

# Some aspects of the reproductive biology of albacore *Thunnus alalunga* from the western Mediterranean Sea

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*Thunnus alalunga* is an important commercial tuna species widely distributed in the three major oceans and the Mediterranean Sea. The Mediterranean population is currently classified as a data-poor stock and little is known about its basic life history parameters. This study provides the first detailed information on some aspects of the reproductive biology of *T. alalunga* from the western Mediterranean Sea. A total of 16 104 specimens were measured between 2005 and 2012. The overall sex ratio of females to males was 1.1:1, although the ratio was female biased in fish <70 cm fork length ( $L_F$ ) and male biased in those >75 cm  $L_F$ . Histological analysis of the ovaries ( $N = 587$ ) and the monthly variation of the gonadosomatic index for both sexes showed that spawning occurred from June to August, which is a much shorter period than the 7 months reported for *T. alalunga* in tropical oceanic waters. *Thunnus alalunga* caught during June and July are capable of spawning daily. The gonadosomatic index values for *T. alalunga* from the western Mediterranean were up to eight times higher than those of *T. alalunga* from other oceans. Histological examination of the ovaries showed that the minimum length at sexual maturity of females was 56 cm  $L_F$ , which is considerably smaller than those estimated for other stocks.

**Keywords:** Size distribution, sex ratio, gonadosomatic index, histology, sexual maturity, spawning season

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## INTRODUCTION

Albacore, *Thunnus alalunga* (Bonnaterre, 1788), is a highly migratory species widely distributed in the major oceans of the world, including the Mediterranean Sea, between latitudes 50°N and 40°S (Collette & Nauen, 1983). For stock assessment purposes, six independent albacore stocks are assumed world-wide, i.e. North and South Pacific, Indian, North and South Atlantic, and Mediterranean stocks (Arrizabalaga *et al.*, 2004). The Mediterranean stock is considered to be independent from the North Atlantic stock, as based on independent spawning areas, tagging experiments, morphological differences, different growth rates and age of first maturity (ICCAT, 2010). Moreover, studies on feeding habits (Bello, 1999; Consoli *et al.*, 2008; Salman & Karakulak, 2009; Goñi *et al.*, 2011; Cardona *et al.*, 2012) and recent genetic studies (Davies *et al.*, 2011; Montes *et al.*, 2012; Albaina *et al.*, 2013) support that the Mediterranean *T. alalunga* stock is an independent population that completes its entire life cycle in the Mediterranean Sea. The International Commission for the Conservation of Atlantic Tunas (ICCAT) stated that the Mediterranean *T. alalunga* is a data-poor stock, and recommended conducting research on its basic life history parameters (Anon., 2012).

Although the life cycle and migration routes of *T. alalunga* in the Mediterranean Sea have been little studied, three spawning grounds have been identified based on larval studies: (1) eastern Mediterranean (Aegean Sea) (Piccinetti *et al.*, 1996); (2) central Mediterranean (Ionian, Tyrrhenian and Adriatic Seas) (Potoschi *et al.*, 1994; Piccinetti *et al.*, 1996; De Ruggieri *et al.*, 1997); and (3) western Mediterranean (Balearic Sea) (Dicenta *et al.*, 1975; Dicenta, 1977; García *et al.*, 2005; Alemany *et al.*, 2010). *Thunnus alalunga* is a multiple spawner with asynchronous oocyte development and indeterminate spawning strategy (Otsu & Uchida, 1959). Like all other tuna species, spawning occurs when the sea surface temperature exceeds 24°C (Schaefer, 2001). Current available information on the reproductive biology of Mediterranean *T. alalunga* is scarce (Arená *et al.*, 1980; Megalofonou, 1990; Akayli *et al.*, 2013), whereas several studies have been published on the stock-related reproductive characteristics of North and South Pacific *T. alalunga* and on the histological analyses of their gonads (Partlo, 1955; Ueyanagi, 1957; Otsu & Uchida, 1959; Otsu & Hansen, 1962; Ratty *et al.*, 1990; Ramon & Bailey, 1996; Chen *et al.*, 2010; Farley *et al.*, 2013, 2014).

An accurate evaluation of the reproductive phases of the gonads should be based on histological examination (Hunter & Macewicz, 1985), which is especially important in relation to females sampled after the spawning season when the resting ovaries may appear to be immature if gonad indices or macroscopic techniques are used (Schaefer, 2001). Thus, this study used both histological and biometric data to

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examine various aspects of the reproductive biology of *T. alalunga* in the western Mediterranean, which is one of the most important spawning grounds of tuna species in the Mediterranean Sea. The study aims were to examine the size frequency, sex ratio, reproductive phase, spawning season and minimum length at maturity of *T. alalunga* caught in the western Mediterranean Sea.

## MATERIALS AND METHODS

The data used in this study were collected from fishing tournaments of the recreational fishery (RF) and from the albacore longline fishery (LLALB) in the western Mediterranean Sea. Recreational and commercial fisheries both target *T. alalunga* in this area (Figure 1).

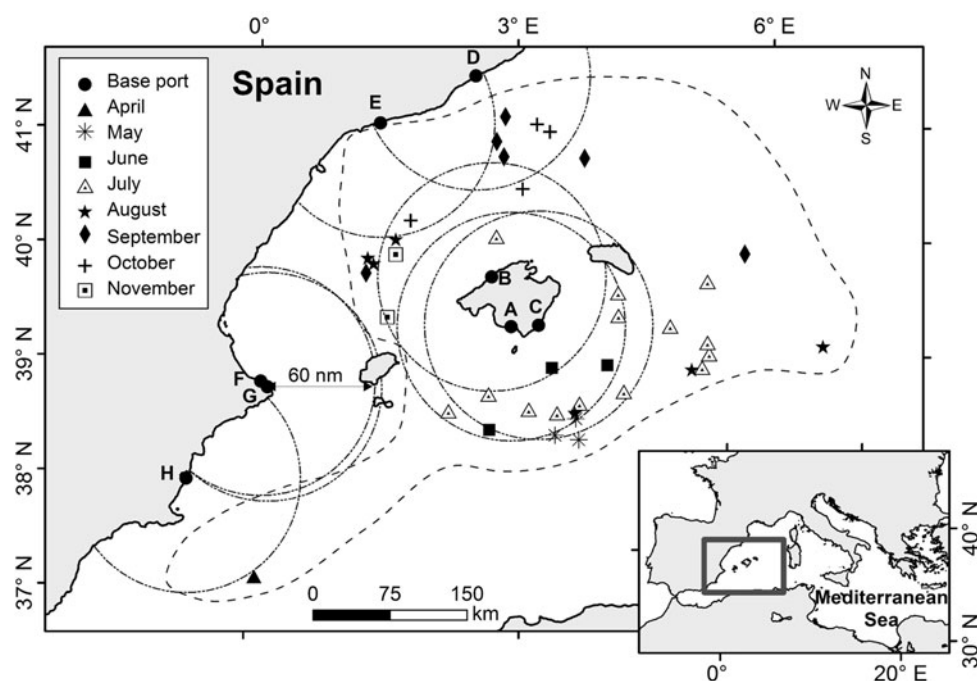
### Fishing description and sampling collection

