

Fatty acid content and profile of round sardinella (*Sardinella aurita*), an expanding thermophilic species in the NW Mediterranean

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Abstract

Over the past few decades, due to sea warming driven by global climate change, the habitat range of round sardinella (*Sardinella aurita*) has expanded into the north-western Mediterranean Sea. This study evaluates the fatty acid content and fatty acid profile of this small, warm-water pelagic fish caught in this area, specifically the northern Catalan coast. The findings provide important insights into the nutritional status of the species under changing environmental conditions. The study confirms that fatty acid content varies according to the individual specimen's maturity stages (immature, pre-spawners, and spawners). Pre-spawners showed higher fat levels compared to spawners, whose lipids are allocated to their gonads to enhance the survival of their offspring. While a high content of omega-3 polyunsaturated fatty acids (n-3 PUFAs) was generally found at all stages of maturity, pre-spawners had higher levels of EPA but lower levels of DHA than immature individuals and spawners. Moreover, compared to small pelagic fish more typical of the temperate waters in the region (European anchovy, *Engraulis encrasicolus*, and European sardine, *Sardina pilchardus*), round sardinella generally have a higher level of PUFAs, especially DHA. Encouraging consumption of this warm water species could provide significant nutritional benefits while reducing fishing pressure on European sardine and European anchovy, whose populations are currently in a very poor state.

Keywords: Fatty acids; small pelagic fish; thermophilic species; NW Mediterranean; *Sardinella aurita*.

Introduction

In the Mediterranean Sea, the expansion of warm-water – i.e., thermophilic – fish species has been well documented in the context of sea warming (Sabatés *et al.*, 2006; Lloret *et al.*, 2015). One of these species is round sardinella (*Sardinella aurita*, Valenciennes, 1847), a small pelagic fish (SPF) commonly found in subtropical and tropical waters, including the southern Mediterranean, due to its preference for warmer waters (Whitehead, 1985; Palomera & Sabatés, 1990; Sabatés *et al.*, 2006, 2009). In response to increasing seawater temperatures, the geographical distribution of this species in the Mediterranean has been gradually shifting northwards over the last two decades (Palomera & Sabatés, 1990; Sabatés *et al.*, 2006; Tsikliras, 2008). Landings of this species along the Catalan coast (NW Mediterranean) have already been correlated with the anomalies in sea surface temperature (SST) observed in the area (Sabatés *et al.*, 2006).

In the NW Mediterranean, while landings of round sardinella have increased, which appears to be benefiting from the changing environmental conditions, those of European anchovy (*Engraulis encrasicolus*, Linnaeus, 1758) and European sardine (*Sardina pilchardus*, Walbaum, 1792), hereafter referred to as anchovy and sardine, have gradually decreased in the region (Palomera *et al.*, 2007; Van Beveren *et al.*, 2014; Lloret *et al.*, 2015; Brosset *et al.*, 2017; Coll *et al.*, 2019). Historically, anchovy and sardine have been the most dominant SPF species in terms of biomass and commercial importance in the NW Mediterranean (Pennino *et al.*, 2020). However, the current situation facing their populations in this region is adverse due to intense fishing and the challenging environmental conditions that have led to a decrease in the quantity or quality of their food supply, thus affecting their nutritional status (Kang, 2011; Van Beveren *et al.*, 2014; Hixson & Arts, 2016; FAO, 2018; Queiros *et al.*, 2019; Biton-Porsmoguer *et al.*, 2020; Lau *et al.*, 2021).

Despite extensive research on the ecological, economic, and nutritional relevance of sardines and anchovies in the Mediterranean (Albo-Puigserver *et al.*, 2020; Biton-Por-smoguer *et al.*, 2020; Šimat *et al.*, 2020), there is a paucity of information regarding the fatty acid composition of round sardinella, particularly within the relatively cold waters of the NW Mediterranean. Previous studies have focused on the fatty acid profiles of round sardinella in the warmer waters of the southern and eastern Mediterranean regions (Rebah *et al.*, 2010; Abouel-Yazeed, 2013).

The assessment of the fatty acid profile of SPF provides an excellent measure of their state of health, while also serving as a good indicator of the health of the ecosystem they inhabit (Dalsgaard *et al.*, 2003; Lloret *et al.*, 2014) due to the ecological role of SPF in marine ecosystems in transferring energy from primary producers to higher trophic levels (Cury *et al.*, 2000). In particular, polyunsaturated fatty acids (PUFAs), which are produced by phytoplankton (Dalsgaard *et al.*, 2003; Puccinelli *et al.*, 2021), play an important role in several biological processes in fish, with impacts on general growth and development, reproduction, behaviour, and immune system (Bell *et al.*, 1986; Watanabe, 1993; Arts & Kohler, 2009). Furthermore, the fatty acid composition of SPF species can indicate alterations in the quantity and/or quality of their diet, thereby reflecting changes in the phytoplankton community, which is increasingly threatened by climate change (Litzow *et al.*, 2006; Pethybridge *et al.*, 2014; Queiros *et al.*, 2019; Grossi *et al.*, 2024). Monitoring fatty acid profiles also facilitates the assessment of ecosystem dynamics, thereby providing insights into fundamental dependencies within the food web (Auel *et al.*, 2002; Dalsgaard *et al.*, 2003).

In addition to providing insights into ecosystem dynamics, monitoring fatty acid profiles serves another crucial purpose. The nutritional composition of fish offers several health benefits to consumers, particularly due to the essential PUFAs that seafood contains (Lund, 2013; Mohanty *et al.*, 2019; Bianchi *et al.*, 2022; Chen *et al.*, 2022). In the case of SPF, PUFAs are concentrated in the muscle (edible part) and therefore are more available to consumers than lipids from benthic fish, which are usually accumulated in their livers (Lloret *et al.*, 2014). The consumption of these fatty acids has been demonstrated to result in favourable health outcomes in humans, including significant contributions to the prevention of certain cancers and in lowering cardiovascular risk (Ruxton *et al.*, 2004; Lloret, 2010; Pauwels, 2011; Hanson *et al.*, 2020). In particular, the omega-3 PUFA series, such as eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), are essential for human health and provide multiple health benefits, including antioxidant, anti-inflammatory, and cardiovascular properties (Ruxton *et al.*, 2004; de Carvalho & Caramujo, 2018; Chen *et al.*, 2022).

To the best of our knowledge, there has been no previous research on the fatty acid profile of round sardinella found in the NW Mediterranean. We present, therefore, the first analysis of the fatty acid content and fatty acid profile of round sardinella in the NW Mediterranean, with the aim of shedding light on the nutritional and ecological

implications of the expansion and increase of this species in the region. In addition, we compare the fatty acid composition of these round sardinella with those of anchovy and sardine from the same area - as documented in the literature. These comparisons shall be used to analyse the potential implications on human nutrition arising from the significant variations observed in recent landings of these species. Finally, we shall discuss the implications of our findings for human health and for fisheries management, while emphasising the importance of round sardinella as a source of essential PUFAs and the need for sustainable management practices in the face of environmental change.

