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Spawning area of the tropical Skipjack Tuna, *Katsuwonus pelamis* (Scombridae), in the western Mediterranean Sea

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Summary: Skipjack is an important commercial species with a tropical distribution, although captures in the Mediterranean Sea have been recorded for decades. The western Mediterranean Sea, specifically the Balearic Sea, is a spawning area for several tuna species. We hypothesized that the western Mediterranean warming in the last few decades could lead to the expansion of skipjack tuna spawning areas from tropical areas to the Mediterranean Sea. We analysed 454 individuals (41.8-81 cm straight fork length) caught by sport fishing vessels in offshore trolling championships in Spanish Mediterranean waters during summer months from 2014 to 2019. Analysis of the gonadosomatic index and microscopic examination of the ovaries (n=192) showed that the skipjack is reproductively active in the western Mediterranean, particularly in the Balearic Sea. These results indicate that the skipjack has expanded its distribution and spawning area from tropical waters to the Mediterranean, probably owing to the gradual warming detected in the area in the last few decades. This new spawning activity in the area should be monitored in the near future to study the possible impact on other tuna species that share the distribution range and spawning area with skipjack tuna in the western Mediterranean.

Keywords: Skipjack; reproductive biology; spawning season; sexual maturity; gonadosomatic index; Mediterranean.

Área de puesta del listado, *Katsuwonus pelamis* (Scombridae), en el Mediterráneo occidental

Resumen: El listado (*Katsuwonus pelamis*) es una especie muy importante a nivel comercial. Aunque su distribución es tropical, desde hace décadas se registran capturas en el Mediterráneo. El Mediterráneo occidental, concretamente el mar Balear, es zona de puesta de varias especies de túnidos. Este trabajo planteó la hipótesis de que el calentamiento registrado en las últimas décadas en el Mediterráneo occidental podría producir la expansión de las áreas de puesta del Listado desde las zonas tropicales hasta el mar Mediterráneo. Analizamos 454 ejemplares (41,8–81 cm SFL) capturados por embarcaciones de pesca recreativa en campeonatos de curricán de altura durante los meses de verano de 2014 a 2019 en aguas del Mediterráneo español. El análisis del Índice Gonadosomático y el análisis microscópico de los ovarios (n=192) mostraron que la especie es reproductivamente activa en el Mediterráneo occidental, particularmente en el mar Balear. Estos resultados indican que el Listado ha ampliado su área de distribución y puesta desde aguas tropicales hasta el Mediterráneo, probablemente debido al calentamiento gradual detectado en la zona en las últimas décadas. Además, es de interés realizar un seguimiento de esta nueva actividad de puesta en un futuro próximo para estudiar el posible impacto sobre otras especies de túnidos con las que comparte tanto área de distribución como zona de puesta en el Mediterráneo occidental.

Palabras clave: atún listado; biología reproductiva; época de puesta; madurez sexual; índice gonadosomático; Mediterráneo.

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INTRODUCTION

The skipjack tuna *Katsuwonus pelamis* (Linnaeus, 1758), hereafter referred to as SKJ, is a cosmopolitan, migratory species distributed in tropical and subtropical waters of all oceans, including the Mediterranean Sea. Its geographical limits are 55-60°N and 45-50°S and it is more abundant in the equatorial region throughout the year (Collete and Nausen 1983, Matsumoto et al. 1984). The SKJ is a commercially important species, being the third species in terms of captures for the eleventh consecutive year, with 2.8 million t in 2020 (FAO 2022). Its catches in the Mediterranean Sea are common, especially in recent decades. In the western Mediterranean Sea, the first catches were recorded in 1968, and the average landing of the last six years (2015-2020) is 168 t (ICCAT 2021). The main Spanish catches come from the traps located in Ceuta (Strait of Gibraltar) and longline surface fisheries targeting albacore tuna. The SKJ is also caught by Spanish recreational offshore trolling fisheries in the Alboran Sea during the summer months, mainly in August and September, and in the Balearic Sea in June and July, coinciding with the reproductive season for tunas in the area (Saber et al. 2015, 2020).

The SKJ has been classified as a multiple batch spawner fish with asynchronous oocyte development (Goldberg and Au 1986, Schaefer 2001a, Grande et al. 2012). Its reproductive potential is considered high because it reaches sexual maturity at around one year of age and spawns opportunistically throughout the year in large areas of the ocean (ICCAT 2019). Knowledge of the biology of the species is required for stock assessment, so it is important to know the reproductive characteristics and phenology of the species.

