPO = postovulatory follicles; A = atretic oocytes).

TABLE 2. – Oocyte development in European hake of the Mediterranean following the description of Sarano (1986) and Murua *et al.* (1998, 2006). PO, Primary oocytes, -primary growth; P, previtellogenic; 1V, 1st vitellogenic stage (cortical alveoli stage); 2V, 2nd vitellogenic stage; 3V, 3rd vitellogenic, migration stage; I, hydration stage. N/C, nucleus/cytoplasm relationship.

Oocyte	Diameter (µm)	N/C	Microscopic characteristics
PO	≤ 20		Small round cells
P	100-120	0.8-0.5	Spherical, large nucleus, basophilic cytoplasm
1V	150-380	0.5-0.3	Lipid globule deposition starts
2V	300-700	0.4-0.2	Yolk eosinophilic granules appear
3V	530-870	0.3-0.15	Nucleus irregular, animal pole migration, oil drops start fusion
I	1050	-----	Nucleus disintegrated. Hydration begins

males included 115 juveniles and 520 adults, whereas in the northern Tyrrhenian Sea they included 1680 juveniles and 1278 adults. For each length class the percentage of adult females was calculated.

Length at first maturity was estimated by means of a logistic model fitted to the percentage of pre-spawning and spawning specimens per length class (Yeates, 1974), whose equation is:

$$f(x) = 1 \times M / 1 + a \times e^{-bx}$$

where $f(x)$ represents the percentage of mature specimens, M the maximum value of $f(x)$, x the length, a and b parameters of the curve, and e the natural logarithm base.

Fecundity

Fecundity was estimated as batch and relative fecundity. Batch fecundity was defined by the number of eggs released for an individual in each spawning event. Females in advanced maturity stage IV were used. Relative fecundity was calculated as the value of batch fecundity per gram of fish ovary-free body weight (fish weight without ovary).

In order to ensure that the location of tissue samples did not affect the batch fecundity estimation, a two-way ANOVA analysis was carried out. For this purpose a total of 20 individuals were used. Three 0.1 g samples of ovary tissue were taken from each ovary, right and left (the positions of the sample were anterior, middle and posterior of the ovarian lobes).

Only ovaries that showed absence of recent postovulatory follicles in the histological analysis, meaning that the current batch had not yet started, were used (Hunter *et al.*, 1985, 1992; Schaefer, 1996). The hydrated oocytes of 3 samples (0.1 g each) per ovary of female in maturity stage IV were counted. Mean value was calculated, expanded to the total ovary weight and expressed as number of oocytes

per ovary. A total of 58 ovaries from the Catalan Sea and 81 from the northern Tyrrhenian Sea were analysed.

Relationships between relative fecundity, batch fecundity, fish total length and fish gonad-free weight were estimated by fitting power functions.

RESULTS

Histology

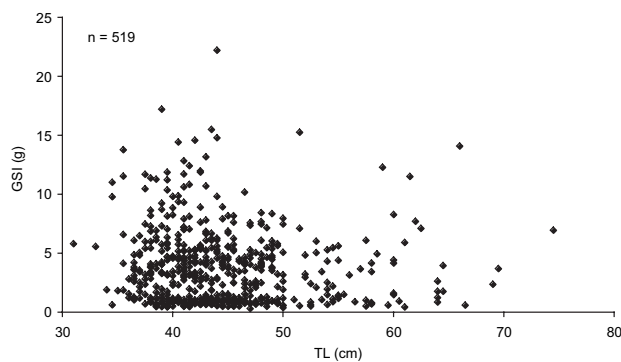
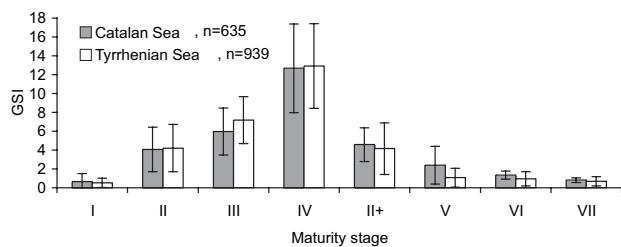
The histological analysis allowed each maturity stage to be characterised following Sarano (1986) (Fig. 2): immature (stage I) (Fig. 2A), in maturation (stage II) (Fig. 2B), prespawning (stage III) (Fig. 2C), spawning (stage IV) (Fig. 2D), partial postspawning (stage II+) (Fig. 2E), total postspawning (stage V) (Fig. 2F), regression (stage VI) (Fig. 2G), and resting (stage VII) (Fig. 2H). Detailed characteristics of oogenesis are listed in Table 2.

The ovary of the spawning females contained oocytes in all development characteristics, hake showing an asynchronous ovary development. The histological analysis was used to determine the minimum oocyte sizes at the beginning and end of vitellogenesis: 150 µm and 870 µm, respectively. A low incidence of oocyte atresia (degeneration of oocytes) occurred throughout the spawning season, but became marked as the spawning season ended and the remaining advanced oocytes in the ovary were reabsorbed.