Materials and Methods

Fish samples

Samples of round sardinella (*Sardinella aurita*) caught by purse seine in the northern Catalan Sea (NW Mediterranean) between May and September 2022 - were collected at the port of L'Escala on the Catalan coast. The collection period coincided with the pre-spawning and spawning season of round sardinella, which occurs from the end of June to September, when the sea surface temperature reaches its highest levels of the year (Palomera & Sabatés, 1990; Tsikliras & Antonopoulou, 2006; Sabatés *et al.*, 2009). During this sampling period, the NW Mediterranean experienced unprecedented marine heatwaves (MHWs) which resulted in summer anomalies of up to 4.6°C in mean sea surface temperatures (SST) (Estaque *et al.*, 2023). The samples were collected and preserved on ice to be transported to the IRTA laboratories in the nearby village of Monells for total lipid and fatty acid profile analyses.

The sampled individuals (620 specimens in total) were measured for length (to the nearest 0.01 cm) and weight (to the nearest 0.01 grams), while sex and reproductive status were determined by visually inspecting their gonads after dissection. The individuals were classified by their level of maturation, as described in Table 1, following the established scales of sexual maturity in individual specimens (Holden & Raitt, 1974; Baali *et al.*, 2021). Specimens were then grouped into sample units consisting of approximately 20 individuals per unit (with a total of 31 sample units), based on the sex and maturation categories. This resulted in 10 sample units of "immature" specimens, 5 sample units of "female pre-spawners", 6 sample units of "male pre-spawners", 5 sample units of "female spawners" and 5 sample units of "male spawners". In September, the sampling period, a few individuals in Stage IV of the post-spawning phase were found, but these were not included in the analysis. After classification into the sample units, each specimen was eviscerated and re-weighed to determine the impact of the weight of the viscera. Then, a muscle fillet from one side of each specimen was extracted, weighed, and stored frozen. Muscle fillets from the other side of each specimen were combined with those from the 20 indi-

Table 1. Adaptation of the sexual maturity scale, based on Baali *et al.*, 2021 and Holden & Raitt, 1974.

Stages of maturity	State	Gonadal size and appearance
Stage I	Immature	Ovary and testis between 33-50% body cavity length. It can be difficult to distinguish between ovaries and testes.
Stage II	Pre-spawning phase / pre-spawners	Ovary and testis about 66% body cavity length. Ovary: pinkish yellow colour with granular appearance Testis: whitish to creamy. No transparent or translucent ova visible.
Stage III	Spawning phase / spawners	Ovary and testis from 66-100% body cavity length. Ovary: orange pink in colour with conspicuous superficial blood vessels. Testis: whitish-creamy, soft. Large transparent, ripe ova visible.
Stage IV	Post-spawning phase / post-spawners	Ovary and testis shrunken to about 50% body cavity length. Walls loose. Ovary: may contain remnants of disintegrating opaque and ripe ova, darkened or translucent. Testis: bloodshot and flabby.

viduals in the respective sample unit, homogenised using a grinder, and kept frozen at -80°C for subsequent biochemical analysis.

Analysis of total fatty acid content and the fatty acids profile

The fatty acid content and fatty acid composition of the round sardinella were analysed from each sample unit of homogenised muscle, as this is where most pelagic fish store most of their energy reserves (Bou *et al.*, 2005; Lloret *et al.*, 2014). Sample lipid extracts were taken in duplicates using the Folch extraction procedure by homogenizing 1.5 g of minced fish muscle in 30 ml of CHCl₃:methanol (2:1, v/v). Additionally, 1,2,3-tritridecanoylglycerol was added in each sample as an internal standard for lipid content quantification. Fatty acid methyl esters (FAMES) were obtained via a two-step methylation procedure (Bou *et al.*, 2005). The fatty acid composition was determined by gas chromatography equipped with a Zebron ZB-FAME capillary column (30 m; 0.25 mm; 0.2 µm) and results were expressed as a % of area normalization whereas the fatty acid content was expressed as mg of internal standard equivalents/100 g fish.

Statistical analysis

Fatty acid content and fatty acid profiles for the different maturity stages of round sardinella were examined using a one-way ANOVA. Normality and homogeneity were verified using Kolmogorov-Smirnov and Levene tests, respectively. For identifying statistical differences between means, a post-hoc Tukey's Honestly Significant Differences (HSD) test was employed. Principal component analyses (PCA) were used to visually identify the primary fatty acids responsible for the observed variations. In all instances, statistical significance was predetermined at $p < 0.05$. The analyses were conducted using

JMP13 software, developed by the SAS Institute in Cary, North Carolina, USA.

Results

Total fatty acid content and profiles

The fatty acid content (g/100 g of sample) and the fatty acid profiles in the muscle of round sardinella are shown in Table 2. Statistical analysis revealed no significant differences in total fatty acid content and fatty acid profile between male and female sardinella. Muscle from pre-spawners showed significantly higher mean fatty acid content compared to immature specimens and spawners. There were no significant differences observed between immature and spawners.

Saturated fatty acids (SFAs) accounted for between 34.91% (in spawners) and 37.06% (in pre-spawners) of the total fatty acids. Significant differences were observed between pre-spawners and the other two categories in the total SFA. In all three categories, the most abundant SFA was C16:0 (P; Palmitic acid), although there was a significant difference between spawners and pre-spawners. Except in the case of C17:0, which presented similar values for all groups, significant differences were observed among the three categories regarding the proportion of particular SFA. The proportion of most of the SFAs was higher in the pre-spawners with the exception of C18:0, which was highest in the spawners, with a significant difference compared to the other categories. The majority of the remaining SFAs showed no significant differences between spawners and the immature.

Monounsaturated fatty acids (MUFAs) comprised between 6.33% (in immature) and 10.83% (in pre-spawners) of the total fatty acids. Apart from C22:1 n-9, pre-spawners displayed a higher content in MUFAs compared to the other two groups. No significant differences in any MUFAs were observed between immature and spawners. The most abundant MUFA in all three categories was C18:1

Table 2. ANOVAs results for the fatty acid content (g/100g sample of wet weight) and fatty acid profiles (as % of total fatty acids) of the muscle of the immature, pre-spawners, and spawners of round sardinella (*Sardinella aurita*) caught between May and September 2022, which included the spawning season (late June to September).