In the Atlantic Ocean SKJ spawn in two main areas: one in the western Atlantic Ocean, where it spawns over two subtropical areas off the coast of South America, and its migration is influenced by season (Andrade and Santos 2004, Benevenuti et al. 2019); and one in the eastern Atlantic Ocean, where it spawns year-round in the equatorial area, from the Gulf of Guinea to 20-30ºW. In the tropical area, spawning occurs only in the warm season (Andrade and Santos 2004). In the Indian Ocean two spawning seasons have been identified, one coinciding with the northeast monsoon and one with the southwest monsoon (Stequert and Ramcharrum 1996, Grande et al. 2014). Though the Balearic Sea is an important spawning area for several tuna species (Alemany et al. 2010), there is no information about the reproduction of SKJ in the area, except for a study in which a few spawning females were recorded (Saber et al. 2012). Temperature is a very important factor determining the distribution of both adult top predators and larvae (Worm et al. 2005, Reglero et al. 2014). An increase in water temperatures before and during spawning is needed for the adult tunas to release eggs (Margulies et al. 2007). The SKJ, like other tunas, breeds at a sea surface temperature (SST) exceeding 24°C, and its spawning season varies according to locality (Cayre and Farrugio 1986, Schaefer 2001b). Geographical differences in the reproductive traits of the SKJ probably occur because the spawning depends on oceanographic conditions (Ashida 2020), and especially on SST (Margulies et al. 2007).

Global warming will directly affect the phenology and spatial distribution of marine organisms and have indirect effects on the productivity and structure of marine ecosystems with important consequences for fisheries. Future changes in the marine environment are expected to affect the physiological rates (reproduction, growth), geographical distribution and migration of SKJ with consequences for their life history. Vargas-Yañez et al. (2010, 2019) analysed trends in different temperature time series in Spanish Mediterranean waters and found warming in intermediate, deep and surface waters from the middle of the last century. We hypothesized that the western Mediterranean warming in the last decades could lead to the expansion of skipjack tuna spawning areas from tropical areas to the Mediterranean Sea. To study the reproductive status of SKJ in the western Mediterranean, we used the gonadosomatic index, microscopic analysis of ovaries and estimates of the daily spawning fraction.

MATERIALS AND METHODS

Study areas and data collection

Specimens of SKJ were obtained from sport fishery during fishing tournaments targeting large pelagic species (mainly albacore *Thunnus alalunga*, skipjack, dolphinfish *Coryphaena hippurus* and Mediterranean spearfish *Tetrapturus belone*) from June to September 2014-2019. Sampling areas located in the western Mediterranean Sea were divided into two areas based on the oceanographic features: (i) the Balearic Sea (Area I) and (ii) the Alboran Sea (Area II) (Fig. 1). The fishing grounds extended 50 to 60 nautical miles around six base ports. Fishes were caught during daylight hours using rod and reel gear by trolling, which consists of fishing lines with hooks and artificial lures, targeting fish in surface waters between 0 and 5 m approximately.

A total of 454 SKJ were randomly collected for sampling collection. Immediately after landing, the round weight (RW, kg), the straight fork length (to the nearest 0.1 cm) and the gonad weight (GW, to the nearest g) were measured. Sex was determined by visual inspection and the sex ratio was calculated as the ratio of females to males. Assuming no systematic differences in ovarian homogeneity throughout the whole ovary, including between the two ovarian lobes (Otsu and Uchida 1959, Stequert and Ramcharrun 1995), a full cross section (2-3 cm wide) from the central part of one of the lobes was fixed in Bouin's fluid for 4 h and then preserved in 70% ethanol for later analysis.

The gonadosomatic index (GSI) was calculated as the ratio of GW to fish gonad-free weight (RW-GW) times 10^2. GW and RW were both measured in grams for males and females to examine monthly changes. The equation of Gibson and Ezzi (1980) was used:

$$GSI = GW / (RW\text{-}GW) \times 100$$

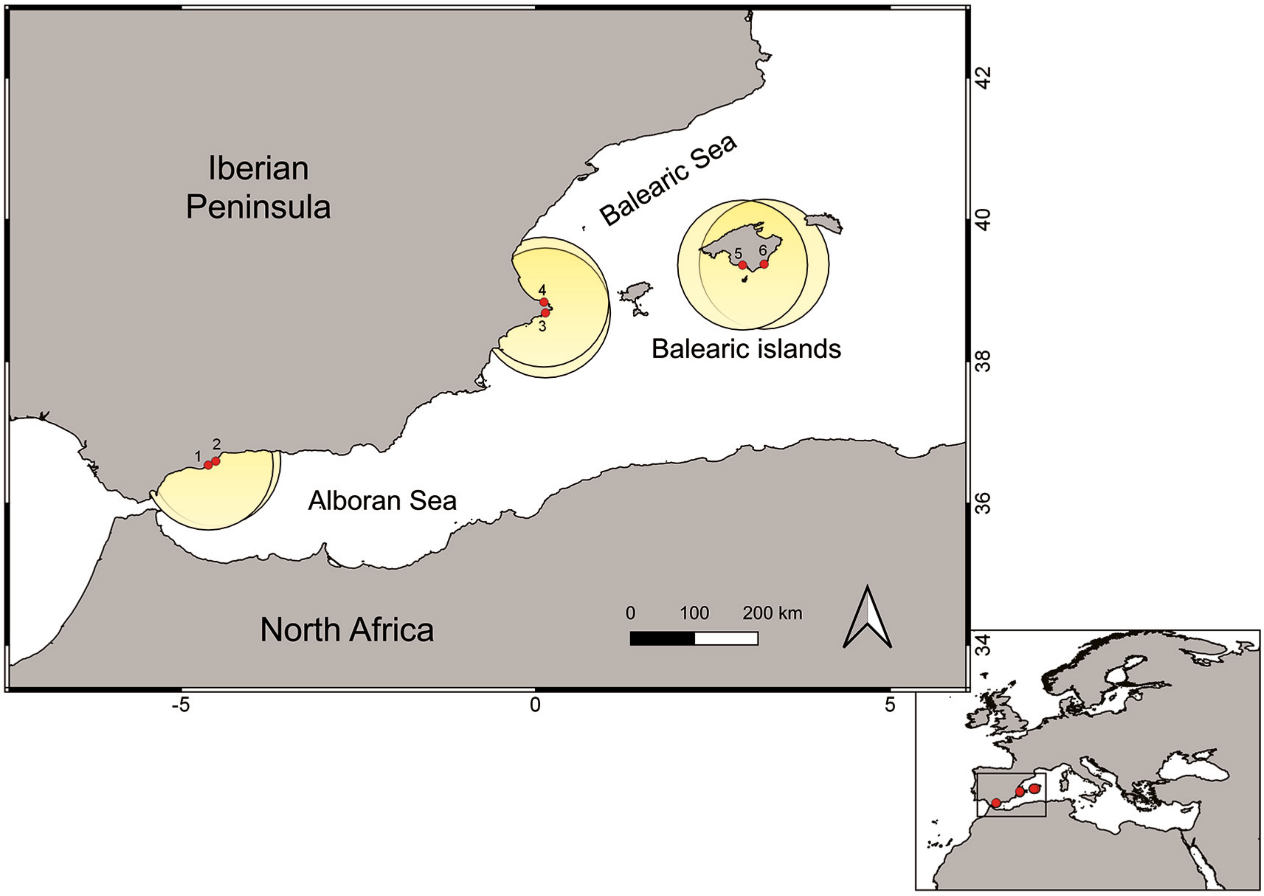

Fig. 1. – The western Mediterranean Sea showing the fishing grounds of recreational fishery (circles around the base ports) during the fishing tournaments. Base ports. Alboran Sea (Area 2): 1, Fuengirola; 2, Benalmadena. Balearic Sea (Area 1): 3, Moraira; 4, Denia; 5 S'Estanyol; 6, Cala D'Or.

An exploratory analysis showed that the relationship between GSI, length and month was non-linear, so generalized additive models (GAM) were used to model the relationships between months, specimen length and monthly means of GSI:

$$\mathrm{GSI} = \boldsymbol{\alpha} + \mathrm{s}\ (\mathrm{FL, month}) + \boldsymbol{\varepsilon}$$

All statistical analyses and graphs were performed using R software (R Core Team 2017). For the GAM, the *mgcv* (Wood 2017) and *ggplot2* packages were particularly useful (Wickhman 2016).

Histological procedures and microscopic classification of ovaries

A sub-sample was taken from each ovary, including the area from the tunica albuginea to the ovarian lumen. These representative sub-samples were then dehydrated through increasing concentrations of ethanol series, embedded in Paraplast Plus® (paraffin), sectioned at a thickness of 10 µm and, stained with Mallory's trichrome stain. A total of 192 ovaries were analysed microscopically.