Concordance between histological maturity stages and macroscopic analysis of the gonads was found for 73% in the Catalan Sea and 59% in the northern Tyrrhenian Sea. Differences in maturity stage determination were centred in stages III and II+, whereas stage IV always showed a good macroscopic and histological concordance. Detailed macroscopic and histological characteristics are listed in Table 3.

TABLE 3. – Correspondence between microscopic and macroscopic maturity ovary staging characteristics.

Stage		Microscopic characteristics	Macroscopic characteristics
I	Juvenile	Only unyolked oocytes: oogonia, primary oocytes growth, previtellogen oocytes	Thin and transparent gonads
II	In maturation	Vitellogenesis has started. Oocytes in 1st (cortical alveoli oocytes) and 2nd vitellogenic phase can be observed	Orange and bigger gonads. Granulated appearance
III	Prespawning	Dominance of oocytes in 2nd and 3rd vitellogenic phase. Migration stage	Orange gonads occupying whole abdominal cavity Oocytes visible
IV	Spawning	Mainly hydrated oocytes are present. Hydration stage	Hydrated oocytes visible, occupying the whole gonad
II+	Partial postspawning	Postovulatory follicles (POF) and oocytes in vitellogenic stage for next batch	Big gonads. Hydrated oocytes present, vascular system conspicuous. Pale orange appearance
V	Total postspawning	Many POFs are present. Most oocytes do not exceed 250 μ m	No hydrated oocytes. Blood spots, vascular system conspicuous. Bloody appearance
VI	Regression	Oocytes > 150 μ m in degeneration	Smaller gonads. Bloody appearance
VII	Resting	Oocytes in previtellogenesis and in 1st vitellogenic phase	Tubular opaque gonads. Pale orange colour.

FIG. 3. – Relation between *M. merluccius* size (TL) expressed in cm and GSI index.FIG. 5. – *Merluccius merluccius* mean female gonadosomatic index (GSI) for each maturity stage. Bars denote SD.

Spawning cycle

There was no relation between fish size and GSI index (Fig. 3). On the other hand, the relationship between fish weight and gonad weight (Fig. 4) was isometric. The t-test carried out with the slope ($b = 1.0119$) shows that b does not differ significantly from 1 ($t = 0.48$, $df = 518$, $prob = 0.63$).

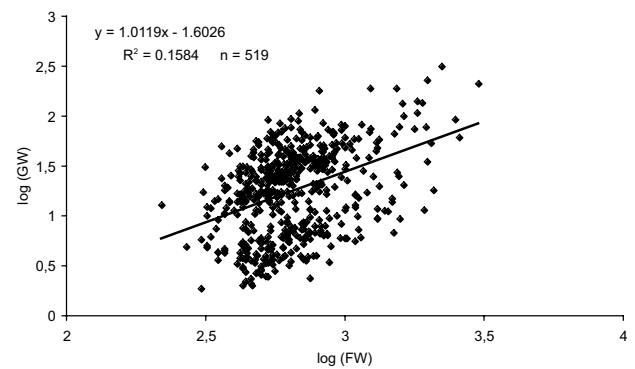


FIG. 4. – Relationship between fish weight (FW) expressed as log (FW) and gonad weight (GW) expressed as log (GW).

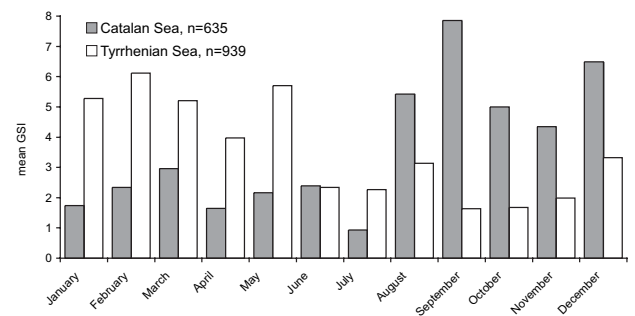


FIG. 6. – Monthly seasonal variation of female gonadosomatic index (GSI).

Female gonadosomatic index (GSI) for each macroscopic maturity stage ranged from a minimum of 0.53-0.68 (maturity stage I) to a maximum of 12.7-12.9 (maturity stage IV), and subsequently decreased after spawning (Fig. 5). Running ripe stage (IV) was easy to distinguish from the other maturity stages and

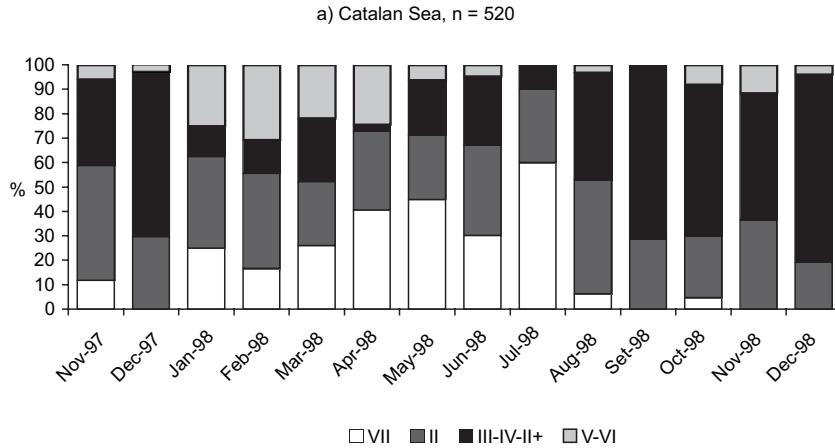


FIG. 7. – Catalan Sea. Monthly percentages of females in different maturity stages during sampling period.