	Immature	Pre-Spawners	Spawners	p-value
Fatty acid content	1.13 ± 0.25 b	2.13 ± 0.36 a	1.04 ± 0.37 b	<0.0001
C14:0	3.57 ± 1.31 b	5.08 ± 0.64 a	2.65 ± 1.46 b	0.0022
C15:0	0.81 ± 0.18 b	1.15 ± 0.15 a	0.77 ± 0.19 b	0.0001
C16:0 (P)	22.67 ± 0.72 ab	23.03 ± 0.34 a	22.20 ± 0.53 b	0.0183
C17:0	1.04 ± 0.11	1.13 ± 0.05	1.08 ± 0.07	ns
C18:0	6.46 ± 0.66 b	5.56 ± 0.25 c	7.51 ± 0.77 a	<0.0001
C20:0	0.17 ± 0.05 b	0.23 ± 0.02 a	0.20 ± 0.06 ab	0.0378
C22:0	0.50 ± 0.18 b	0.80 ± 0.10 a	0.46 ± 0.13 b	<0.0001
Total SFA	35.24 ± 0.80 b	37.06 ± 0.68 a	34.91 ± 1.43 b	0.0067
C16:1 n-7 (PO)	1.56 ± 0.72 b	2.81 ± 0.24 a	1.29 ± 0.82 b	0.0002
C18:1 n-9	3.86 ± 0.93 b	6.39 ± 0.59 a	4.29 ± 1.53 b	0.0003
C20:1 n-9	0.40 ± 0.22 b	0.69 ± 0.10 a	0.37 ± 0.13 b	<0.0001
C22:1 n-9	0.07 ± 0.04	0.10 ± 0.01	0.09 ± 0.03	ns
C24:1 n-9	0.34 ± 0.15 b	0.49 ± 0.05 a	0.33 ± 0.12 b	0.0253
Total MUFA	6.33 ± 2.06 b	10.83 ± 0.91 a	6.48 ± 2.46 b	0.0001
C18:3 n-3	0.96 ± 0.36 b	2.04 ± 0.20 a	0.87 ± 0.43 b	<0.0001
C20:5 n-3 (EPA)	7.40 ± 1.20 b	9.76 ± 0.62 a	6.04 ± 1.67 b	<0.0001
C22:5 n-3	0.34 ± 0.15 b	0.49 ± 0.04 a	0.33 ± 0.12 b	0.0065
C22:6 n-3 (DHA)	45.76 ± 4.08 a	35.26 ± 2.10 b	47.23 ± 5.92 a	<0.0001
Total n-3 PUFA	54.55 ± 2.56 a	47.68 ± 1.43 b	54.55 ± 4.01 a	0.0002
C18:2 n-6	1.63 ± 0.25 b	2.17 ± 0.10 a	1.67 ± 0.27 b	0.0004
C18:3 n-6	0.03 ± 0.02 b	0.09 ± 0.02 a	0.02 ± 0.03 b	0.0004
C20:2 n-6	0.37 ± 0.04 a	0.31 ± 0.03 b	0.39 ± 0.05 a	0.0377
C20:3 n-6	0.10 ± 0.01	0.13 ± 0.02	0.11 ± 0.01	ns
C20:4 n-6	1.71 ± 0.39	1.71 ± 0.08	1.84 ± 0.14	ns
Total n-6 PUFA	3.84 ± 0.59 b	4.42 ± 0.16 a	4.01 ± 0.29 ab	0.0085
Total PUFA	58.39 ± 2.47 a	52.10 ± 1.48 b	58.57 ± 3.79 a	0.0004

n-9 (oleic acid).

Polyunsaturated fatty acids (PUFAs) accounted for between 52.10% (in pre-spawners) and 58.57% (in spawners) of the total fatty acids. The majority of these were n-3 PUFAs, which ranged from 47.68% (in pre-spawners) to 54.55% (in both spawners and the immature). Significant differences were observed in the total amount of PUFAs, and more specifically, in the levels of n-3 and n-6 PUFA, between the pre-spawners and the other two categories. The PUFA with the highest concentration was C22:6 n-3 (DHA), with notable variance between pre-spawners (with the lowest mean value), and the immature as well as spawners (which had the highest mean value). Among the n-3 PUFAs, DHA was the most abundant, with a mean of 47.23% in spawners, while EPA was more abundant in pre-spawners (9.76%). Whereas there were no significant differences in C20:3 n-6 and C20:4 n-6 (arachidonic acid, ARA) values, the remaining n-6 PUFAs showed signifi-

cant differences between pre-spawners and the other two groups.

Principal component analysis

A Principal Component Analysis (PCA) was performed to assess the differences in fatty acid composition among the three maturity stages (immature, pre-spawners, and spawners) of *Sardinella aurita* (Fig. 1). The first two components of the model accounted for 84.8% of the variance. The first component explained 68.3% of the variance and grouped DHA, total n-3 PUFAs, C18:0, and C20:2 n-6 on one side, opposite oleic acid (C18:1 n-9), total MUFAs, and EPA. The first component seems to differentiate distinctly between pre-spawners and spawners. The difference appears to arise mainly because EPA, which is abundant in pre-spawners, and DHA, which is

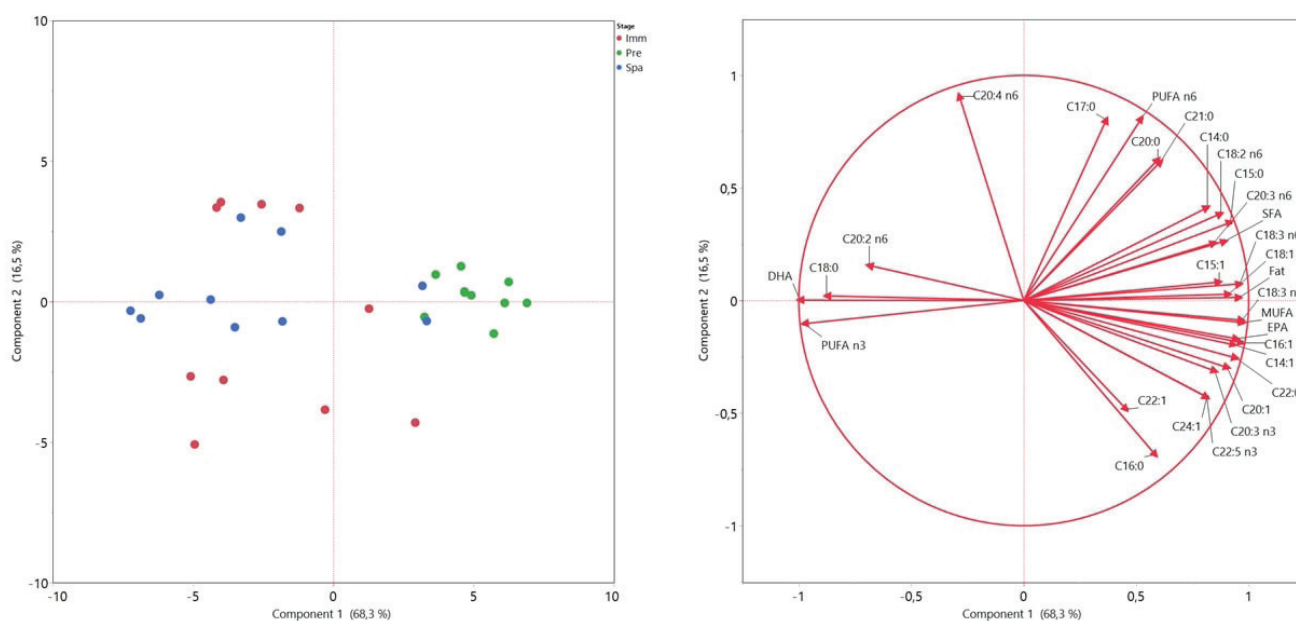


Fig. 1: Plots of scores and loadings of the PCA of round sardinella (*Sardinella aurita*) fatty acid composition corresponding to sexual maturity stage of the specimens: immature (red), pre-spawners (green), and spawners (blue).