Trolling is the fishing method used by recreational fishery and consists of using fishing lines (30 or 50 lb) with hooks and artificial lures. Fishing tournaments take place during the daytime (approximate effective fishing time: between 08:00 and 17:00 hours) and the fishing grounds extend 60 nautical miles around the base ports (Figure 1). *Thunnus alalunga* were caught during 21 fishing tournaments (38 fishing days) between 2005 and 2012 (Table 1). In this period, the tournaments were mainly held between mid-June and mid-July, but were only held in September in 2005 and 2006. A total of 287 positive fishing operations (sets with albacore catch) were recorded between 2006 and 2012 by scientific observers on fishing boats. The main characteristics of the gear are as follows: shallow mainline, i.e. hook depth ranges from 20 to 50 m; between 2000 and 6000 hooks are usually set in each

fishing operation; and the most commonly used bait is frozen sardine *Sardina pilchardus* and round sardinella *Sardinella aurita*. The fishing operation lasts around 24 h, and thus the effective fishing time includes the day and night hours. Further details on the LLALB can be found in García-Barcelona et al. (2010). In 2008, Spanish legislation on the LLALB (Order APA/254/2008, 7 February of Ministry of Agriculture, Fisheries and Food) prohibited the use of albacore longline gear between 15 October and 31 May. However, in 2010, a new order (Order ARM/2023/2010, 26 July of Ministry of Environment, and Rural and Marine) allowed its use from 1 May to 30 September. Fortunately, historical data are available for the period March–December, before the current legislation was introduced.

Sampling from fishing tournaments was conducted by qualified staff from the Spanish Institute of Oceanography (IEO), and by scientific observers on longline fishing vessels. According to the ICCAT recommendations, onboard observers were assigned to vessels based on a standard ICCAT time-area stratum ( $5^\circ \times 5^\circ \times$  month). Positive fishing operations alone were used in the current study to identify the fishing areas where the commercial albacore longline fishery usually operates (Figure 1).

In total, 3952 *T. alalunga* were measured of the 4016 fish caught during the recreational fishery (RF) tournaments and 12,152 were measured from the LLALB catch (Tables 1 and 2). Fork length ( $L_F$ ) was measured either to the nearest 0.1 cm (fish caught by the RF) or to the nearest cm (fish measured on longline vessels). Total weight ( $W_T$ ) was measured to the nearest 0.1 kg. During the fishing tournaments in 2005 and 2006, observers on sports vessels monitored the catch and recorded fish that were not retained. The observers reported that no *T. alalunga* were discarded during any of the



**Fig. 1.** Study area. The western Mediterranean Sea showing the fishing grounds of albacore longline fishery (dashed line) and of recreational fishery (circles around the base ports) during the fishing tournaments. Locations (according to the month) are shown where *Thunnus alalunga* ovaries were collected on albacore longline vessels. Base ports: A, S'Estanyol; B, Sóller; C, Cala D'Or; D, Port Balis; E, Torredembarra; F, Dénia; G, Jávea; H, Torrevieja.

**Table 1.** Number of individuals caught (N), individuals measured (number and range of fork length), males and females, ovaries sampled and ovaries histologically examined of *Thunnus alalunga* caught at fishing tournaments in the western Mediterranean Sea by month (pooled across years).

Month	Fishing days	Ind. caught	Ind. measured	Sex		Ovaries (sampled)	Ovaries (histology)
				male	female		
June	10	483	474	192	199	192	110
July	26	3513	3458	504	571	550	405
September	2	20	20	7	13	13	13
Total	38	4016	3952	703	783	755	528

tournaments. In the subsequent years up to 2012, surveys of the tournament participants were conducted at landing sites and also showed that no small *T. alalunga* were caught and discarded.

All the fish were sampled to identify their sex when the total catches at fishing tournaments were small, whereas a subset was randomly selected when a large number of fish were caught. Macroscopic examination of the gonads was performed to determine the sex of 1486 fish caught by the RF (Table 1) and the sex ratio was calculated as the ratio of females to males. A total of 755 ovaries were removed and the weights of the gonads ( $N = 753$ ) ( $W_G$ ) were recorded to the nearest g. A 2–3 cm cross-section from the central part of the right or left lobe was fixed in Bouin's fluid for 4 h, and preserved in 70% ethanol. A total of 55 females, 54 males and five undetermined fish were dissected on longline vessels and their gonads were fixed and preserved as previously described. Histological examination showed that the five individuals of undetermined sex were four immature females and one male. Given that an examination of testes did not form part of the study aim, the results concerning the immature male are not discussed further. Figure 1 shows the localities by month where females were caught by the LLALB.

Gonadosomatic index (GSI) was calculated for males and females sampled in both fisheries to determine the spawning period. In order to compare our results with those reported in other albacore studies, two alternative formulations were used:

$$GSI^a = 10^4 \times W_G / L_F^3,$$

where  $GSI^a$  is the GSI calculated from the ratio of gonad weight to fork length times  $10^4$ ;  $W_G$  in grams and  $L_F$  in cm.

$$GSI^b = 100 \times W_G / W_T,$$

**Table 2.** Number of individuals measured (N) and ovaries histologically examined of *Thunnus alalunga* caught by LLALB in the western Mediterranean Sea by month (pooled across years).