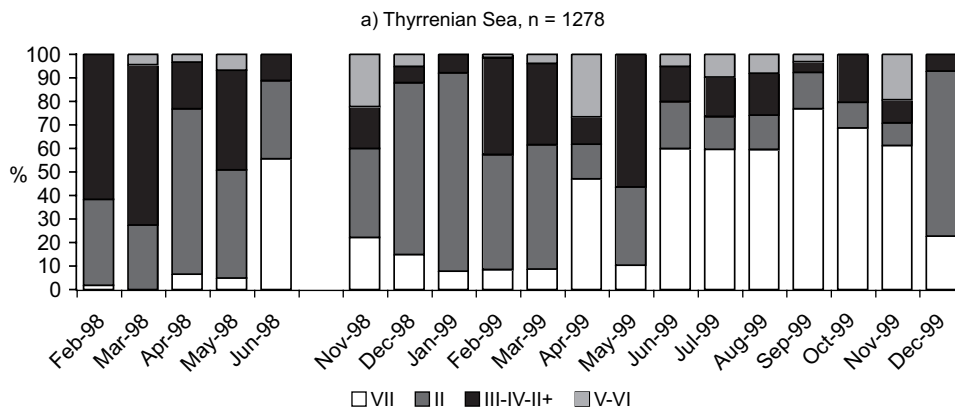


FIG. 8. – Northern Tyrrhenian Sea. Monthly percentages of females in different maturity stages during sampling period.

its range of GSI variation showed a low overlap with stage III and no overlap with other maturity stages.

In both study areas, the monthly evolution of the mean GSI (Fig. 6) and the maturity stages (Figs. 7 and 8) showed that females in advanced maturity (III), spawning (IV) and partial postspawning (II+) were present all year round, but there were considerable differences in the spawning peaks: in the northern Tyrrhenian Sea the reproductive activity was concentrated from January to May, with spawning peaks in February and May, while in the Catalan Sea the main reproductive season occurred from August to December, with spawning peaks in September and December.

Length at first maturity

Length at first maturity was determined as 35.8 cm in the Catalan Sea and 35.1 cm in the northern Tyrrhenian Sea (Fig. 9a,b). The length at which all the females matured at least once was 45-50 cm in both areas.

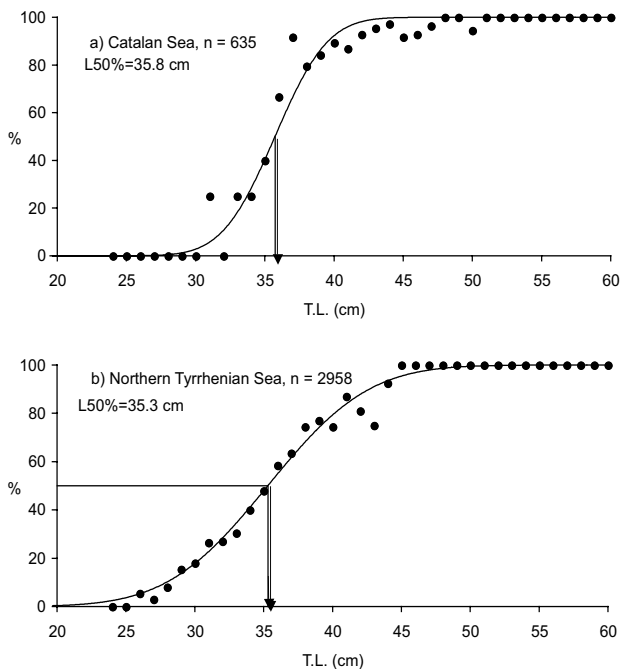


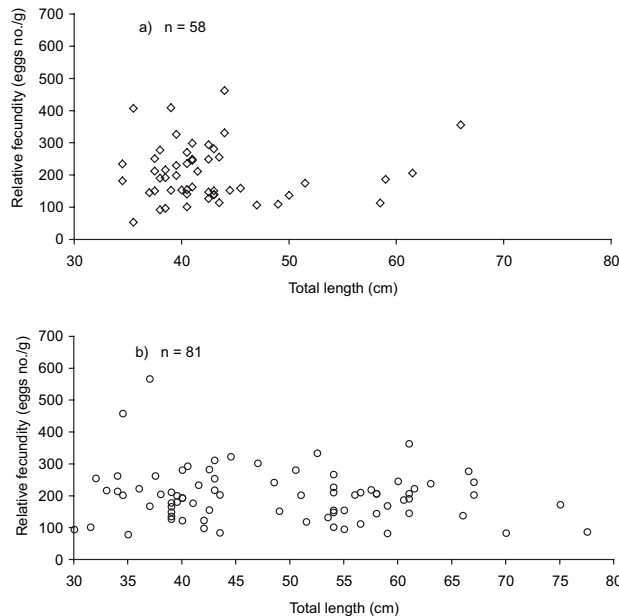
FIG. 9. – Females length at first maturity (50%) in a) Catalan Sea and b) northern Tyrrhenian Sea.