abundant in spawners, are in opposite positions in the PCA. The second component explained 16.5% of the variance, which is mainly determined by ARA (C20:4 n-6), n-6 PUFAs, and various SFAs, which were present in opposite coordinates to palmitic acid (C16:0) and C22:1. Pre-spawners and spawners occupied central positions in the second component, whereas the immature group seemed to be more affected by this component.

Discussion

Total fatty acid content and profile of round sardinella in relation to reproduction, feeding and environmental conditions

This study provides novel information on the lipid composition among immature, pre-spawners and spawners specimens of round sardinella in the NW Mediterranean, highlighting, in particular, variations in fish lipid content, which is known to fluctuate due to environmental conditions, dietary patterns, reproductive status and seasonality (Zlatanos & Laskaridis, 2007; Linder *et al.*, 2010; Lloret *et al.*, 2014; Taşbozan & Gökçe, 2017). The results reveal that pre-spawners had a higher fat content than spawners, in line with the reproductive strategy of round sardinella, which accumulates energy reserves prior to spawning and expends them during spawning (Albo-Puigserver *et al.*, 2017). In other words, spawners exhibit a reduction of fat content in their muscles as they allocate the energy-rich lipids to their gonads to ensure the survival of their offspring (McBride *et al.*, 2015). Our investigation was limited to a specific period (from May to September), and, therefore, further year-round investigations are required, considering that the quantity of fatty acids may fluctuate significantly throughout the year due to various factors such as environmental conditions, feeding habits, and reproductive cycle.

The feeding behaviour and environmental conditions of round sardinella are thought to be linked with their fatty acid content and fatty acid composition. Spawning of round sardinella in the NW Mediterranean occurs during the highest seasonal water temperature, which is associated with low phytoplankton availability, minimal chlorophyll *a* values, and an increased presence of zooplankton (Calbet *et al.*, 2001). Previous research has indicated that round sardinella is an opportunistic predator with a diverse diet, comprising of copepods, fish eggs, diatoms, *chaetognatha*, decapods, and *salpidae* (Tsikliras *et al.*, 2005; Bayhan *et al.*, 2015; Albo-Puigserver *et al.*, 2019). Most of these phytoplankton and zooplankton groups are rich in lipids and essential fatty acids (Persson & Vrede, 2006; Brett *et al.*, 2009; Hartwich *et al.*, 2013), which contribute to the overall health of round sardinella. The results of our study are in line with previous research on the trophic ecology of round sardinella in the Mediterranean. During the summer, they feed mainly on copepods and *cladocerans* (Tsikliras *et al.*, 2005; Madkour, 2012; Bayhan *et al.*, 2015; Albo-Puigserver *et al.*, 2019), which is consistent with high DHA levels, as DHA content is known to be almost twice that of EPA in most copepod species (Kattner & Hagen, 2009). It is also consistent with the idea that *cladocerans* accumulate EPA almost exclusively, whereas copepods predominantly accumulate DHA (Farkas, 1979). Several fatty acids and their ratios may be employed to compare dietary changes within a population over time (Dalsgaard *et al.*, 2003; Parrish, 2009; Pethybridge *et al.*, 2014; Biton-Porsmoguer *et al.*, 2020). Prior to our study, no data existed regarding the concentrations of fatty acids in round sardinella on the NW Mediterranean, yet the data and results provided here might prove valuable for future research on biological, fisheries and nutritional aspects of species, such as round sardinella, whose range and abundance is increasing due to sea warming.

Environmental conditions, particularly the increasing water temperatures due to climate change, are fundamen-

tal to the status of the Mediterranean round sardinella. Several studies, including those of Hixson & Arts (2016) and Holm *et al.* (2022), have explored the potential impacts of increasing water temperature on the production of n-3 PUFAs in phytoplankton. Any changes in the quantity of EPA and DHA in phytoplankton can disrupt the marine food chain, affecting the entire ecosystem's balance (Jin *et al.*, 2020). In particular, sea warming could lead to a significant decline in EPA levels, which have a negative correlation with temperature (Holm *et al.*, 2022). The correlation between planktonic EPA and temperature indicates a potential reduction in EPA production by plankton at the base of the food chain in response to rising ocean temperatures (Holm *et al.*, 2022). This could result in restricted availability of omega-3 fatty acids across the food chain. Moreover, elevated water temperatures may cause stratification, which limits the nutrient intake of phytoplankton, resulting in a decline in their populations, leading to a further lowering of lipid content and PUFA levels (Kang, 2011). Although sampling took place in 2022, which was a year with the highest SST anomaly observed in the Mediterranean Sea in recent decades (Estaque *et al.*, 2023), we were unable to assess the impact of sea warming on the fatty acid profile and energy reserves of round sardinella due to the lack of previous studies on fatty acid profiles in this region with which to make comparisons.

There have, however, been previous investigations in other areas of the Mediterranean Sea, for example in the southern and eastern areas, which have examined the total lipid content and fatty acid profile of round sardinella. For instance, Barakat *et al.* (2022) investigated the chemical composition of round sardinella and observed fluctuations in fat content over the course of a year, with higher levels observed during autumn and lower levels in summer, coinciding with the species' spawning period. A synthesis of findings on total lipid and fatty acid contents from two studies conducted in Tunisia and Egypt and the

present study is presented in Table 3 (Rebah *et al.*, 2010; Abouel-Yazeed, 2013). It is important to remember that these studies were conducted in different years, regions, and months of the reproductive period of round sardinella. However, some general trends can be observed. Studies such as those of Rebah *et al.* (2010) and Abouel Yazeed (2013), which reported higher total lipid contents, appear to have been conducted outside the spawning season, which could lead to higher lipid reserves in the muscle. Conversely, during the spawning period, these lipid reserves in the muscle are redirected towards gonadal development to support offspring maturation which, in turn, may help to explain our findings. While the total SFA levels were similar between the studies, our study exhibited notably lower total MUFA levels compared to the others. Although EPA levels were similar, DHA levels were higher in our study. However, further investigation into any variations in total lipid content and fatty acid profiles of round sardinella populations inhabiting waters with differing temperature regimes would be required to enhance our understanding of the various factors that affect the fatty acid content of the species.