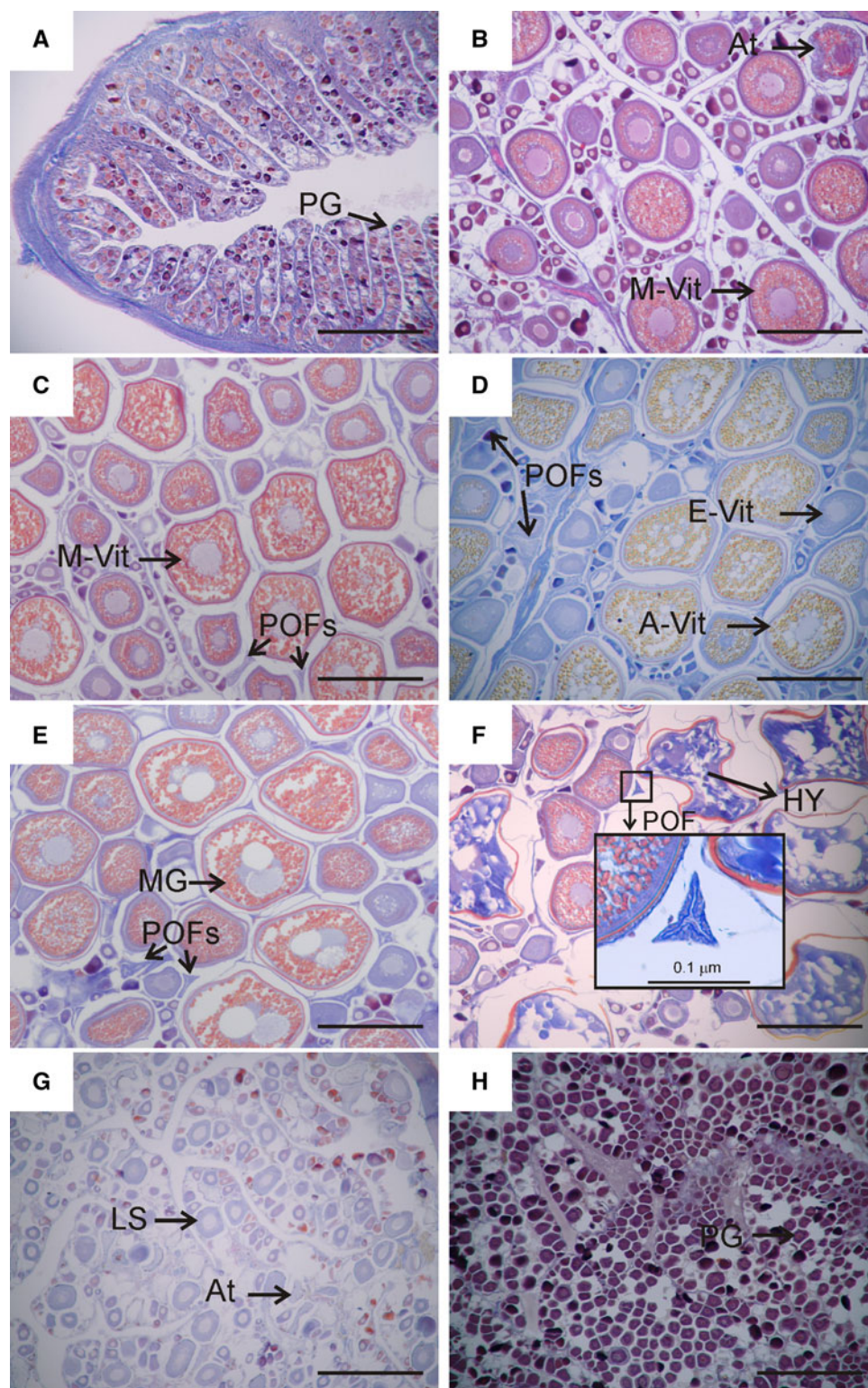
Month	N	Ovaries (histology)
March	47	–
April	20	1
May	581	3
June	4574	3
July	4477	23
August	1715	12
September	476	9
October	110	6
November	145	2
December	7	–
Total	12,152	59

where  $GSI^b$  is the GSI calculated from the ratio of gonad weight to total weight times  $10^2$ ;  $W_G$  and  $W_T$  both in grams.

## Laboratory processing and histological classification

A total of 587 ovaries were histologically examined (Tables 1 and 2). A representative portion of the preserved ovarian tissue (from the *tunica albuginea* to the ovarian lumen) was dehydrated in ascending concentrations of ethanol, cleared with *n*-butanol, and embedded in paraffin. Sections were cut at 10  $\mu$ m and stained with Mallory's trichrome stain. The most advanced group of oocytes (MAGO) was determined for each ovary; primary growth, lipid-stage, early vitellogenic, medium vitellogenic, advanced vitellogenic, migratory nucleus and hydrated oocyte stages (Figure 2). The presence of postovulatory follicles (POFs) and atretic follicles was also recorded to determine the reproductive phases of the ovaries (Schaefer, 1998). Subsequently, histological criteria based on the work of Schaefer (1998) and Farley *et al.* (2013) were applied to determine the maturity status of each female and its ovarian phase. Females were classified as immature if their ovaries only contained primary growth oocytes or early vitellogenic oocytes, but no signs of atresia (Figure 2A); whereas they were classified as mature if the ovaries contained vitellogenic, migratory nucleus or hydrated oocyte stages, POFs, atresia of vitellogenic oocytes (alpha or beta atresia) and/or late stages of atresia. Ovaries of mature females were classified into the following five ovarian phases: Developing phase, when they contained early vitellogenic oocytes as MAGO, no POFs and no atresia; spawning capable phase if ovaries showed medium or advanced vitellogenic oocytes as MAGO, some atresia of vitellogenic oocytes could be present, but no POFs (Figure 2B); spawning phase, when they showed evidence of past spawning (POFs present) or imminent spawning (migratory nucleus or hydrated oocytes present), and atresia, when present at all, only in limited amounts (Schaefer, 1998; Farley *et al.*, 2013) (Figure 2C–F); regressing phase, when they had lipid-stage or early vitellogenic oocytes, abundant alpha and/or beta atresia, and no POFs (Figure 2G); and regenerating phase, if ovaries contained primary growth or lipid-stage oocytes, late stages of atresia, and no POFs (Figure 2H). As not only oocytes in the latter two advanced developmental stages but also the presence of POFs reflects spawning tunas (Schaefer, 1998; Chen *et al.*, 2010; Farley *et al.*, 2013), spawning ovaries were further classified into four subphases according to the MAGO present in the ovary: medium vitellogenic subphase, advanced vitellogenic subphase, migratory nucleus subphase and hydrated subphase.