TABLE 4. – Two-way ANOVA of No. eggs/g of ovary tissue in hake. Effect of the position of ovarian tissue samples on the number of hydrated eggs per unit sample weight (g). Positions of the sample were anterior, middle and posterior of ovarian lobes. ns = not significant

Effect	df effect	Mean square effect	df error	Mean square error	F	p-level	
Right vs left ovary	1	1604.44	84	144707.5	0.011	0.916	ns
Position within ovary	2	2080.00	84	144707.5	0.014	0.985	ns
Interaction	2	1524.44	84	144707.5	0.011	0.989	ns

TABLE 5. – Catalan and northern Tyrrhenian Sea fecundity values for hake. SD, Standard Deviation.

		mean num. eggs/fish	SD	minimum	maximum
Batch fecundity	Catalan Sea	126035	100574	17296	681489
	Tyrrhenian Sea	185821	132411	25238	562440
		mean num. eggs/g (gonad free)	SD	minimum	maximum
Relative batch fecundity	Catalan Sea	204.29	87.87	53.07	461.9
	Tyrrhenian Sea	202.35	83.12	80.05	568.6

FIG. 10. – Relative fecundity (eggs number/g) of *M. merluccius* in both areas. a) Catalan Sea; b) Northern Tyrrhenian Sea.

In the northern Tyrrhenian Sea, the minimum size at which specimens were mature was 26.5 for a female of stage II. In the Catalan Sea, a female of 31 cm and stage III was the smallest one in maturation.

Fecundity

The position of the samples of hydrated oocytes within the ovaries had no significant effect on oocyte density. Hydrated oocytes were homogeneously distributed within the ovary, so samples could be taken from any location, right or left, without bias (Table 4).

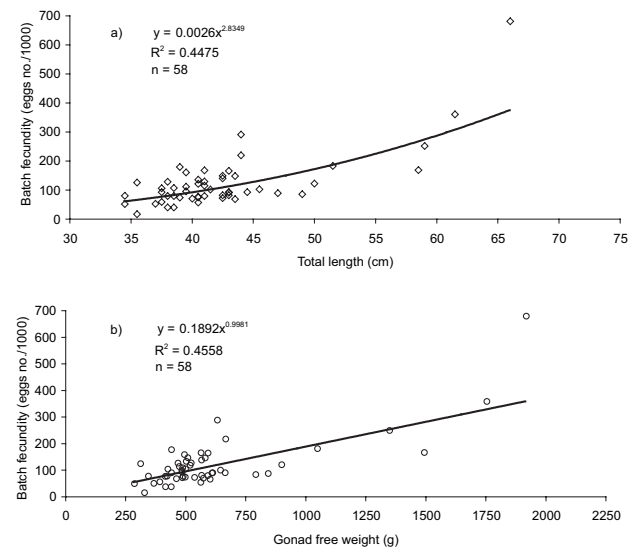


FIG. 11. – Catalan Sea. Relationships between batch fecundity (eggs number/female) and a) total length (cm); b) female gonad-free weight (g). Number of females = 58.

The estimations of the batch fecundity were similar in the two zones. In the Catalan sea it ranged from 17296 for a female of 35.5 cm TL to 681489 for a female of 66 cm TL. In the northern Tyrrhenian Sea it ranged from 25238 for a female of 31.5 cm TL to 562440 for a female of 66.5 cm TL.

In the Catalan Sea the mean relative batch fecundity was 204 eggs g⁻¹ (gonad free female weight) (Table 5), whereas in the northern Tyrrhenian Sea it was 202 eggs g⁻¹ (gonad free). Concerning the relationship between relative batch fecundity and the size of hake, the results indicate that relative fecundity is not size-dependent (Fig. 10) in either area.

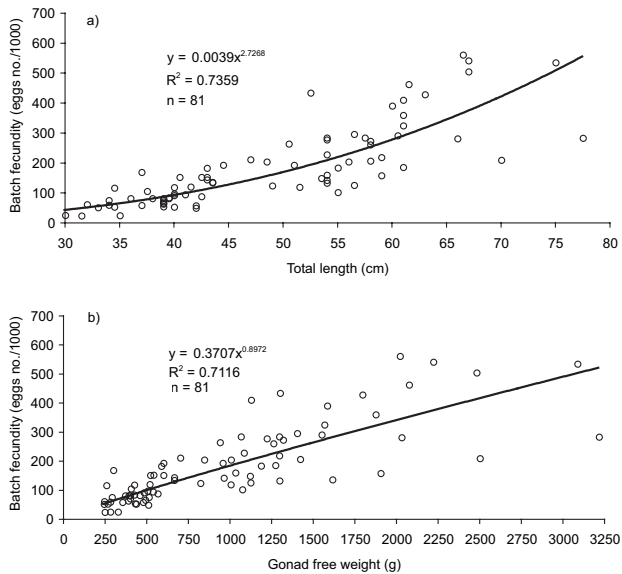


FIG. 12. – Northern Tyrrhenian Sea. Relationships between batch fecundity (eggs number/female) and a) total length (cm); b) female gonad-free weight (g). Number of females = 81.

