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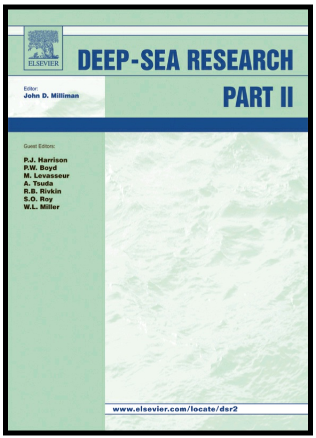

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Ecological energetics of forage fish from the Mediterranean Sea: seasonal dynamics and interspecific differences

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ABSTRACT

Small and medium pelagic fishes play a central role in marine food webs by transferring energy from plankton to top predators. In this study, direct calorimetry was used to analyze the energy density of seven pelagic species collected over four seasons from the western Mediterranean Sea: anchovy *Engraulis encrasicolus*, sardine *Sardina pilchardus,* round sardinella *Sardinella aurita,* horse mackerels *Trachurus trachurus* and *T. mediterraneus,* and mackerels *Scomber scombrus* and *S. colias*. Inter-specific differences in energy density were linked to spawning period, energy allocation strategies for reproduction and growth, and feeding ecologies. Energy density of each species varied over time, with the exception of *S. colias*, likely due to its high energetic requirements related to migration throughout the year. In general, higher energy density was observed in spring for all species, regardless of their breeding strategy, probably as a consequence of the late-winter phytoplankton bloom. These results provide new insights into the temporal availability of energy in the pelagic ecosystem of the Mediterranean Sea, which are pivotal for understanding how the population dynamics of small and medium pelagic fishes and their predators may respond to environmental changes and fishing impacts. In addition, the differences found in energy density between species highlighted the importance of using species specific energy-values in ecosystem assessment tools such as bioenergetic and food web models.

Keywords

energy density, bioenergetics, food webs, Mediterranean Sea, environmental variability

1. Introduction

The amount of energy available to an individual during its lifecycle affects its ability to grow and reproduce and this in turn, affects ecological energetics, that is, how energy is acquired, retained and transferred from one trophic level to another in the food web (Rossoll et al., 2012). Ecosystem energetics underpins many food web models that are increasingly being used to assist ecosystem-based fisheries and conservation management (Christensen and Maclean, 2011). Knowing the energetic value of the main ecological groups is needed in these models to understand energy transfer from lower to higher trophic levels and also to validate model outputs. One of the most cost-effective and quantitative ways to assess ecological energetics is through energy density analysis which provides a direct measure of the nutritional condition and quality of an individual or population. Energy density is positively correlated with lipid content (Rand et al., 1994; Van Pelt et al., 1997), which is important for energy storage and often the first macro-molecule to be catabolized (Lloret et al., 2014). Instead, proteins and carbohydrates remain rather constant in most species and have a much lower energy density than lipids (Anthony et al., 2000; Lloret et al., 2014).

Energy storage and nutritional quality of fish may fluctuate during the year due to different biological processes (i.e. growth, maintenance or reproduction) and external factors (i.e. temperature). In temperate regions, pelagic marine environments show important seasonal fluctuations with cyclical changes in temperature and food availability (Coma et al., 2000; Mazzocchi and Ribera d'Alcalà, 1995). In response to this, marine organisms have developed different life-history and energy allocation strategies in order to optimise their reproduction and population growth (Houston et al., 2006). Some marine species acquire and store energy in periods of high food abundance, which is then used for reproduction (they are named 'capital breeders'). Others use their current energy income for reproduction (named 'income breeders'), and there are also intermediate strategies (Alonso-Fernández and Saborido-Rey, 2012; McBride et al., 2015).

Species of fish with faster life cycles and smaller body size, such as small and medium sized pelagic fish, also known as forage fish, are thought to respond rapidly to environmental fluctuations that have been shown to have important implications for fish recruitment and ecosystem structure (Perry et al., 2005; Peck et al., 2013). Changes in the energy density of forage fish have been shown to be responsible for declines in top-predator populations through negatively impacting their breeding success and fitness (Doney et al., 2012; Österblom et al., 2008). For example, the decline of the common guillemots (*Uria aalge*) in the North Sea was linked to a reduction in the energetic value of their main prey (sprat *Sprattus sprattus* and lesser sandeels *Ammodytes marinus*) (Wanless et al., 2005). Furthermore, the decline of Steller sea lions (*Eumetopias jubatus*) in the Gulf of Alaska was also partially related to a reduction of fattier fishes such as herring (*Clupea harengus*) within their feeding grounds (Rosen and Trites, 2000). Moreover, small and medium pelagic fishes are a good source of food nutrition for humans and in some areas, such as sub-Saharan countries, their consumption represent the main protein supply (Kawarazuka and Béné, 2011; Tacon and Metian, 2013).