**Fig. 2.** Reproductive phases of the ovaries of *Thunnus alalunga* caught in the western Mediterranean Sea. Immature (A), spawning capable (B), spawning (C–F) [medium vitellogenic subphase (C), advanced vitellogenic subphase (D), migratory nucleus subphase (E), hydrated subphase (F)], regressing (G), and regenerating (H) showing the different developmental stages of oocytes and follicles: PG, primary growth oocyte; LS, lipid-stage oocyte; E-Vit, early vitellogenic oocyte; M-Vit, medium vitellogenic oocyte; A-Vit, advanced vitellogenic oocyte; MG, migratory nucleus oocyte; HY, hydrated oocyte; POFs, postovulatory follicles; At, atretic follicles. Histological sections were stained with Mallory's trichrome. Scale bar = 500 µm.

### Spawning frequency

The estimation of the spawning frequency of female *T. alalunga* from the western Mediterranean Sea was calculated

following the postovulatory follicle method of Hunter & Macewicz (1985), which is commonly used in tuna (Hunter *et al.*, 1986; Farley & Davis, 1998; Medina *et al.*, 2002; Chen

*et al.*, 2006, 2010). This method is based on the assumption that POFs are resorbed within 24 h after spawning, which has been demonstrated in South Pacific *T. alalunga* (Farley *et al.*, 2013). Spawning frequency was estimated as the inverse of the spawning fraction, which is defined as the number of females whose ovaries contained POFs divided by the total number of mature females. The spawning fraction was also estimated using mature active females (females whose ovaries are either in the spawning-capable or spawning phase), i.e. mature specimens whose ovaries were reproductively inactive (either in the regressing or regenerating phase) were not included.

## Statistical analyses

All statistical analyses were conducted using R statistical software (R Core Team, 2013).

A two-sample Kolmogorov–Smirnov test was performed to test for differences in length distributions from LLALB data between months (pooled across years) with sufficient sample sizes (May–September). The same approach was applied to test for differences in length distributions (pooled across months and years) between the RF and the LLALB. A binomial generalized linear model (GLM) was used to examine the effect of  $L_F$  on the proportion of females. A significance level of  $\alpha = 0.01$  was assumed in all statistical tests.

## RESULTS

### Size composition

During the study period, observers on the LLALB boats measured a total of 12,152 *T. alalunga*. Their sizes ranged between 33 and 109 cm  $L_F$  (mean  $\pm$  SD =  $72.4 \pm 8.3$  cm) (Figure 3A). No statistically significant differences in size distribution between months were found ( $P > 0.01$ ). The sizes of the 3952 specimens from the RF ranged between 57 and 103 cm  $L_F$  (mean  $\pm$  SD =  $70.7 \pm 7.0$  cm) (Figure 3B). Statistically significant differences in size distributions between fisheries were found ( $P = 0.01$ ). Only 5.4% of the 16,104 *T. alalunga* measured fell outside the length range of 60–90 cm  $L_F$ .

### Sex ratio

The overall sex ratio was 1.1 ♀:1 ♂ ( $n = 1486$  fish). In total, 99.5% were measured ( $n = 1478$  fish; 779 females and 699 males). The size of males ranged between 57.5 and 98.0 cm  $L_F$  (mean =  $74.7 \pm 8.3$  cm) and females ranged between 57.2 and 90.5 cm  $L_F$  (mean =  $69.4 \pm 5.7$  cm). Significant differences in the proportion of females were found between length classes ( $P < 0.01$ ). The predictions of the GLM analysis showed that females predominated in the length classes less than 70 cm  $L_F$ , whereas males were more abundant in the length classes greater than 75 cm  $L_F$ ; that is, the sex ratio was 1:1 for a 72.6 cm  $L_F$  fish and for a length class of between approximately 71 and 74 cm  $L_F$  (95% confidence interval) (Figure 4).

### Histological classification

With the exception of the developing phase, all ovarian phases were represented in the ovarian samples examined (Figure 2).

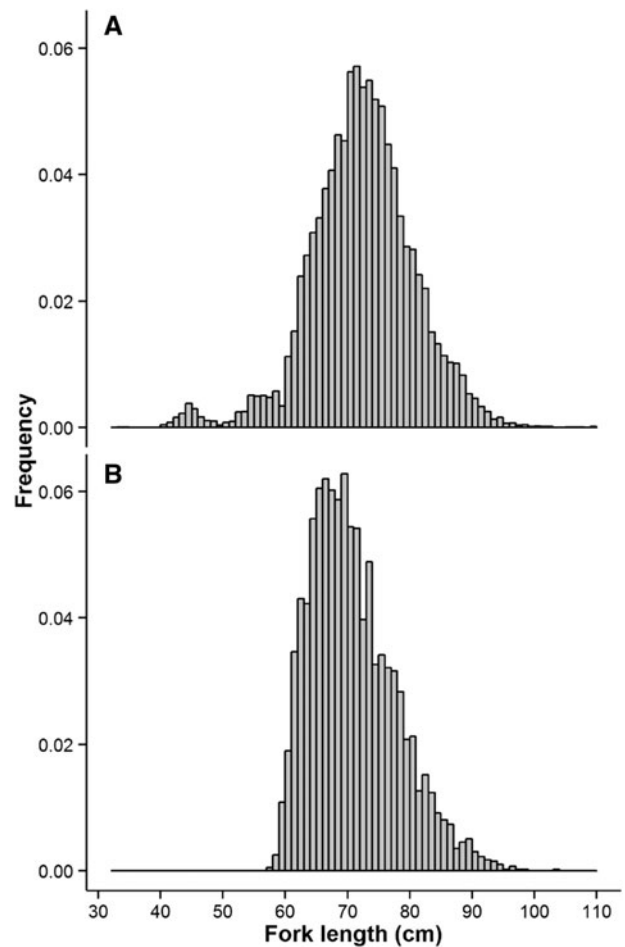


Fig. 3. Fork length frequency distributions of *Thunnus alalunga* caught by albacore longline fishery ( $N = 12,152$  fish) (A) and by recreational fishery ( $N = 3952$ ) (B) in the western Mediterranean Sea.