Fecundity relationships were established for females with hydrated oocytes. Batch fecundity was related to fish length and fish weight (gonad free). The results show a positive relation between these variables and similar values in both areas (Figs. 11 and 12).

DISCUSSION

Histological observations of the maturity stages of the ovaries showed certain differences from the macroscopic evaluations of the gonads (73% agreement in the Catalan Sea and 59% in the northern Tyrrhenian Sea) caused by a more subjective assignment of the macroscopic stage, indicating the importance of the histological approach in performing studies of maturity assessment. This problem could be solved through the joint consideration of reproductive stages such as pre-spawning (III), spawning (IV) and partial post-spawning (II+), and also total post-spawning (V) and regression (VI). The results indicate asynchronous ovary maturation for this species, in which oocytes at all stages of development are present at the same time throughout the reproductive season. The contemporary presence of developing yolked oocytes and postovulatory follicles in the ovaries of many females indicated that *M. merluccius* is a partial spawner, as was suggested previously in the Tyrrhenian Sea (Biagi *et al.* 1995; Nannini *et al.* 2001) and is in agreement with At-

lantic populations (Sarano 1986; Murua *et al.* 1998; Murua and Saborido, 2003).

In the Mediterranean, hake populations seem to have an active reproduction throughout the year, as is shown in this paper and has been reported previously (Papaconstantinou and Stergiou, 1995; Recasens *et al.*, 1998). The same protracted spawning pattern has recently been described for Atlantic hake populations (Murua and Motos, 2006), so this protracted spawning period is a specific characteristic for *M. merluccius*. This pattern has been observed in other *Merluccius* species like *M. capensis* (Kainge *et al.*, 2007) but for other ones like *M. hubbsi* (Macchi *et al.*, 2004) the spawning season lasted fewer months. In our results, advanced mature females (prespawning, III; spawning, IV and partial postspawning, II+) were present during all the sampled months in both study areas, confirming that hake spawns continuously throughout the year. In fact, juvenile recruitment has also been observed throughout the year (Recasens *et al.*, 1998; Belcari *et al.*, 2001; Morales-Nin and Moranta, 2004; Belcari *et al.*, 2006).

The gonadosomatic index by maturity stages showed similar numeric values in the two areas and these values are not dependent of hake size. Thus, we can assume that hake gonads have a similar development in the Catalan and northern Tyrrhenian Seas.

The reproductive pattern shows the alternation of a period of 4-6 months of high activity followed by a period of low activity. Nevertheless, there is a temporal displacement of the spawning season, with spawning peaks occurring earlier in the northern Tyrrhenian Sea (winter and spring) than in the Catalan Sea (summer and autumn). The occurrence of these spawning peaks was confirmed by the finding of eggs and larvae in the study areas (Sartini *et al.*, 2002; Olivar *et al.*, 2003). There is also a correspondence with an autumn recruitment peak in the northern Tyrrhenian Sea (Belcari *et al.*, 2001) and a spring-summer recruitment peak in the Catalan Sea (Recasens *et al.*, 1998; Maynou *et al.*, 2003).

In Atlantic populations, the main spawning peak is centred in winter and early spring (Pérez and Pereiro, 1985; Lucio *et al.*, 2000; Piñeiro and Saínza, 2003; Murua and Motos, 2006), which coincide with the spawning peak in the northern Tyrrhenian.

The influence of temperature does not seem to be a key factor for the determination of spawning peaks of European hake. In the northern Atlantic and western Mediterranean areas sea surface temperature (SST) seasonal variation follows the same trend. Data ob-

tained from the Levitus Atlas (Levitus and Boyer, 1994) show slightly lower temperatures in the Atlantic zone (Biscayan Gulf), but the same trend as in the Catalan and northern Tyrrhenian Seas, with a high correlation between the three series (0.98) (Table 6).

The particular oceanographic conditions of the Catalan Sea may be responsible for the different spawning patterns observed. The phenomenon of surface dense water formation and later cascading events, which occur during the coldest and windiest winters in the Gulf of Lions from January until mid-April, with a current speed that reaches more than 80 cm s^{-1} (Font *et al.*, 2007), can cause unfavourable conditions for hake spawning. These events have been proven to influence recruitment and abundance of deeper species like red shrimp (*Aristeus antennatus*) (Company *et al.*, 2008). In cascading events displacements of shelf water to deeper areas through submarine canyons (Canals *et al.*, 2006) can extend to whole Catalan Sea (Salat *et al.*, 2006). This geographical feature is common in the Gulf of Lions and in the Catalan Sea up to 41°N and 2°E , where the shelf becomes wider due to the effect of the Ebro river delta. Bearing in mind that hake spawners concentrate at the end of the shelf near submarine canyons (Recasens *et al.*, 1998), these strong currents may diminish hake spawning concentration in winter. Therefore, hake population in the Catalan Sea and in the Gulf of Lions develops its spawning peak previously (summer-autumn) (Recasens *et al.*, 1998) when these cascading events do not occur.