The oocytes were classified into six developmental stages using the terminology of Brown-Peterson et al. (2011) and Ashida et al. (2017): primary growth, cortical alveolar, early or primary vitellogenic, advanced (secondary or tertiary) vitellogenic, germinal vesicle migration and hydrated oocytes. The microscopic maturity scale for skipjack females (Table 1) was based on a modification of the criteria of Schaefer (1998), Farley et al. (2013) and Saber et al. (2015). Each ovary was examined to record the most advanced group of oocytes, the presence of both postovulatory and atretic follicles (alpha and beta stages) and maturity markers. The maturity markers were well-defined muscle bundles and numerous Brown bodies (Farley et al. 2013) and the relative thickness of the gonad wall (Schaefer and Fuller 2019). Ovaries of mature females were classified into one of four ovarian phases, namely: developing, spawning capable, spawning and postspawning (including regressing and regenerating phases).

Data on SST come from the Earth System Research Laboratory, Physical Science Division NOAA (National Oceanic and Atmospheric Administration, www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html, Reynolds et al. 2022).

Spawning frequency

Postovulatory follicles of SKJ can be observed in the ovary for one day or less after ovulation (Schaefer and

Table 1. – Microscopic classification criteria for females based on a modification of Schaefer (1998), Farley et al. (2013) and Saber et al. (2015).

Female Maturity stage	Microscopic characteristics
1. Immature (virgin)	Only oogonia; primary growth or cortical alveolar oocytes present. No atresia. Absence of post-ovulatory follicles (POFs). Thin ovarian wall and little space between oocytes.
2. Developing	Early vitellogenic oocytes present as the most advanced group of oocytes (MAGO). Some atretic follicles may be present. Absence of POFs. Little space between oocytes.
3. Spawning capable	Advanced vitellogenic oocytes present as the MAGO. Atresia can be present. Absence of POFs.
4. Spawning	POFs present and/or migratory nucleus or hydrated oocytes present as the MAGO. Atresia, when present at all, only in limited amounts.
5a. Regressing	Cortical alveolar or early vitellogenic oocytes as the MAGO. Abundant alpha and/or beta atresia. Absence of POFs. Disorganization of ovary structures, with spaces. Thick and/or wrinkled gonad wall is observed (in some ovaries).
5b. Regenerating	Only primary growth oocytes as the MAGO or cortical alveolar oocytes present, with some spaces between oocytes. Absence of POFs. Late stages of atresia. Maturity markers. Thick and/or wrinkled gonad wall is observed (in some ovaries).

Fuller 2019). Spawning female frequency was estimated as the inverse of the spawning fraction for individuals collected in Area I. The spawning fraction was estimated following the postovulatory follicles method (Hunter and Macewicz 1985) as the ratio between the active spawning females (females with postovulatory follicles) and the total mature active females (females whose ovaries are either in the spawning capable or spawning stage). Female mature specimens whose ovaries were reproductively inactive (regressing or regenerating) were not included.

Table 2. – Sampled individuals by year, zone, fishing sport and month in offshore trolling championships.

Year	Area	Fishing port	Month	Sampled individuals
2014	Balearic Sea	Cala D'Or	June	30
	Alboran Sea	Benalmádena	August	6
2015	Balearic Sea	S'Estanyol	June	9
		Cala D'Or	July	37
	Alboran Sea	Benalmádena	August	7
2016	Balearic Sea	Moraira	June	4
		S'Estaniol		6
		Cala D'Or	July	32
		Dénia		2
	Alboran Sea	Benalmádena	August	13
		Fuengirola	September	10
2017	Balearic Sea	S'Estanyol	June	8
			July	7
		Cala D'Or		18
	Alboran Sea	Benalmádena	August	41
		Fuengirola	September	26
2018	Balearic Sea	S'Estanyol	June	2
		Cala D'Or	July	37
	Alboran Sea	Benalmádena	August	101
		Fuengirola	September	26
2019	Balearic Sea	S'Estanyol	June	4
		Cala D'Or	July	28