Histological analysis classified 583 females as mature and only four as immature. Immature females were caught in July; the smallest was 52 cm  $L_F$  and the largest was 60 cm  $L_F$ , whereas mature females ranged between 56 and 90 cm  $L_F$ . Figure 5 shows the gonad phases of mature females by month. The absence of ovaries in the developing phase (the phase before the spawning capable phase) may have been due to the number of females sampled (four) between April and May. The only three ovaries collected in May were in the spawning capable phase. The majority of females were caught in June, July and August and their ovaries presented POFs ( $N = 548$ ). Then, spawning ovaries were classified into the four subphases: Medium vitellogenic subphase (24.6%); advanced vitellogenic subphase (43.6%); migratory nucleus subphase (28.6%); and hydrated subphase (only 3.1%). Ovaries in the hydrated subphase represented 1.2% ( $n = 6$ ) of the spawning ovaries analysed from the RF and 33.3% ( $n = 11$ ) from the LLALB. A total of 32 ovaries (5.5% of mature females) were classed as either regressing or regenerating; only one of these ovaries was collected in August (Table 3 and Figure 5).

### Spawning season and spawning frequency

The GSI was calculated for 803 females (753 from the RF and 50 from the LLALB) and 736 males (682 from the RF and 54



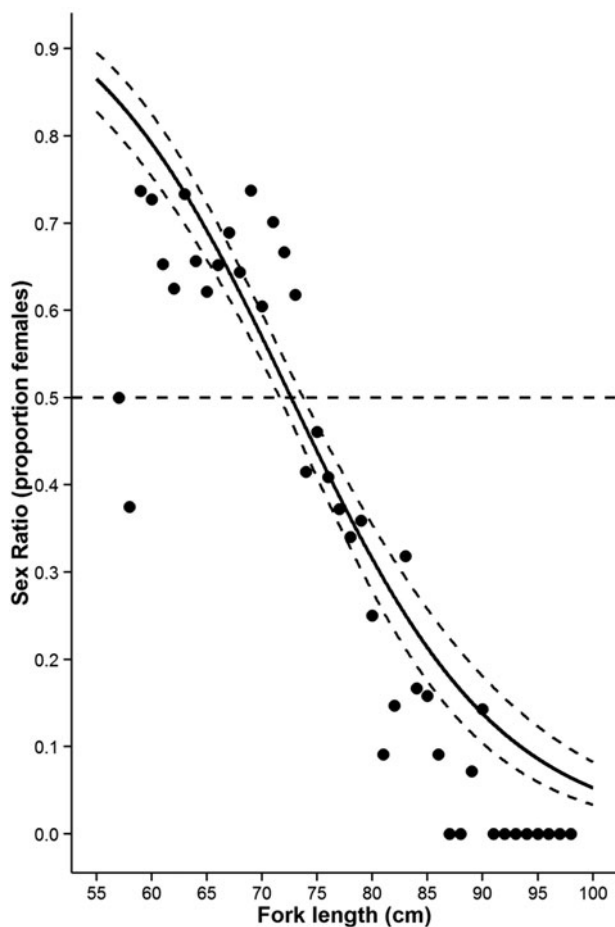


Fig. 4. Predicted trend in sex ratio (proportion female) with fork length. Dashed lines indicate confidence interval ( $\pm 95\%$  CI).

from the LLALB) (Table 4). The mean monthly GSI values calculated by using the two formulas increased gradually from May and reached a peak during June and July (Figure 6). Although few ovaries ( $N = 39$ ) and testes ( $N = 41$ ) were sampled between August and November, a clear downward trend in GSI values was observed (Table 4 and Figure 6).

The maximum values of the GSI calculated in relation to the length (17.4) and weight (8.7) were observed in ovaries in the hydrated subphase (Table 3). Mean maximum GSI values were also observed in ovaries in the hydrated subphase (mean  $\pm$  SD =  $11.6 \pm 3.7$ ), whereas the minimum values were observed in ovaries in the regenerating phase (mean  $\pm$  SD =  $1.5 \pm 0.6$ ) (Table 3). The combined monthly GSI values for females and males and histological examination of the ovaries suggest that the spawning season for albacore in the western Mediterranean Sea is between June and August.

Histological analysis showed that all ovaries classified as spawning presented POFs. The POFs found in ovaries in the hydrated subphase were small and scarce (Figure 2) with the exception of one ovary in which the POFs were fresh and few hydrated oocytes were observed. The spawning fraction calculated considering all the mature females was 0.94 and the mean spawning interval was 1.06 days (i.e.  $1/0.94$ ). The proportion of active females whose ovaries had POFs (548) to all active females (551 ovaries, in phase III and IV) was 0.99, and the spawning frequency 1.01 days (i.e.  $1/0.99$ ). If only mature females caught during the peak spawning

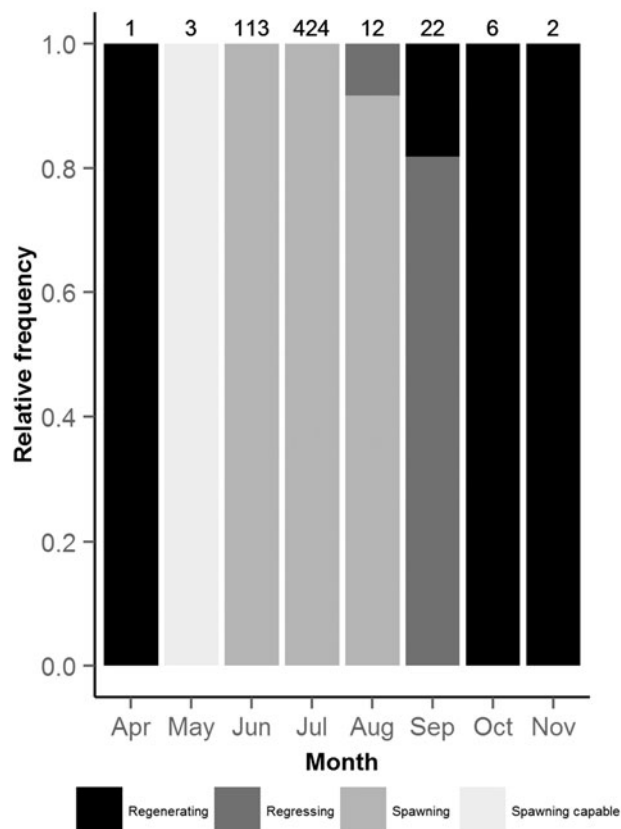


Fig. 5. Monthly relative frequency of gonad phases (by microscopic examination) for mature female *Thunnus alalunga* in the western Mediterranean Sea (immature fish are not included). Numbers on bars represent the number of individuals.

months (June and July) ( $N = 537$ ) are considered, then the spawning fraction is 1; therefore, in these months, *T. alalunga* from the western Mediterranean Sea are capable of spawning every day.