Values of length at first maturity for females are in agreement with previous studies performed in the Iberian Mediterranean area (Larraneta, 1970; Sánchez and Martín, 1985; Oliver, 1991; Recasens, 1992; Recasens *et al.*, 1998). A slightly greater length at first maturity of about 42–45 cm TL is also reported in the Mediterranean (Aldebert and Carries, 1989; Biagi *et al.*, 1995) and about 45 cm TL in Atlantic areas (Lucio *et al.*, 2000; Piñeiro and Saínza, 2003).

The fecundity results presented in this study represent the first estimation of reproductive potential of the Mediterranean hake population. Relative batch fecundity shows similar values in the two zones: around 200 eggs g^{-1} (gonad-free weight). These values, which are not significantly different from those obtained in Atlantic populations (165 eggs g^{-1}) (Murua *et al.*, 1998; Murua *et al.*, 2006), represent medium values in comparison with other *Merluccius* species, are higher than those of *M. capensis* (160 eggs g^{-1}) (Osborne *et al.*, 1999) and are lower than

TABLE 6. – 1994 mean monthly sea surface temperature (SST) ($^{\circ}\text{C}$) series data in the northern Atlantic and western Mediterranean areas. Data obtained from Levitus and Boyer (1994).

1994	SST Catalan Sea	SST Northern Tyrrhenian	SST Bizkaian Gulf
January	13	13.3	12.2
February	12.3	12.8	12.5
March	12.4	12.8	12
April	13.4	14	14
May	15.2	16.2	16
June	19	20	19
July	22	23	21.2
August	23	23.8	22
September	22.6	22	21
October	19.4	19.8	17
November	17.2	16.8	16.4
December	14.4	14.4	14

those of *M. hubbsi* (551 eggs g^{-1}) (Macchi *et al.*, 2004). Relationships between fecundity estimations and hake size indicate that the total of eggs number per female increases with size, but in relative terms the egg production per gram of female is similar.

In conclusion, the reproductive parameters of Mediterranean hake populations—size at maturity, oocyte development, reproductive modality and fecundity—have similar biological characteristics in the Catalan and northern Tyrrhenian seas. Furthermore, the results can be included in the normal range for this species in Atlantic waters. However, differences in the occurrence of the spawning peak in the Catalan Sea suggest that environmental factors such as strong winter currents can affect the synchronisation of the hake spawning cycle. These winter events, which originate in the surface water of the Gulf of Lions, can affect biological and ecological characteristics of marine populations, especially those of deeper species but also those of species that spawn or recruit in the shelf-break area.

ACKNOWLEDGEMENTS

This work was supported by the EU LLUCET Project (FAIR CT-97-3522). We wish to thank the LLUCET team and especially Nila Nannini, Loïc Lancou, Dr. Jordi Leonart and two anonymous referees who helped to improve the manuscript.

REFERENCES

- Aldebert, Y. and C. Carries. – 1989. L'exploitation du merlu dans le golfe du Lion. Données complémentaires. *Bull. Soc. Zool. France*, 114: 15-20.