Comparison of total fatty acid content and profile of round sardinella with those of other small pelagic fish species in the NW Mediterranean

In the NW Mediterranean, round sardinella coexist with sardine, and anchovy. These three SPF species have larger populations and may compete due to their overlapping distribution in shallow waters (Palomera *et al.*, 2007), shared food resources (Ablo-Puigserver *et al.*, 2019; Bachiller *et al.*, 2021), and similar reproductive patterns (Palomera *et al.*, 2007). In order to gain insight into the dietary preferences, trophic interactions, potential competition for food resources, and to provide valuable information on the nutritional quality of these fish

Table 3. Total lipid (g/100g of wet weight) and fatty acid profiles (as % of total fatty acids) of round sardinella (*Sardinella aurita*) in Gulf of Gabès (Tunisia) (Ben Rebah *et al.*, 2010), in Alexandria Governorate (Egypt) (Abouel-Yazeed, 2013) and in N Catalan Sea (this study).

Location	Gulf of Gabès (Tunisia)	Alexandria Governorate (Egypt)	N Catalan Sea (Spain)
Collection period	February (prior to 2008)	March 2012	May-September 2022
Reproductive period	Non-spawning period	Non-spawning period	Spawning period
Fatty acid method	Soxhlet method	Folch method	Folch method
Total lipid	9.33	10.27	1.43
Total SFA	37.5	27.92	35.73
Total MUFA	21.2	36.84	7.88
C20:5 n-3 (EPA)	11.0	2.57	7.73
C22:6 n-3 (DHA)	9.8	19.22	42.75
Total n-3 PUFA	25.0	23.64	52.26
Total n-6 PUFA	4.3	11.65	4.09
Total PUFA	31.6	35.29	56.35

species as food sources for consumers, a comparison was conducted between the fatty acid content and fatty acid profile of sardine and anchovy in the NW Mediterranean (Biton-Porsmoguer *et al.*, 2020), and the results of round sardinella from this study (Table 4). The comparison, it should be pointed out, concerns specimens caught only during the spawning season: sardine spawn in the autumn/winter, anchovy in early spring/summer, and round sardinella in late spring/summer (Tsikliras & Antonopoulou, 2006; Palomera *et al.*, 2007; Ablo-Puigserver *et al.*, 2019). Notably, round sardinella have the highest levels of total PUFAs, whereas sardines have higher levels of SFA and MUFA than round sardinella, and anchovies have higher EPA levels than round sardinella. The higher total PUFA levels in round sardinella is primarily attributed to elevated levels of DHA present in the fish muscle, compared to sardines and anchovies. This elevated PUFA levels observed in round sardinella compared to the other SPF highlight the increasing ecological and nutritional relevance of this species within the NW Mediterranean ecosystem. The lower PUFA levels observed in anchovy and sardine in the NW Mediterranean may be attributed to the challenging environmental conditions present in this region (Biton-Porsmoguer *et al.*, 2020; Báez *et al.*, 2022). Round sardinella and other SPF contribute to support various trophic levels within the ecosystem, including predatory species such as swordfish (*Xiphias gladius*), little tunny (*Euthynnus alletteratus*), Atlantic bonito (*Sarda sarda*), and Atlantic bluefin tuna (*Thunnus thynnus*) (Palomera *et al.*, 2007; Navarro *et al.*, 2017).

The importance of PUFAs for the health of humans and oceans

The importance of PUFAs, particularly EPA and DHA, in maintaining the well-being of both marine ecosystems and human health is undeniable. The consump-

tion of EPA and DHA has a multitude of beneficial effects on human health, from infancy to adulthood, improving quality of life and reducing the risk factors associated with premature death (Ruxton *et al.*, 2004). DHA is the primary PUFA component found in brain neurons, retinal cells, testicles, and sperm, where it appears to play a central role in the development and function of these organs and systems and plays a crucial role in both prenatal and postnatal brain development (Sidhu, 2003; Kidd, 2007; Mohanty *et al.*, 2019). It is also vital for maintaining the well-being of most vertebrates (Colombo *et al.*, 2020). EPA, on the other hand, is believed to be particularly effective in regulating mood and behaviour, while also demonstrating potential benefits in mitigating various conditions, including dementia, Huntington's disease, depression, bipolar disorder, and schizophrenia (Kidd, 2007; Mohanty *et al.*, 2019). Research suggests that a combination of EPA and DHA is beneficial for several clinical conditions, including the prevention and the reversal of cardiovascular disease, hypertension, asthma, high cholesterol, diabetes, rheumatoid arthritis, cancer, depression, dementia, and Alzheimer's disease (Sidhu, 2003; Ruxton *et al.*, 2004; Mohanty *et al.*, 2019; Chen *et al.*, 2022).

Our study, in conjunction with previous research, such as that of Mathieu-Resuge *et al.* (2023), supports the notion that SPF are rich in essential fatty acids, making them a favourable choice for consumers. Round sardinella, characterised by its high PUFA levels and an expanding population, emerges as a promising and sustainable fishing alternative for fisheries in the NW Mediterranean. By diversifying fishing practices with the incorporation of warm-water fishes like round sardinella, small-pelagic fisheries in the NW Mediterranean could enhance their resilience and ecological sustainability. Interestingly, despite its favourable fatty acid profile, round sardinella is not commonly consumed in France and Spain, possibly due to the historical abundance of other SPF species in

Table 4. Total lipid (g/100g of wet weight) and fatty acid profiles (as % of total fatty acids) during the spawning period for European anchovy (*Engraulis encrasicolus*), sardine (*Sardina pilchardus*), and round sardinella (*Sardinella aurita*) in the northern Catalan Sea (NW Mediterranean Sea) (Biton-Porsmoguer *et al.*, 2020) and this study.

Species	<i>Sardina pilchardus</i>	<i>Engraulis encrasicolus</i>	<i>Sardinella aurita</i>
Collection period	November-April 2019-2020		May-September 2022
Total lipid	1.78	2.46	1.43
Total SFA	46.33	33.52	35.73
Total MUFA	20.33	15.59	7.88
C20:5 n-3 (EPA)	7.88	14.13	7.73
C22:6 n-3 (DHA)	20.86	32.02	42.75
Total n-3 PUFA	30.13	47.53	52.26
Total n-6 PUFA	3.19	3.37	4.09
Total PUFA	33.32	50.90	56.35

the region and to an ignorance of its gastronomic and culinary potential. Furthermore, given that SPF account for over a quarter of global landings (FAO, 2022), the significance of these findings cannot be overstated, emphasizing the importance of leveraging sustainable fishing practices to ensure the continued availability of nutritious seafood resources.