## DISCUSSION

Although *T. alalunga* is a resource of high economic value for both large-scale industrial and small-scale artisanal fisheries, the reproductive biology of the Mediterranean population of *T. alalunga* remains poorly understood (Juan-Jordá *et al.*, 2013). In the present study a total of 16,104 specimens were measured and 587 females were examined to determine their maturity status and to gauge their spawning season in the western Mediterranean Sea. Thus, this study presents new information on aspects of the reproductive biology of this species in the western Mediterranean that could be of value to future fishery management.

Only 5.4% of the large number of *T. alalunga* measured was less than 60 cm  $L_F$  and greater than 90 cm  $L_F$ . Specimens over 90 cm  $L_F$  have been frequently observed in other oceans, e.g. up to 110 cm  $L_F$  in the South Pacific Ocean (Otsu & Hansen, 1962; Ramon & Bailey, 1996; Farley *et al.*, 2013), 120 cm  $L_F$  in the Indian and North Pacific Oceans (Wu & Kuo, 1993; Chen *et al.*, 2010), and even 130 cm  $L_F$  in the South Atlantic Ocean (Anon., 2012). Although statistically significant differences were found in size distributions between the RF and the LLALB, the length distribution pattern in the present

**Table 3.** Gonadosomatic index values for mature female according to their gonad phase. GSI<sup>a</sup> = ratio of gonad weight to fork length times 10<sup>4</sup>; GSI<sup>b</sup> = ratio of gonad weight to total weight times 10<sup>2</sup>.

Phase/Subphase	<i>n</i>	GSI <sup>a</sup>	GSI <sup>b</sup>
		Range (mean $\pm$ SD)	Range (mean $\pm$ SD)
-Spawning capable	3	4.6–6.6 (5.3 $\pm$ 1.1)	–
-Spawning:			
Medium vitellogenic subphase	135	1.5–16.4 (8.7 $\pm$ 2.2)	1.0–8.0 (4.4 $\pm$ 0.9)
Advanced vitellogenic subphase	239	1.8–16.2 (9.9 $\pm$ 2.0)	0.8–9.2 (4.9 $\pm$ 0.9)
Migratory nucleus subphase	157	4.8–16.8 (10.6 $\pm$ 1.9)	2.4–8.4 (5.2 $\pm$ 0.9)
Hydrated subphase	17	5.0–17.4 (11.6 $\pm$ 3.7)	2.7–8.7 (6.3 $\pm$ 1.9)
- Regressing	19	0.8–4.3 (2.4 $\pm$ 0.9)	0.5–2.0 (1.2 $\pm$ 0.4)
- Regenerating	13	0.5–2.3 (1.5 $\pm$ 0.6)	0.3–1.4 (0.8 $\pm$ 0.4)

**Table 4.** Gonadosomatic index ranges for female and male *Thunnus alalunga* by month (pooled across years). GSI<sup>a</sup> = ratio of gonad weight to fork length times 10<sup>4</sup>; GSI<sup>b</sup> = ratio of gonad weight to total weight times 10<sup>2</sup>.

Month	Female				Male			
	GSI <sup>a</sup>		GSI <sup>b</sup>		GSI <sup>a</sup>		GSI <sup>b</sup>	
	N	Range	N	Range	N	Range	N	Range
April	1	2.3	1	1.1	2	0.5	2	0.2
May	3	4.6–6.6	–	–	3	0.3–3.2	2	0.2–1.4
June	195	4.8–17.4	193	2.4–8.0	191	1.1–11.7	191	0.5–5.9
July	565	1.8–16.8	561	0.8–9.2	498	1.8–15.6	496	1.0–8.6
August	11	1.5–16.7	7	2.6–8.7	18	1.0–5.0	14	0.5–2.2
September	22	0.5–4.3	22	0.3–2.0	13	0.3–2.1	12	0.2–1.1
October	5	0.9–2.2	5	0.5–1.4	10	0.2–2.9	8	0.1–1.8
November	1	0.9	1	0.5	–	–	–	–

study is consistent with that observed in other fisheries, including artisanal ones, throughout the Mediterranean Sea [e.g. Aegean Sea and Antalya Bay (eastern Mediterranean): 54–101 cm  $L_F$  (Megalofonou, 1990, 2000; Karakulak *et al.*, 2011); Ionian, Adriatic and Tyrrhenian Seas (central-southern Mediterranean): 32–111 cm  $L_F$  (Arena *et al.*, 1980; Megalofonou, 2000; Marano *et al.*, 2005; Consoli *et al.*, 2008; Di Natale *et al.*, 2011); and the present study (western Mediterranean): 33–109 cm  $L_F$ ].

The overall estimated sex ratio for *T. alalunga* in the western Mediterranean was 1.1♀:1♂. Similar results were reported for *T. alalunga* in the south-western Atlantic, South Pacific (Ratty *et al.*, 1990; Anon., 2012) and eastern Mediterranean Sea (calculated from Megalofonou, 2000; Table I). However, *T. alalunga* males were more abundant than females in autumn in the Aegean Sea, with an estimated sex ratio of 0.48♀:1♂ (Megalofonou, 1990). The analysis of sex ratio by length showed that the sex ratio was close to 1:1 for length classes between 71 and 74 cm  $L_F$ , with females being predominant in small length classes. A predominance of *T. alalunga* females in length classes less than 75 cm  $L_F$  was found in the eastern Mediterranean, suggesting that females cease growing at smaller sizes than males (Karakulak *et al.*, 2011). A greater abundance of males in larger length classes (above 95 cm  $L_F$  to 100 cm  $L_F$ ), has also been reported in *T. alalunga* from the Pacific Ocean (Chen *et al.*, 2010; Farley *et al.*, 2013) and in other tuna species (Schaefer, 1998; Aranda *et al.*, 2013). According to Schaefer (2001) and Schaefer *et al.* (2005), the almost complete absence of females in tuna species within larger size classes

seems to be related to differences in natural mortality and vulnerability to capture rather than to differential growth. However, recent studies have reported that male *T. alalunga* from the eastern Mediterranean Sea (Megalofonou, 2000; Karakulak *et al.*, 2011) and the North and South Pacific (Chen *et al.*, 2012; Williams *et al.*, 2012) grow faster and reach greater sizes at age than females, suggesting that once the size at maturity is reached, reproductive investment rather than somatic growth is higher in females than in males (Chen *et al.*, 2012; Williams *et al.*, 2012; Farley *et al.*, 2013).