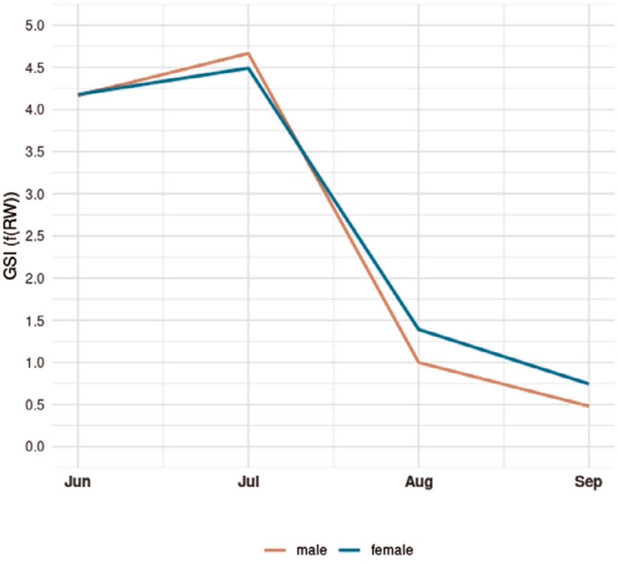

Fig. 2. – Monthly average of GSI as a function of round weight (RW): females (blue line) and males (red line).

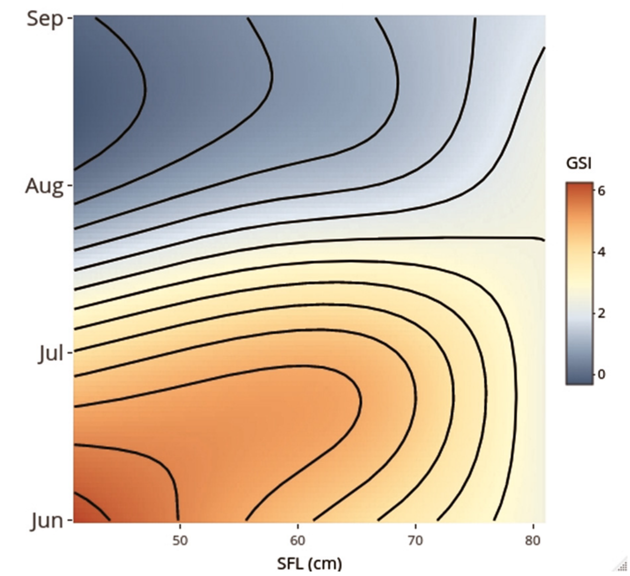

Fig. 3. – Contour plot of the fitted GAM for the GSI as a function of months and size. Straight fork length on the x-axis, month on the y-axis and the response values (GSI) given by the isolines (gray colour indicates the lowest and orange the highest GSI values).

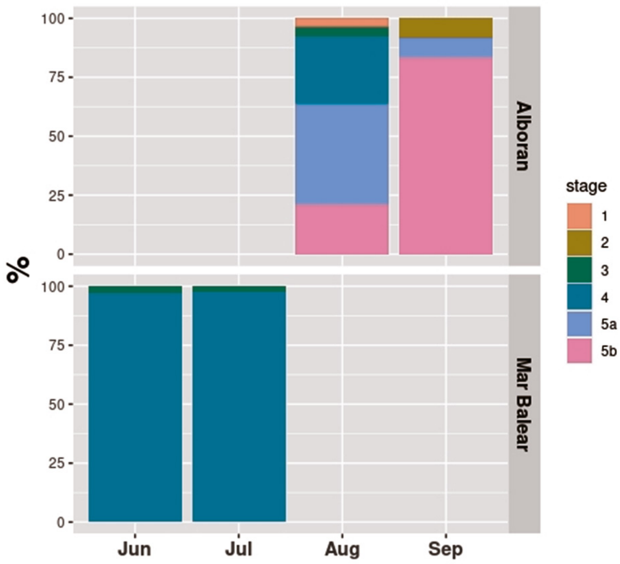

Fig. 4. – Monthly relative frequency of ovarian stages found by microscopic eamination in the Alboran Sea and the Balearic Sea.

RESULTS

Between 2014 and 2019 we attended a total of 21 sport fishing championships. A total of 224 SKJ were sampled in the Balearic Sea (Area I) and 230 in the Alboran Sea (Area II). For more detail of the number of individuals sampled per year, month or fishing port, see Table 2.