In marine ecosystems, PUFAs contribute to the structural integrity of cell membranes in phytoplankton and other marine organisms, enhancing their resilience to environmental stressors (de Carvalho & Caramujo, 2018; Hernando *et al.*, 2022). As these PUFAs are transferred from primary producers to higher trophic levels through consumption, they exert a significant influence on the health and stability of entire marine ecosystems (Bell & Tocher, 2009). Consequently, the health of marine ecosystems directly affects the availability and quality of PUFAs in seafood, highlighting the links between ocean health and human health and well-being and emphasising the importance of preserving marine ecosystems as a whole. Moreover, it is important to comprehend how environmental alterations can influence the nutritional composition of marine organisms is essential. For instance, fluctuations in the fatty acid content and fatty acid profile of phytoplankton can diminish the nutritional value of marine species consumed by humans, potentially leading to deficiencies of these essential PUFAs and increased consumption of SFAs (Hixson & Arts, 2016; Jónasdóttir, 2019; Jin *et al.*, 2020). The study by Jin *et al.* (2020) provides valuable insights, indicating that short-term warming scenarios may decrease phytoplankton lipid content, although prolonged exposure to warming conditions can partially or fully restore this content. It is important to continue monitoring the lipid content and fatty acid profile of such marine species given their potential impact on both marine ecosystems and human health. This emphasises the importance of mitigating climate change and safeguarding marine ecosystems to preserve the nutritional integrity of seafood resources, which are important not only for the health of marine ecosystems, but also for human health as well.

In the future, climate change-induced anomalies in oceanic temperatures are expected to result in a significant redistribution of species, especially with regard to those adapted to warm waters, such as the round sardinella. As warmer waters become more pervasive, the spawning and habitat range of the round sardinella is highly likely to continue to expand (Sabatés *et al.*, 2006; Maynou *et al.*, 2020). Understanding the health benefits associated with the consumption of these species, rich in beneficial fatty acids and newly-arrived in the NW Mediterranean, becomes crucial. Additionally, it is essential to implement sustainable fisheries management strategies for their populations, such as size regulations, in order to guarantee their preservation and the overall stability of the ecosystem.

Conclusion

This study highlights the importance of understanding the fatty acid content and fatty acid profile of populations of round sardinella, a small, warm-water pelagic fish that has become more abundant in the NW Mediterranean due to sea warming. It is important to point out that, the present study represents the first investigation of the lipid composition and fatty acid profile of the round sardinella in the NW Mediterranean region. This is particularly important given that populations of traditional, more temperate SPF such as sardine and anchovy, have suffered from impoverishment or depletion in the NW Mediterranean due to deteriorating environmental conditions and fishing. It also highlights the high-quality nutritional profile of round sardinella as a source of healthy PUFAs both for their natural predators, as well as for humans. In addition, it emphasises the potential consequences of climate change on the nutritional composition of the species, underscoring the importance of sustainable fishing practices.

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References

- Abouel-Yazeed, A.M., 2013. Fatty acids profile of some marine water and freshwater fish. *Journal of Arabian Aquaculture Society*, 8 (2), 283-292.
- Albo-Puigserver, M., Muñoz, A., Navarro, J., Coll, M., Pethybridge, H. *et al.*, 2017. Ecological energetics of forage fish from the Mediterranean Sea: Seasonal dynamics and inter-specific differences. *Deep Sea Research Part II: Tropical*

- Studies in Oceanography*, 140, 74-82.
- Albo-Puigserver, M., Borne, D., Coll, M., Tirelli, V., Palomera, I. *et al.*, 2019. Trophic ecology of range-expanding round sardinella and resident sympatric species in the NW Mediterranean. *Marine Ecology Progress Series*, 620, 139-154.
- Albo-Puigserver, M., Sánchez, S., Coll, M., Bernal, M., Sáez-Liante, R. *et al.*, 2020. Year-round energy dynamics of sardine and anchovy in the north-western Mediterranean Sea. *Marine Environmental Research*, 159, 105021.
- Arts, M.T., Kohler, C.C., 2009. Health and condition in fish: The influence of lipids on membrane competency and immune response. In: Kainz, M., Brett, M., Arts, M. (eds) *Lipids in aquatic ecosystems*, 237-256. Springer, New York.
- Auel, H., Harjes, M., Da Rocha, R., Stübing, D., Hagen, W., 2002. Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. *Polar Biology*, 25 (5), 374-383.
- Baali, A., Belhsen, O.K., Ouazzani, K.C., Amenouz, K., Yahyaoui, A., 2021. Age, Growth and Ovarian Histology of *Sardinella aurita* (Valenciennes, 1847) in the South of Atlantic Moroccan coast. *Turkish Journal of Fisheries and Aquatic Sciences*, 21 (4), 191-204.
- Bachiller, E., Giménez, J., Albo-Puigserver, M., Pennino, M.G., Mari-Mena, N., *et al.* 2021. Trophic niche overlap between round sardinella (*Sardinella aurita*) and sympatric pelagic fish species in the Western Mediterranean. *Ecology and Evolution*, 11 (22), 16126-16142.
- Báez, J.C., Pennino, M.G., Czerwinski, I.A., Coll, M., Bellido, J.M. *et al.*, 2022. Long term oscillations of Mediterranean sardine and anchovy explained by the combined effect of multiple regional and global climatic indices. *Regional Studies in Marine Science*, 56, 102709.
- Bayhan, B., Sever, T.M., Kaya M., 2015. Diet composition of the round sardinella *Sardinella aurita* Valenciennes, 1847 (Osteichthyes: Clupeidae) in the Turkish Aegean Sea. *International Journal of Fauna and Biological Studies*, 2 (4), 38-42.
- Bell, M.V., Henderson, R.J., Sargent, J.R., 1986. The role of polyunsaturated fatty acids in fish. *Comparative Biochemistry and Physiology Part B: Comparative Biochemistry*, 83 (4), 711-719.
- Bell, M.V., Tocher, D.R., 2009. Biosynthesis of polyunsaturated fatty acids in aquatic ecosystems: general pathways and new directions. In: Kainz, M., Brett, M., Arts, M. (eds) *Lipids in aquatic ecosystems*, 211-236. Springer, New York.
- Bianchi, M., Hallström, E., Parker, R.W., Mifflin, K., Tyedmers, P. *et al.*, 2022. Assessing seafood nutritional diversity together with climate impacts informs more comprehensive dietary advice. *Communications Earth & Environment*, 3 (1), 188.
- Biton-Porsmoguer, S., Bou, R., Lloret, E., Alcaide, M., Lloret, J., 2020. Fatty acid composition and parasitism of European sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) populations in the northern Catalan Sea in the context of changing environmental conditions. *Conservation Physiology*, 8 (1), coaa121.
- Bou, R., Codony, R., Tres, A., Baucells, M.D., Guardiola, F., 2005. Increase of geometrical and positional fatty acid isomers in dark meat from broilers fed heated oils. *Poultry science*, 84 (12), 1942-1954.
- Brett, M.T., Müller-Navarra, D.C., Persson, J., 2009. Crustacean zooplankton fatty acid composition. In: Kainz, M., Brett, M., Arts, M. (Eds) *Lipids in Aquatic Ecosystems*. 115-146 Springer, New York.
- Brosset, P., Fromentin, J.M., Van Beveren, E., Lloret, J., Marques, V. *et al.*, 2017. Spatio-temporal patterns and environmental controls of small pelagic fish body condition from contrasted Mediterranean areas. *Progress in oceanography*, 151, 149-162.
- Calbet, A., Garrido, S., Saiz, E., Alcaraz, M., Duarte, C.M., 2001. Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions. *Journal of Plankton research*, 23 (3), 319-331.
- Chen, J., Jayachandran, M., Bai, W., Xu, B., 2022. A critical review on the health benefits of fish consumption and its bioactive constituents. *Food Chemistry*, 369, 130874.
- Coll, M., Albo-Puigserver, M., Navarro, J., Palomera, I., Dambacher, J.M., 2019. Who is to blame? Plausible pressures on small pelagic fish population changes in the northwestern Mediterranean Sea. *Marine Ecology Progress Series*, 617-618, 277-294.
- Colombo, S.M., Rodgers, T.F., Diamond, M.L., Bazinet, R.P., Arts, M.T., 2020. Projected declines in global DHA availability for human consumption as a result of global warming. *Ambio*, 49 (4), 865-880.
- Cury, P., Bakun, A., Crawford, R.J., Jarre, A., Quinones, R.A. *et al.*, 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. *ICES Journal of Marine Science*, 57 (3), 603-618.
- Dalsgaard, J., John, M.S., Kattner, G., Müller-Navarra, D., Hagen, W., 2003. Fatty acid trophic markers in the pelagic marine environment. *Advances in Marine Biology*, 46, 225-340.
- De Carvalho, C.C., Caramujo, M.J., 2018. The various roles of fatty acids. *Molecules*, 23(10), 2583.
- Estaque, T., Richaume, J., Bianchimani, O., Schull, Q., Mériot, B. *et al.*, 2023. Marine heatwaves on the rise: One of the strongest ever observed mass mortality event in temperate gorgonians. *Global change biology*, 29 (22), 6159-6162.
- FAO, 2018. The state of Mediterranean and Black Sea fisheries. Rome: Food and Agriculture Organization of the United Nation.
- FAO, 2022. The State of World Fisheries and Aquaculture: Towards a Blue transformation. Rome: FAO.
- Farkas, T., 1979. Adaptation of fatty acid composition to temperature -a study on carp (*Cyprinus carpio* L.) liver slices. *Comparative Biochemistry and Physiology Part B: Comparative Biochemistry*, 79 (4), 531-535.
- Grossi, F., Lagasio, M., Napoli, A., Provenzale, A., Tepsich, P., 2024. Phytoplankton spring bloom in the NW Mediterranean Sea under climate change. *Science of The Total Environment*, 914, 169884.
- Hanson, S., Thorpe, G., Winstanley, L., Abdelhamid, A.S., Hooper, L., 2020. Omega-3, omega-6 and total dietary polyunsaturated fat on cancer incidence: systematic review and meta-analysis of randomised trials. *British journal of cancer*, 122 (8), 1260-1270.
- Hartwich, M., Martin-Creuzburg, D., Wacker, A., 2013. Seasonal changes in the accumulation of polyunsaturated fat-