In the Mediterranean Sea, small pelagic fishes such as *Sardina pilchardus* (sardine), *Engraulis encrasicolus* (anchovy) and *Sardinella aurita* (round sardinella), and medium pelagic fishes such as *Trachurus* spp. (horse mackerels) and *Scomber* spp. (mackerels) play key roles in the food-web, due to their high abundances and fast population turnover rates (Coll et al., 2008; Palomera et al., 2007). Despite this, while the energy density of multiple forage fishes has been reported in the Atlantic and the Pacific Oceans (Anthony et al., 2000; Dubreuil and Petitgas, 2009; Pedersen, 2001; Spitz and Jouma'a, 2013), such data are very scarce in the Mediterranean Sea (Tirelli et al., 2006; Vivien et al., 2012).

In the present study, we investigated the ecological energetics of seven forage fishes, *E. encrasicolus, S. pilchardus, S. aurita, T. trachurus, T. mediterraneus, S. scombrus* and *S. colias,* that are ecologically and economically important in the western Mediterranean Sea (see Table 1). The study aims were to (1) provide reference values of the energy densities of their whole-body, (2) examine potential seasonal changes, and (3) make inter-specific comparisons. These results are needed to better understand the different life-history strategies of these fishes and regional ecological energetics. Energy density analyses are relevant as input data for bioenergetics and food web models, increasingly used to predict the cumulative effects of climate change and fishing impacts on population and ecosystem dynamics.

2. Material and methods

2.1. Study area

The present study was conducted in the continental shelf and upper slope areas associated with the Ebro River Delta, northwestern Mediterranean Sea (Fig. 1). As a consequence of particular oceanographic conditions, such as wind conditions, vertical mixing and river discharges (Salat et al., 2002), this area is an important fishing ground of the Mediterranean Sea (Lleonart and Maynou 2003) and has been identify as a priority area for conservation (Coll et al., 2015; Piante and Ody, 2015). Sea surface temperature and primary production follow annual cycles characterized by strong seasonality. From May to October the ecosystem is characterized by stratification of the water column, resulting in a reduction of nutrients in the photic zone. In contrast, from November to April, the water temperature is at its lowest and the water column is mixed, leading to higher nutrient availability at the surface, with a peak of phytoplankton in late-winter and spring (Salat et al., 2002).

2.2. Sampling procedures

Individuals of sardine, anchovy, round sardinella, Atlantic horse mackerel (*Trachurus trachurus*), Mediterranean horse-mackerel (*Trachurus mediterraneus*), Atlantic mackerel (*Scomber scombrus*) and Atlantic chub mackerel (*Scomber colias*) were collected during spring-2012, summer-2012, fall-2012 and winter-2013 from commercial vessels of the harbours of Tarragona, Torredembarra and Cambrils working in the study area (Table 1; Fig. 1). Due to the lack of catches of *T. trachurus* in summer 2012 in the area of study, this species was not sampled that summer.

All individuals were immediately frozen after capture and stored at -20 ºC. Total body length and weight was recorded for all individuals. From the samples collected, for each species, from 10 to 20 individuals per season with similar body size and both sexes were selected to measure the energy density (kJ·g^{-1}). To reduce the potential variation in energy density due to ontogenetic changes, only individuals larger than the size at first maturity of each species (length at which 50% of the fish at that size are mature) were selected.

2.3. Energy density analyses

In total, the energy density of 354 individuals of the seven forage fish species was determined. This metric is widely used as a proxy of food quality and is thus perfectly suitable for comparative studies (Spitz et al., 2012). For determination of energy density we used direct calorimetry measuring the heat of combustion of small samples (Parr 6725 Semimicro Oxygen Bomb Calorimeter). The calorimeter system was calibrated with the combustion of benzoic acid standard. Prior to the determination of energy density, each individual was homogenized with a blender and the entire individual in the case of *E. encrasicolus*, *S. pilchardus* and *S. aurita* and two subsamples in the case of *T. trachurus*, *T. mediterraneus*, *S. scombrus* and *S. colias* were oven-dried at 70ºC to constant mass for 48 – 72 hours. After determining the dry weight, each sample was homogenised in a mixer (Retsch Mixer Mill MM-200) and two pellets of 100-200 mg for each individual were obtained with a press for the determination of the energy density. If energy densities of the two pellets from an individual differed by more than

3%, a third pellet was analysed. The average of the two or three subsamples was used to calculate the energy density of each individual.

The energy density was originally measured on dry samples (kJ·g^{-1} of dry weight) and was converted to wet mass basis (kJ·g^{-1} of wet weight) by taking into account the water content of each fish (% dry weight=100· dry weight· wet $weight^{-1}$; Lloret et al., 2014). The prey quality of each species was determined following the classification proposed by Spitz et al. (2010): Low Quality (ED < 4 kJ g^{-1}), Moderate Quality (4 < ED < 6 kJ g^{-1}) and High Quality (ED > 6 kJ g^{-1}).