The straight fork length of 233 females ranged between 41.8 and 76 cm (mean±sd=61.5±6.2 cm) and the weight between 9.6 and 1.54 kg (5.4±1.7 kg). The sizes of 221 males ranged between 46.5 and 81 cm (61.2±6.3 cm) and the weight between 2.1 and 12.1 kg (5.4±1.8 kg). The sex ratio was 1:0.98 (F:M). Females were more abundant than males in the study sample. However, using a binomial test we concluded that there were no significant differences in the population analysed ($p=0.6057$, $p>0.05$). The SKJ belonging to Area I were slightly larger than those in Area II in both size (65.2±5.1 cm versus 57.7±5.0 cm) and weight (6.5±1.5 kg vs 4.3±1.3 kg).

We used total weight to calculate the GSI. The Balearic Sea samples had the highest mean GSI values (4.46±1.04 vs 1.04±0.66). In general, females always showed slightly higher values than males (2.81±1.8 vs 2.64±2.04). The highest GSI value for females was 7.82 (56.5 cm, 4.3 kg) and that for males was 7.44 (67 cm, 6.8 kg), both found in spawning individuals sampled in July in Balearic waters.

The mean monthly GSI was calculated for both males and females (Fig. 2). In June, a slight increase was observed until the maximum was reached at the beginning of July. After that date, the mean GSI decreased rapidly until it reached the minimum values in September. The monthly evolution showed a similar trend in both sexes, suggesting that the spawning season for SKJ in western Mediterranean occurs between June and August. Mean GSI showed an increasing trend during the maturation progress. The immature females showed the lowest GSI values, followed by developing and postspawning ones. The spawning capable females followed by spawning females showed the highest values. The GAM analysis (Fig. 3) revealed that larger-sized individuals showed the highest GSI values in June and July and the lowest in August and September.

The monthly frequencies of gonad stages by area are shown in Figure 4. Regarding the ovaries analysed, 76 females belonged to fishing championships in the Alboran Sea and 116 to ones in the Balearic Sea. The majority (n=113) of the samples from the Balearic Sea

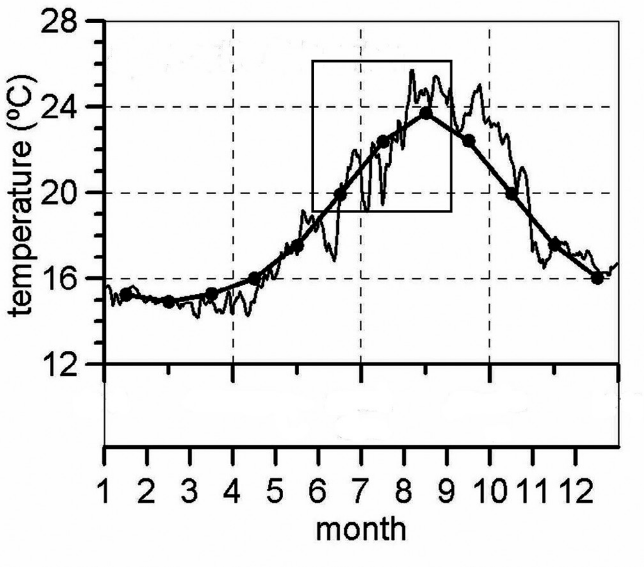

Fig. 5. – Mean daily SST for the northern zone of the Alboran Sea in 2018 and monthly mean values for the period 1981-2021 (line with points). The rectangle highlights the biological sample (June to September).