Histological analysis of the ovaries and GSI values (for males and females) suggest that the spawning season in the western Mediterranean Sea is from June to August. These results are in line with a larval study conducted in the Balearic Sea by Alemany *et al.* (2010), who suggested that the peak *T. alalunga* spawning season occurs in mid-July. The estimated spawning season duration of around 3 months was similar to that observed for male *T. alalunga* in the eastern Mediterranean Sea (Akayli *et al.*, 2013), but much shorter than the 6 and 7 months reported for *T. alalunga* in the tropical waters of the South Atlantic (Anon., 2012) and the North and South Pacific (Chen *et al.*, 2010; Farley *et al.*, 2013). It is known that *T. alalunga* larvae in the western Mediterranean Sea avoid temperatures lower than 23°C (Alemany *et al.*, 2010), which are only exceeded in summer in this area (Vargas-Yáñez *et al.*, 2010). Thus, the spawning period of *T. alalunga* in the Mediterranean Sea will rarely exceed 4 months, due to the inherent climatology of the Mediterranean Sea (the environmental conditions

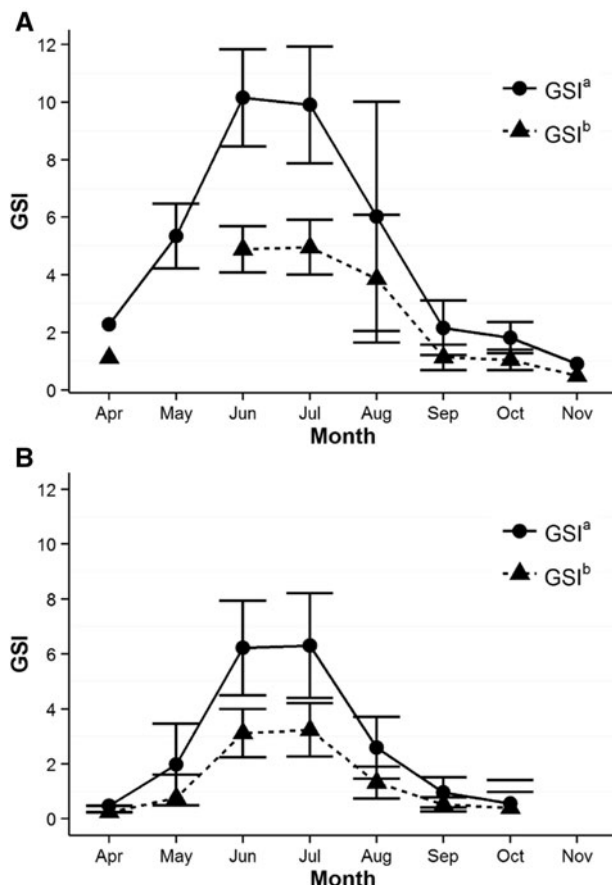


Fig. 6. Monthly variations of the gonadosomatic index (GSI) for mature female *Thunnus alalunga* (A) and for male *Thunnus alalunga* (B). GSI<sup>a</sup> = ratio of gonad weight to fork length times  $10^3$ ; GSI<sup>b</sup> = ratio of gonad weight to total weight times  $10^2$ .

suitable for spawning are a surface water temperature of over  $24^{\circ}\text{C}$ ; Schaefer, 2001). These differences between the Mediterranean and oceanic populations in the duration of the spawning season are also found in other species. For example, it has been reported that the spawning period of little tunny *Euthynnus alletteratus* (Rafinesque, 1810) in the central Mediterranean Sea is between June and September (Hajje et al., 2010), whereas in the Atlantic Ocean the spawning season is between about April and November (Collette & Nauen, 1983). Likewise, the spawning period of the swordfish *Xiphias gladius* is shorter, between June and August, in the western Mediterranean Sea (De la Serna et al., 1996) and between December and June in the north-west Atlantic Ocean (Arocha & Lee, 1996). Our findings are in line with those of Arocha (2007), who reported that these differences are due to the fact that the  $24^{\circ}\text{C}$  isotherm only appears in the Mediterranean between late spring and late summer.

Given that the majority of the ovaries examined were collected from the RF, which operates during the day, the scarcity of females with hydrated oocytes would suggest that spawning takes place at night as reported for other tuna species (Schaefer, 2001) including South Pacific *T. alalunga* (Farley et al., 2013). These results are in line with those of Hunter et al. (1986), who suggested that sampling should be conducted after 21:00 hours in order to capture a significant number of skipjack tuna *Katsuwonus pelamis* (L. 1758) with

hydrated oocytes. Furthermore, the higher proportion of ovaries in the hydrated subphase in fish caught by the LLALB ( $N = 11$ ) compared with those caught by the RF ( $N = 6$ ) could be due to the fact that tournament fishing takes place during the day, whereas sets from the LLALB can also be placed during the night. Another explanation for these results may be due to the differences in the potential time-lapse between the moment the fish bite the hook and their death, i.e. the fish die almost immediately in a sports vessel, whereas tuna species such as albacore could be caught hours before eventually dying in a LLALB, and thus the stress caused by the capture could induce the hydration process (Hunter et al., 1986). With the exception of one ovary in which the POFs were fresh and only few hydrated oocytes were observed, the small size and the scarcity of POFs in ovaries in the hydrated subphase together with the high surface water temperature of  $25.2^{\circ}\text{C} \pm 1.3$  (mean  $\pm$  SD) from June to August in the western Mediterranean ([www.mai.ieo.es/gcc](http://www.mai.ieo.es/gcc)) suggest that POFs are reabsorbed before the following batch.