- Aldebert, Y., L. Recasens and J. Lleonart. – 1993. Analysis of gear interactions in a hake fishery: the case of the gulf of Lions (NW Mediterranean). *Sci. Mar.*, 57(2-3): 207-217.
- Aldebert, Y. and L. Recasens. – 1996. Comparison of methods for stock assessment of European hake *Merluccius merluccius* in the Gulf of Lions (Northwestern Mediterranean). *Aquat. Living Resour.*, 9(1): 13-22.
- Alheit, J. and T.J. Pitcher. – 1995. *Hake. Fisheries, Ecology and Markets*. Fish and Fisheries Series 15. Chapman and Hall, London.
- Belcari P., S. De Ranieri, B. Reale, P. Sartor, M. Sbrana and C. Viva. – 2001. Spatial distribution and seasonal concentration of juveniles of European hake (*Merluccius merluccius*). *Rapp. Comm. int. Mer Médit.*, 36: 238.
- Belcari P., A. Ligas and C. Viva. – 2006. Age determination and growth of juveniles of the European hake, *Merluccius merluccius* (L., 1758), in the northern Tyrrhenian Sea (NW Mediterranean). *Fish. Res.*, 78: 211-217.
- Belcari P., C. Viva and P. Martín. – 2004. Discard composition of the European hake *Merluccius merluccius* (Linnaeus, 1758) bottom trawl fishery in two areas of the NW Mediterranean Sea, northern Tyrrhenian Sea and Catalan Sea. *Rapp. Comm. int. Mer Médit.*, 37: 310.
- Biagi F., A. Cesarini, M. Sbrana and C. Viva. – 1995. Reproductive biology and fecundity of *Merluccius merluccius* (Linnaeus, 1758) in the Northern Tyrrhenian Sea. *Rapp. Comm. int. Mer Médit.*, 34: 23.
- Bozzano, A., L. Recasens and P. Sartor. – 1997. Diet of the European hake *Merluccius merluccius* (Pisces: Merlucciidae) in the Western Mediterranean (Gulf of Lions). *Sci. Mar.*, 61(1): 1-8.
- Canals, M., P. Puig, X. Durrieu de Madron, S. Heussner, A. Palanques and J. Fabrés. – 2006. Flushing submarine canyons. *Nature*, 444: 354-357. doi:10.1038/nature05271.
- Company, J.B., P. Puig, F. Sardà, A. Palanques, M. Latasa and R. Scharek. – 2008. Climate Influence on Deep Sea Populations. *PLoS ONE* 3(1): e1431. doi:10.1371/journal.pone.0001431.
- FAO Fishery Resources Division. – 2005. Review of the state of world marine fishery resources. *FAO Fish. Tech. Pap.*, 457: 235 pp.
- Font, J., P. Puig, J. Salat, A. Palanques and M. Emelianov. – 2007. Sequence of hydrographic changes in NW Mediterranean deep water due to the exceptional winter of 2005. *Sci. Mar.*, 71(2): 339-346.
- García-Rodríguez, M. and A. Esteban. – 1995. Algunos aspectos sobre la biología y pesca de la merluza mediterránea *Merluccius merluccius* (Linnaeus, 1758) en la Bahía de Santa Pola (sureste de la Península Ibérica). *Bol. Inst. Esp. Oceanogr.*, 11(1): 3-25.
- Hunter J. R. and B.J. Macewicz. – 1985. Measurement of spawning frequency in multiple spawning fishes. In: R. Lasker (ed.), *An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, Engraulis mordax*, pp. 79-94. Washington, D.C.: U.S. Department of Commerce.
- Hunter J. R., N.C.H. Lo, R.J. Leong and B.J. Macewicz. – 1985. Batch fecundity in multiple spawning fishes. In: R. Lasker (ed.), *An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, Engraulis mordax*, pp. 67-78. Washington, D.C.: U.S. Department of Commerce.
- Hunter J. R., B.J. Macewicz, Lo N. Chyan Huei and C.A. Kimbrell. – 1992. Fecundity spawning and maturity of female Dover sole *Microstomus pacificus*, with an evaluation of assumptions and precision. *Fis. Bull., U.S.*, 90: 101-128.
- Kainge, P., O.S. Kjesbu, A. Thorsen and A.G. Salvanes. – 2007. *Merluccius capensis* spawn in Namibian waters, but do *M. paradoxus*? *Afr. J. Mar. Sci.*, 29(3): 379-392.
- Larrañeta, M.G. – 1970. Sobre la alimentación, la madurez sexual y la talla de primera captura de *Merluccius merluccius* (L.). *Inv. Pesq.*, 34: 267-280.
- Levitius, S. and T. Boyer. – 1994. World Ocean Atlas 1994 Volume 4: Temperature. *NOAA Atlas NESDIS 4*, U.S. Department of Commerce, Washington, D.C.
- Lleonart, J., F. Maynou, L. Recasens and R. Franquesa. – 2003. A bioeconomic model for Mediterranean fisheries, the hake off Catalonia (western Mediterranean) as a case study. *Sci. Mar.*, 67(Suppl. 1): 337-351.
- Lucio, P., H. Murua, and M. Santurtun. – 2000. Growth and reproduction of hake (*Merluccius merluccius*) in the Bay of Biscay during the period 1996-1997. *Ozeanografika*, 3: 325-354.
- Macchi, G.J., M. Pájaro, and M. Ehrlich. – 2004. Seasonal egg production pattern of the Patagonian stock of Argentine hake (*Merluccius hubbsi*). *Fish. Res.*, 67: 25-38.
- Maynou, F., J. Lleonart, and J.E. Cartes. – 2003. Seasonal and spatial variability of hake (*Merluccius merluccius* L.) recruitment in the NW Mediterranean. *Fish. Res.*, 60: 65-78.
- Morales-Nin, B. and J. Moranta. – 2004. Recruitment and post-settlement growth of juvenile *Merluccius merluccius* on the western Mediterranean shelf. *Sci. Mar.*, 68(3): 399-409.
- Morales-Nin B., G.J. Torres, A. Lombarte and L. Recasens. – 1998. Otolith growth and age estimation in the European hake. *J. Fish Biol.*, 53: 1155-1168.
- Murua, H. and L. Motos. – 2006. Reproductive strategy and spawning activity of the European hake, *Merluccius merluccius* (L.), in the Bay of Biscay. *J. Fish Biol.*, 69: 1288-1303.
- Murua, H. and F. Saborido-Rey. – 2003. Female reproductive strategies of marine fish species of the North Atlantic. *J. Northw. Atl. Fish. Sci.*, 33: 23-31.
- Murua, H., L. Motos, and P. Lucio. – 1998. Reproductive modality and batch fecundity of the European hake (*Merluccius merluccius* L.) in the bay of Biscay. *CalCOFI Rep.*, 39: 196-203.
- Murua, H., P. Lucio, M. Santurtún and L. Motos. – 2006. Seasonal variation in egg production and batch fecundity of European hake *Merluccius merluccius* (L.) in the Bay of Biscay. *J. Fish Biol.*, 69: 1304-1316.
- Nannini N., D. Pinna, V. Chiericoni, F. Biagi and P. Belcari. – 2001. Ciclo ovarico di *Merluccius merluccius* (Linnaeus, 1758) nel mar Tirreno settentrionale. *Biol. Mar. Médit.*, 8(1): 745-748.
- Olivar, M.P., G. Quílez and M. Emelianov. – 2003. Spatial and temporal distribution and abundance of European hake, *Merluccius merluccius*, eggs and larvae in the Catalan coast (NW Mediterranean). *Fish. Res.*, 60: 321-331.
- Oliver, P. – 1991. *Dinámica de la población de merluza (Merluccius merluccius L.) de Mallorca (Reclutamiento, Crecimiento y Mortalidad)*. PhD thesis, Univ. Illes Balears.
- Oliver, P. and E. Massutí. – 1995. Biology and fisheries of western Mediterranean hake (*M. merluccius*). In: J. Alheit and T.J. Pitcher (eds.), *Hake. Fisheries, Ecology and Markets*. Fish and Fisheries Series 15, pp. 181-202. Chapman and Hall, London.
- Osborne, R.F., Y.C. Melo, M.D. Hofmeyr and D.W. Japp. – 1999. Serial spawning and batch fecundity of *Merluccius capensis* and *M. paradoxus*. *Afr. J. Mar. Sci.*, 21: 211-216.
- Papaconstantinou, C. and K.I. Stergiou. – 1995. Biology and fisheries of eastern Mediterranean hake (*M. merluccius*). In: J. Alheit and T.J. Pitcher (eds.), *Hake. Fisheries, ecology and markets*, Fish and Fisheries Series, 15, pp. 149-180. Chapman and Hall, London.
- Pérez, N. and F.J. Pereiro. – 1985. Aspectos de la reproducción de la merluza (*Merluccius merluccius* L.) de la plataforma gallega y cantábrica. *Bol. Inst. Esp. Oceanogr.*, 2(3): 39-47.
- Piñero, C. and M. Sainza. – 2003. Age estimation, growth and maturity of the European hake (*Merluccius merluccius* (Linnaeus, 1758)) from Iberian Atlantic waters. *ICES J. Mar. Sci.*, 60: 1086-1102.
- Recasens, L. – 1992. *Dinàmica de poblacions i pesqueria del lluç (Merluccius merluccius) al golf de Lleó i la mar Catalana*. PhD thesis, Univ. Barcelona, 398 pp.
- Recasens, L., A. Lombarte, B. Morales-Nin and G.J. Torres. – 1998. Spatiotemporal variation in the population structure of the European hake in the NW Mediterranean. *J. Fish Biol.*, 53: 387-401.
- Salat, J., M. Emelianov and J.L. López-Jurado. – 2006. Proceso extraordinario de formación de agua profunda en el Mediterráneo Occidental durante el invierno de 2005. In: *Proc. 5ª Asamblea Hispano-Portuguesa de Geodesia y Geofísica*. Sevilla, Spain.
- Sánchez, P. and P. Martín. – 1985. Talla de primera madurez y selectividad en algunas especies demersales de interés comercial del litoral Catalán. *Inf. Téc. Inst. Esp. Oceanogr.*, 100: 19-27.
- Sánchez, P., P. Sartor, L. Recasens, A. Ligas, J. Martín, S. De Ranieri and M. Demestre. – 2007. Trawl catch composition during different fishing intensity periods in two Mediterranean demersal fishing grounds. *Sci. Mar.*, 71(4): 765-773.
- Sarano, F. 1986. Cycle ovarien du merlu, *Merluccius merluccius*, poisson à ponte fractionnée. *Rev. Trav. Inst. Pêches marit.*, 48(1-2): 65-76.
- Sartini M., P. Belcari and S. De Ranieri. – 2002. Occurrence of eggs and larvae of European hake *Merluccius merluccius* (L.,