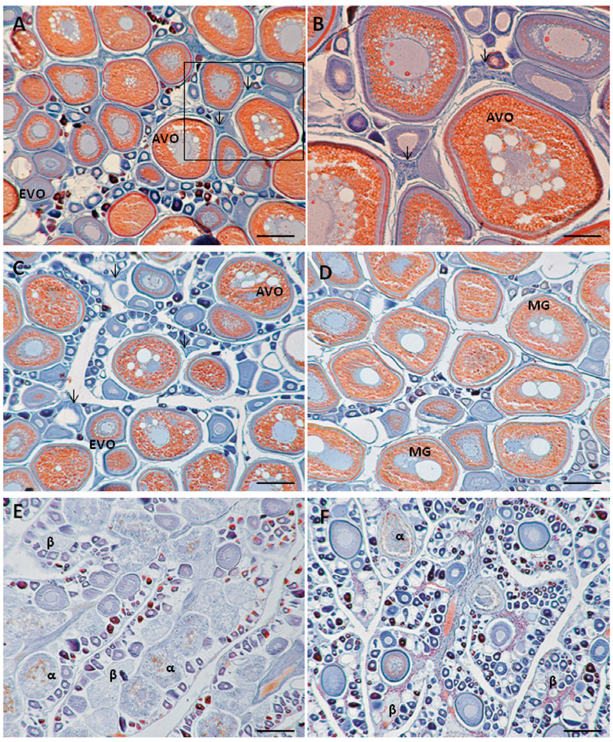

Fig. 6. – Microphotographs of spawning females. A. Ovary with early (EVO) and advanced (AVO) vitellogenic oocytes; arrows point to postovulatory follicles. B. Squared area in A, detail of postovulatory follicles (arrows show POFs) and AVOs. C. Ovary with vitellogenic oocytes and POFs. D. Ovary with migratory oocyte nucleus (MG). E and F. Ovary in regression after spawning, α and β atresia. Bar on images A, C, D and F=250 µm and on image B=100 µm.

were spawning females and the rest were spawning capable. We consistently found spawning females in the Balearic Sea throughout the study period. The ovaries collected in the Alboran Sea showed greater variability in all possible gonad stages: two immature individuals, two specimens in the developing stage, two in the spawning capable stage, 15 in the spawning stage, 24 in the regressing stage and 31 in the regenerating stage. In 2018 all spawning capable and spawning females were captured in the Benalmadena sport fishing championship. This unusual episode was recorded for the first time.

Figure 5 shows the mean daily SST in 2018 for northern zone of the Alboran Sea (5°W to 2°W and 36.4°N to 37°N) and the monthly mean values for the period 1981-2021. A few days before the sport championship, an SST peak occurred there (25.4°C), with higher temperatures than expected for these dates (23.7±0.94°C).

Figure 6 shows microphotographs of ovaries in spawning and postspawning phases, confirming the reproduction of the species in the western Mediterranean. The spawning female fraction calculated considering the proportion of spawning females (n=116) to all active females (n=119, that is, the spawning capable and spawning stages) was 0.97, and the mean spawning frequency was 1.03 days. Therefore, SKJ from the Balearic Sea are capable of spawning every day.

DISCUSSION

Though the SKJ is of great economic importance and several studies have been carried out on it worldwide, there is a lack of knowledge about its biology and migrations in the Mediterranean Sea.

An upward trend in the CPUE of SKJ was observed in the Balearic Sea, where the specimens caught were slightly larger than in the Alboran Sea. Catches in the Alboran Sea also showed an upward trend in CPUE. However, this trend is more irregular than in the Balearic Sea (Saber et al. 2012, 2015, 2020). Our results on CPUE trends agree with those reported by Saber et al. (2015), which indicate an increase in the abundance, weight and average size of individuals caught in the area during the study period.

The sex ratio we found was close to 1:1. However, in Atlantic waters Cayré and Farrugio (1986) identified a global sex ratio in favour of males. In the Indian Ocean, Stequert and Ramcharrum (1996) and Timohina and Romanov (1996) observed the same for larger fishes.

The estimated length at which 50% of the female population of the species reached maturity (L_{50}) is below the sizes sampled in our study. The minimum size at which SKJ reached maturity in the western Mediterranean was at least 53.5 cm straight fork length. This finding agrees with studies in the Indian Ocean, where the L_{50} reaches 41 to 43 cm in females, corresponding to 1.5 years (Stequert and Ramcharrun 1996, Hartaty et al. 2020). In the southwest Atlantic L_{50} was estimated at 45.6 cm for both sexes, 43.2 cm for females and 46.2 cm for males (Benevenuti et al. 2019). Grande et al. (2014) used cortical alveolar oocytes as an indicator of maturation in the western Indian Ocean and the L_{50} of the female population that reached maturity was 39.9 cm. When these authors used advanced vitellogenic oocytes as an indicator, the L_{50} was similar to that in other areas and estimated as 43.5 cm. In our study, the lack of small-sized and immature specimens did not allow us to calculate the L_{50} in the western Mediterranean. We will have to resolve this lack of information in further studies.

The monthly variation of the mean GSI values for males and females and the results obtained from the GAM indicated that the western Mediterranean is a spawning area for SKJ. GAM results indicated that larger specimens reached their maximum GSI earlier than smaller specimens, suggesting that larger specimens start their spawning period earlier than smaller ones. Our results agree with those of other studies conducted on other tuna species in the western Mediterranean Sea (e.g. Macías et al. 2005, Saber et al. 2018). These results were confirmed by histological analysis. The majority of the females sampled in Area I in June and July were spawning females. SKJ spawned in the Mediterranean in the summer months when the environmental conditions were suitable. Several tuna larval surveys carried out by Alemany et al. (2010) and Reglero et al. (2012) have demonstrated that the Balearic Sea is an important spawning ground for tuna species. Moreover, Alemany et al. (2010) and Reglero et al. (2014) reported larvae of SKJ around the Balearic Islands, confirming this area as a spawning ground for the species in the western Mediterranean Sea.