- ty acids in zooplankton. *Journal of Plankton Research*, 35 (1), 121-134.
- Hernando, M.P., Schloss, I.R., De La Rosa, F., De Troch, M., 2022. Fatty acids in microalgae and cyanobacteria in a changing world: Contrasting temperate and cold environments. *Biocell*, 46 (3), 607-621.
- Hixson, S.M., Arts, M.T., 2016. Climate warming is predicted to reduce omega-3, long-chain, polyunsaturated fatty acid production in phytoplankton. *Global Change Biology*, 22 (8), 2744-2755.
- Holden, M.J., Raitt, D.F.S., 1974. Manuel de science halieutique. Pt. 2: Méthodes de recherches sur les ressources et leur application. FAO, *Document Technique sur les Pêches* (FAO) fre no. 115 (Rev. 1).
- Holm, H.C., Fredricks, H.F., Bent, S.M., Lowenstein, D.P., Ossolinski, J.E. *et al.*, 2022. Global ocean lipidomes show a universal relationship between temperature and lipid unsaturation. *Science*, 376 (6600), 1487-1491.
- Jin, P., González, G., Agustí, S., 2020. Long-term exposure to increasing temperature can offset predicted losses in marine food quality (fatty acids) caused by ocean warming. *Evolutionary Applications*, 13 (9), 2497-2506.
- Jónasdóttir, S.H., 2019. Fatty acid profiles and production in marine phytoplankton. *Marine drugs*, 17 (3), 151.
- Kang, J.X., 2011. Omega-3: a link between global climate change and human health. *Biotechnology advances*, 29 (4), 388-390.
- Kattner, G., Hagen, W., 2009. Lipids in marine copepods: latitudinal characteristics and perspective to global warming. In: Kainz, M., Brett, M., Arts, M. (eds) *Lipids in Aquatic Ecosystems*. (pp. 257-280). Springer, New York.
- Kidd, P.M., 2007. Omega-3 DHA and EPA for cognition, behavior, and mood: clinical findings and structural-functional synergies with cell membrane phospholipids. *Alternative medicine review*, 12 (3), 207.
- Lau, D.C., Jonsson, A., Isles, P.D., Creed, I.F., Bergström, A.K., 2021. Lowered nutritional quality of plankton caused by global environmental changes. *Global Change Biology*, 27 (23), 6294-6306.
- Linder, M., Belhaj, N., Sautot, P., Tehrany, E.A., 2010. From Krill to Whale: an overview of marine fatty acids and lipid compositions. *Oléagineux, Corps gras, Lipides*, 17 (4), 194-204.
- Litzow, M.A., Bailey, K.M., Prahl, F.G., Heintz, R., 2006. Climate regime shifts and reorganization of fish communities: the essential fatty acid limitation hypothesis. *Marine Ecology Progress Series*, 315, 1-11.
- Lloret, J., 2010. Human health benefits supplied by Mediterranean marine biodiversity. *Marine pollution bulletin*, 60 (10), 1640-1646.
- Lloret, J., Shulman, G., Love, R.M., 2014. Condition and health indicators of exploited marine fishes. John Wiley & Sons. 247.
- Lloret, J., Sabatés, A., Muñoz, M., Demestre, M., Solé, I. *et al.*, 2015. How a multidisciplinary approach involving ethnoecology, biology and fisheries can help explain the spatio-temporal changes in marine fish abundance resulting from climate change. *Global Ecology and Biogeography*, 24 (4), 448-461.
- Lund, E.K., 2013. Health benefits of seafood; is it just the fatty acids? *Food chemistry*, 140 (3), 413-420.
- Madkour, F.F., 2012. Feeding ecology of the round sardinella, *Sardinella aurita* (Family: Clupeidae) in the Egyptian Mediterranean waters. *International Journal of Environmental Science and Engineering*, 2, 83-92.
- Mathieu-Resuge, M., Le Grand, F., Brosset, P., Lebigre, C., Soudant, P. *et al.*, 2023. Red muscle of small pelagic fishes' fillets are high-quality sources of essential fatty acids. *Journal of Food Composition and Analysis*, 120, 105304.
- Maynou, F., Sabatés, A., Raya, V., 2020. Changes in the spawning habitat of two small pelagic fish in the Northwestern Mediterranean. *Fisheries Oceanography*, 29 (2), 201-213.
- McBride, R. S., Somarakis, S., Fitzhugh, G. R., Albert, A., Yaragina, N. A., *et al.*, 2015. Energy acquisition and allocation to egg production in relation to fish reproductive strategies. *Fish and Fisheries*, 16 (1), 23-57.
- Mohanty, B.P., Ganguly, S., Mahanty, A., Mitra, T., Patra, S. *et al.*, 2019. Fish in human health and nutrition. *Advances in fish research*, 7, 189-218.
- Navarro, J., Sáez-Liante, R., Albo-Puigserver, M., Coll, M., Palomera, I., 2017. Feeding strategies and ecological roles of three predatory pelagic fish in the western Mediterranean Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, 140, 9-17.
- Palomera, I., Sabatés, A., 1990. Co-occurrence of *Engraulis encrasicolus* and *Sardinella aurita* eggs and larvae in the northwestern Mediterranean. *Scientia Marina*, 57 (1), 61-67.
- Palomera, I., Olivar, M.P., Salat, J., Sabatés, A., Coll, M. *et al.*, 2007. Small pelagic fish in the NW Mediterranean Sea: an ecological review. *Progress in Oceanography*, 74 (2-3), 377-396.
- Parrish, C.C., 2009. Essential fatty acids in aquatic food webs. *Lipids in aquatic ecosystems*, 309-326. In: Kainz, M., Brett, M., Arts, M. (eds) *Lipids in Aquatic Ecosystems*. Springer, New York, NY.
- Pauwels, E.K., 2011. The protective effect of the Mediterranean diet: focus on cancer and cardiovascular risk. *Medical principles and practice*, 20 (2), 103-111.
- Pennino, M.G., Coll, M., Albo-Puigserver, M., Fernández-Corredor, E., Steenbeek, J. *et al.*, 2020. Current and future influence of environmental factors on small pelagic fish distributions in the Northwestern Mediterranean Sea. *Frontiers in Marine Science*, 7, 566340.
- Persson, J., Vrede, T., 2006. Polyunsaturated fatty acids in zooplankton: variation due to taxonomy and trophic position. *Freshwater Biology*, 51 (5), 887-900.
- Pethybridge, H., Bodin, N., Arsenaault-Pernet, E.J., Bourdeix, J.H., Brisset, B. *et al.*, 2014. Temporal and inter-specific variations in forage fish feeding conditions in the NW Mediterranean: lipid content and fatty acid compositional changes. *Marine Ecology Progress Series*, 512, 39-54.
- Puccinelli, E., Sardenne, F., Pecquerie, L., Fawcett, S.E., Machu, E. *et al.*, 2021. Omega-3 pathways in upwelling systems: the link to nitrogen supply. *Frontiers in Marine Science*, 8, 664601.
- Queiros, Q., Fromentin, J.M., Gasset, E., Dutto, G., Huiban, C. *et al.*, 2019. Food in the sea: size also matters for pelagic fish. *Frontiers in Marine Science*, 6, 385.
- Rebah, F.B., Abdelmouleh, A., Kammoun, W., Yezza, A., 2010.