- 1758) in the northern Tyrrhenian Sea. *Biol. Mar. Medit.* 9(1): 358-365.
- Sartor, P., L. Recasens, C. Viva and J. Lleó. – 2001. Analysis of the impact of the fishery on the adult population of European hake in the Northwestern Mediterranean. *Rapp. Comm. Int. Mer Médit.*, 36: 321-322.
- Sbrana M. and P. Belcari. – 1993. Nota sulla presenza di femmine mature di *Merluccius merluccius* (L.) nell'arcipelago toscano meridionale. *Biol. Mar., suppl. al Notiz. S.I.B.M.*, 1: 375-376.
- Sbrana, M., P. Belcari, S. De Ranieri, P. Sartor and C. Viva. – 2007. Comparison of the catches of European hake (*Merluccius merluccius*, L. 1758) taken with experimental gillnets of different mesh sizes in the northern Tyrrhenian Sea (western Mediterranean). *Sci. Mar.*, 71(1): 47-56.
- Schaefer K.M. – 1996. Spawning time, frequency and batch fecundity of yellowfin tuna, *Thunnus albacares*, near Clipperton Atoll in the eastern Pacific Ocean. *Fish. Bull.*, 94: 98-112.
- Yeates, J. – 1974. *An introduction to quantitative analysis in human geography*. J. Yates and J.R. Belser (eds.), Mc Graw-Hill series in geography.
- Scient. ed.: M.P. Olivar.
Received February 14, 2007. Accepted June 27, 2008.
Published online October 21, 2008.