All the ovaries in the spawning phase presented POFs. Thus, assuming that POFs do not persist for more than 24 h after ovulation, which has been confirmed in *K. pelamis* (Hunter et al., 1986), *T. albacares* (Schaefer, 1996) and South Pacific *T. alalunga* (Farley et al., 2013), the spawning frequency of *T. alalunga* in the western Mediterranean Sea would be almost daily. Similar spawning rates have been reported for other tuna species in 'prime reproductive condition': 1.11 days in *K. pelamis* (Hunter et al., 1986) and 1.09 days in *Thunnus obesus* (Lowe 1839) (Nikaido et al., 1991) in the western Pacific; 1.14 days in *T. albacares* in the eastern Pacific (Schaefer, 1996); 1.1 days in Southern bluefin tuna *Thunnus maccoyii* (Castelnau 1872) in the south-east Indian Ocean (Farley & Davis, 1998); and  $\sim 1.15$  days in Atlantic bluefin tuna *Thunnus thynnus* (L. 1758) in the Balearic Sea (Medina et al., 2002; Aranda et al., 2013). However, spawning frequency during the peak spawning activity of North and South Pacific *T. alalunga* has been estimated at 1.7 days and 1.3 days, respectively (Chen et al., 2010; Farley et al., 2013). Furthermore, differences have been found in estimated spawning frequencies according to the type of fishing gear used and the vertical distribution of spawning tuna (Itano, 2000; Medina et al., 2007). Thus, to address the issue of possible sampling bias, it would be very useful to conduct a comparative study on the estimated spawning frequency of Mediterranean *T. alalunga* based on catches using non-shallow gear.

The estimated GSI values of *T. alalunga* from the western Mediterranean (current study) are strikingly different from those estimated in other oceans. The mean GSI<sup>a</sup> value for the hydrated subphase was 11.6 in *T. alalunga* from the western Mediterranean, whereas it was 5.3 in North Pacific *T. alalunga* (Chen et al., 2010). Similarly, the highest GSI<sup>a</sup> value of 17.4 in *T. alalunga* from the western Mediterranean is higher than the value of 5.2 (Ramon & Bailey, 1996) or the value of nearly 7 (Farley et al., 2013) in South Pacific *T. alalunga*. Likewise, the largest GSI<sup>b</sup> values found in male and female *T. alalunga* in the western Mediterranean were 8.6 and 9.2, respectively, which are much higher than the values of 0.97 and 2.23 in male and female *T. alalunga* in the Indian Ocean, respectively (Wu & Kuo, 1993). However, our results are in line with those of Akayli et al. (2013). These authors studied male *T. alalunga* in the eastern



Mediterranean Sea and found similar mean GSI<sup>b</sup> values in June and July (greater than 3.0).

It has been suggested that tuna species would reach the spawning grounds following a migration pattern structured by age and size: larger or older fish would arrive in advance and would therefore have a longer spawning season than smaller or younger fish (Schaefer, 1998; Zudaire *et al.*, 2013). Our results show that there were no significant differences in size distributions among months, therefore indicating that the *T. alalunga* spawning in the western Mediterranean does not follow the spawning migration pattern suggested above and that estimated size at maturity would not differ based on a time-limited sampling scheme. Given that only five immature individuals were found, it was not possible to estimate the length at 50% maturity ( $L_{50}$ ) using the most common method, i.e. fitting a logistic model to the proportion of mature fish by age-length class. Histological analysis showed that the minimum size at maturity for females was 56 cm  $L_F$ . Similar minimum size at maturity were reported by Akayli *et al.* (2013) for males (63 cm  $L_F$ ) in the eastern Mediterranean and by Arena *et al.* (1980), who estimated the age at first maturity of 2 years (mean size 66.3 cm  $L_F$ ) and the minimum size of 62 cm  $L_F$  in the Tyrrhenian Sea. In contrast, a minimum size at maturity of between 71 and 90 cm  $L_F$  has been reported in North and South Pacific *T. alalunga* (Otsu & Uchida, 1959; Otsu & Hansen, 1962; Ratty *et al.*, 1990; Ramon & Bailey, 1996; Chen *et al.*, 2010; Farley *et al.*, 2013) and the  $L_{50}$  of 87 cm  $L_F$  has recently been estimated for South Pacific *T. alalunga* by Farley *et al.* (2014). These estimates are in agreement with those found in *T. alalunga* in the Indian Ocean by Kikawa & Ferraro (1967) and by Wu & Kuo (1993), who estimated that *T. alalunga* reached maturity at a minimum length of between 90 and 96 cm  $L_F$ , and between 83 and 90 cm  $L_F$ , respectively. Based on studies by Bard, the  $L_{50}$  and age at 50% maturity ( $A_{50}$ ) of North Atlantic *T. alalunga* are assumed to be 90 cm  $L_F$  and 5 year (Bard, 1981 in ICCAT, 2010). The  $L_{50}$  of South Atlantic *T. alalunga* is estimated to be 92 cm  $L_F$  for females and 100 cm  $L_F$  for males (Anon., 2012). Therefore, *T. alalunga* in the Mediterranean Sea reaches sexual maturity at a smaller size than all of their counterparts in all other regions worldwide; suggesting different reproductive tactics between the Mediterranean *T. alalunga* population and the oceanic ones. Other species also follow this pattern of earlier maturation. The smallest  $L_{50}$  of *X. gladius*, 142 cm LJFL (lower jaw – fork length), has been found for the Mediterranean population (De la Serna *et al.*, 1996). In contrast, in the Indian Ocean the  $L_{50}$  for female *X. gladius* was estimated at 170 cm LJFL by Poisson & Fauvel (2009) and in the North Atlantic Ocean it was estimated at 179 cm LJFL by Arocha & Lee (1996). However, in the South Atlantic the  $L_{50}$  has been estimated at 146.5 cm LJFL, which is slightly larger than that estimated for the Mediterranean population (Mejuto, 2007).

In summary, the present study provides new information on some key aspects of the reproductive biology of *T. alalunga* in western Mediterranean Sea. The results suggest that the reproductive traits (lower maximal length, higher GSI values during the spawning season, lower minimum length at maturity and shorter spawning season) of *T. alalunga* in this area differ from those determined for the oceanic populations. These differences are consistent with those found between Mediterranean and North Atlantic *T. alalunga* in previous studies, such as different growth rates (Megalofonou, 2000),

different gill parasites (Mele *et al.*, 2010) and genetic differences (Arrizabalaga *et al.*, 2004; Nakadate *et al.*, 2005; Davies *et al.*, 2011; Montes *et al.*, 2012; Albaina *et al.*, 2013), suggesting a reproductive isolation of the Mediterranean *T. alalunga* (Davies *et al.*, 2011). It may be the case that the reproductive strategy of Mediterranean *T. alalunga* would represent an adaptation to the environmental conditions of the Mediterranean Sea. Additional studies incorporating other spawning sampling localities within the Mediterranean Sea are needed for further and better understanding of the differences in reproductive strategies between the *T. alalunga* Mediterranean population and the oceanic populations.

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