- Seasonal variation of lipid content and fatty acid composition of *Sardinella aurita* from the Tunisian coast. *Journal of the Marine Biological Association of the United Kingdom*, 90 (3), 569-573.
- Ruxton, C.H.S., Reed, S.C., Simpson, M.J.A., Millington, K.J., 2004. The health benefits of omega-3 polyunsaturated fatty acids: a review of the evidence. *Journal of human nutrition and dietetics*, 17 (5), 449-459.
- Sabatés, A.N.A., Martín, P., Lloret, J., Raya, V., 2006. Sea warming and fish distribution: the case of the small pelagic fish, *Sardinella aurita*, in the western Mediterranean. *Global change biology*, 12 (11), 2209-2219.
- Sabatés, A., Salat, J., Raya, V., Emelianov, M., Segura-Noguera, M., 2009. Spawning environmental conditions of *Sardinella aurita* at the northern limit of its distribution range, the western Mediterranean. *Marine Ecology Progress Series*, 385, 227-236.
- Sidhu, K.S., 2003. Health benefits and potential risks related to consumption of fish or fish oil. *Regulatory toxicology and pharmacology*, 38 (3), 336-344.
- Šimat, V., Hamed, I., Petričević, S., Bogdanović, T., 2020. Seasonal changes in free amino acid and fatty acid compositions of sardines, *Sardina pilchardus* (Walbaum, 1792): Implications for nutrition. *Foods*, 9(7), 867.
- Taşbozan, O., Gökçe, M.A., 2017. Fatty acids in fish. In: *Fatty acids*, InTech 1, 143-159.
- Tsikliras, A.C., Torre, M., Stergiou, K.I., 2005. Feeding habits and trophic level of round sardinella (*Sardinella aurita*) in the northeastern Mediterranean (Aegean Sea, Greece). *Journal of Biological Research*, 3, 67-75.
- Tsikliras, A.C., Antonopoulou, E., 2006. Reproductive biology of round sardinella (*Sardinella aurita*) in north-eastern Mediterranean. *Scientia Marina*, 70 (2), 281-290.
- Tsikliras, A.C., 2008. Climate-related geographic shift and sudden population increase of a small pelagic fish (*Sardinella aurita*) in the eastern Mediterranean Sea. *Marine Biology Research*, 4 (6), 477-481.
- Van Beveren, E., Bonhommeau, S., Fromentin, J.M., Bigot, J.L., Bourdeix, J.H. *et al.*, 2014. Rapid changes in growth, condition, size and age of small pelagic fish in the Mediterranean. *Marine biology*, 161, 1809-1822.
- Watanabe, T., 1993. Importance of docosahexaenoic acid in marine larval fish. *Journal of the World Aquaculture Society*, 24 (2), 152-161.
- Whitehead, P.J.P., 1985. Clupeoid fishes of the world (suborder Clupeoidei): Chirocentridae, Clupeidae, and Pristigasteridae. Food and Agriculture Organization of the United Nations.
- Zlatanov, S., Laskaridis, K., 2007. Seasonal variation in the fatty acid composition of three Mediterranean fish-sardine (*Sardina pilchardus*), anchovy (*Engraulis encrasicolus*) and picarel (*Spicara smaris*). *Food chemistry*, 103 (3), 725-728.