Schaefer and Fuller (2019) found that SKJ spawning in the eastern Pacific Ocean occurred from 24°C to 30°C. The optimal temperatures for tuna spawning are only reached in the Balearic Sea precisely on the dates when spawning SKJ were found in this study. For more details on the oceanography of the western Mediterranean Sea, see Vargas-Yañez et al. (2010, 2019). Our results confirm the preliminary study carried out by Saber et al. (2012) showing spawning-stage fish in the Balearic Sea.

SKJ from the Balearic Sea were capable of spawning every day (spawning frequency=1.03 d) during the spawning season. This result is slightly less than that found by Schaefer and Fuller (2019) in the eastern Pacific Ocean (spawning frequency=1.18 d) and by Ashida (2020) in the western Pacific Ocean (spawning frequency ranged from 4.38 d in the Kuroshio-Oyashio transition area to 2.16 d in the Nasei Islands area).

Given the subtropical and tropical distribution of the species and its high plasticity, the increasing presence of SKJ in the western Mediterranean and the new spawning area detected in the Balearic Sea could be related to the trend towards an increase in SST in the region. Vargas-Yañez et al. (2010, 2019) analysed a long-term time series of temperature generated by the monitoring programmes supported by the Spanish Oceanography Institute in Spanish Mediterranean Waters, complemented with meteorological information from the Spanish Meteorological Agency (AEMET), satellite data from the NOAA and data from meteorological stations to assess the possible impact of climate change. All the areas analysed by these authors, including the Alboran Sea and the Balearic Sea, show a trend to increase in temperature. Analysing the intermediate and deep waters, the same authors detected an increase since the mid-20th century of between 0.13 and 0.3°C/100 years. The increasing temperature trend was confirmed in surface waters, and at a higher rate since 1970. According to Ashida (2020), the reproductive investment of spawning fish in high-latitude areas of the western Indian Ocean may be lower than in tropical and subtropical zones because of shorter durations of favourable oceanographic conditions. These results agree with our results in the western Mediterranean, where the reproductive season only occurs in the summer months.

The specimens caught in the Balearic Sea were reproductively active, while those captured in the Alboran Sea were reproductively inactive and would be migrating towards the Atlantic at the end of the summer once the spawning season was over and SST in the western Mediterranean was decreasing. The exceptional SST conditions in the Alboran Sea in August 2018 could explain the unusual presence of spawning females in Area II. Using NOAA data, we saw that a few days before the championship there was an SST peak maintaining higher temperatures than expected for these dates. However, it must be taken into consideration that the SST in 2018 were above the historical monthly means, a phenomenon that may be related to global warming (Vargas-Yañez M., pers. com. 13/03/2022). This information could be related to changes in the oceanographic conditions (mainly temperature) or changes in the migratory behaviour of the species. Varela et al. (2019) found that SKJ feeds actively between the two areas in our study. This result supports the “income breeding strategy” described for the species. Spawning individuals can adjust their reproductive investment in response to environmental factors, indicating that higher investments in reproduction can be made when food resources are available (McBride et al. 2015) and when they have optimal environmental conditions.

As shown above, SST is of high importance for the highly migratory species, as it impacts spawning activity (Medina et al. 2002), and climate change will directly affect the physiology and spatial distribution of marine organisms, and is expected to affect SKJ. Dueri et al. (2014) projecting the impacts of climate change on SKJ abundance and spatial distribution, found that under present climatic conditions, the biomass peaks at the Equator. In addition, the model projected an increase of biomass at the latitudes 10°N and 10°S for 2050 and a displacement of the biomass peak from the Equator to 10°N. The reproduction rate showed a temporal trend similar to biomass abundance. Our study confirms that the Balearic Sea is a new spawning ground for this species in the western Mediterranean Sea and agrees with the expanding habitats projected for the species in the future.

The presence of a new reproductive species in the study area could be affecting the larval ecology and recruitment of local tuna species. This issue must be studied in the near future to assess its implications for tuna management and conservation in the region.

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