2.4. Statistical analyses

Inter-specific and seasonal differences in energy density were tested using one-way semi-parametric permutation multivariate analyses of variance tests (PERMANOVA test) on the Euclidean distance matrix (Anderson et al., 2008). In the case of a significant difference in the energy density of each species between seasons or between species, pairwise tests were performed. Potential differences between sexes were not tested since the number of females or males was not always sufficient for all species and seasons. Nonetheless, previous studies on small pelagic fishes have revealed no relationship of gender with lipid dynamics of the entire fish (Garrido et al., 2008). PERMANOVA allows for the analysis of complex designs without the constraints of multivariate normality and homoscedasticity (Anderson et al., 2008). The method calculates a pseudo-F statistic directly analogous to the traditional F-statistic for multifactorial univariate ANOVA models, using permutation procedures to obtain p-values for each term in the model (Anderson et al. 2008). PERMANOVA tests were carried out with PRIMER-E 6 software.

3. Results

3.1. Inter-specific differences in energy density

The annual energy density was significantly different between species (Pseudo-$F_{6,348}$= 22.45; p-value < 0.01) with the lower values for *E. encrasicolus* and the higher values for *S. scombrus* (Table 2; Fig. 2). Within small pelagic fish, *S. pilchardus* showed significantly higher energy density than *E. encrasicolus* and similar to *Trachurus* spp. *S. aurita* had similar energy density to both, *E. encrasicolus* and *S. pilchardus*. Within the medium pelagic fishes, *T. trachurus* and *T. mediterraneus* had similar energy density, which was lower than the *Scomber* spp. Both *Scomber* species had significantly higher energy density than the rest of the species analysed (Fig. 2). The body length of the individuals analysed was also significantly different between all species (Pseudo-$F_{6,348}$= 309.47; p-value < 0.01). Body lengths of *S. pilchardus* and *E. encrasicolus* were smaller than 20 cm, *S. aurita* and *T. trachurus* had mean body lengths between 20 and 25 cm while *T. mediterraneus* and *Scomber* spp. had body lengths larger than 25 cm (Table 2).

None of the seven species studied here were classified as species with low nutritional quality. *E. encrasicolus*, *S. aurita* and *T. mediterraneus* were classified as forage species of moderate nutritional quality, while *S. pilchardus, T. trachurus, S. scombrus* and *S. colias* were classified of high prey quality (Table 2). However, within the moderate prey quality category, only *E. encrasicolus* could be classified as moderate during all seasons, while within the high quality group only the two *Scomber* spp. had values greater than 6 kJ · g^{-1} across seasons.

3.2. Seasonal differences in energy density

Seasonal differences in energy density were found in most of the species; only *S. colias* showed similar energy density through the year (Table 3). Among the small pelagic fishes, energy density of *E. encrasicolus* was significantly highest during spring and lowest during fall. The energy density of *S. pilchardus* increased in spring and was significantly similar in summer, and declined to a minimum during fall and winter. For *S. aurita* energy density in spring and fall were significantly similar and higher than in summer and winter (Figure 3).

Among the medium pelagic fishes, the energy density of *T. trachurus* slightly increased in winter and had similar low values in spring and fall. For the congeneric species, *T. mediterraneus*, energy density was lowest in summer and fall, and increased during winter with a peak in spring. *S. scombrus* had significantly lower energy density in winter than in spring and fall. On the contrary, the energy density of *S. colias* was significantly similar between seasons (Table 3, Fig. 3).

4. Discussion

This study reports new energetic data on 354 individuals of seven ecological and economical important pelagic fish species in the Mediterranean Sea. Results revealed clear differences in energy density between species and between seasons. These differences are related to species life-history and energy allocation strategy in addition to their feeding ecology. In consequence, predators of these small and medium sized pelagic fish could gain more or less energy per unit of food intake depending on the preyed species and period of the year.

4.1. Inter-specific differences in energy density

The two fishes that had the lowest energy density, *E. encrasicolus* and *S. aurita*, are species with fast growth, small body size and a lifespan of 4-5 years (Morales-Nin and Pertierra, 1990; Tsikliras and Antonopoulou, 2006). Both species have a greater reliance on a planktivorous diet (Palomera et al., 2007). In contrast, the two species with higher energy density, *Scomber* scombrus and *S. colias* are both highly migratory species that feed on wide range of prey sizes, have bigger body sizes than clupeiforms and a longer lifespan (10-15 years; Bachiller and Irigoien, 2013, 2015; Velasco et al., 2011; Table 1).

Previous studies in the same study area found that *Scomber* species occupy a higher trophic level in the food web than the small pelagic fish and segregate completely their trophic niche (Albo-Puigserver et al., 2016). Trophic level and body size are often collinear and represent important features of species since larger size fishes may have larger mouth size and may be able to feed on larger prey with higher energy content (Cohen et al., 1993; Jennings et al., 2008; Bachiller and Irigoien, 2013). Moreover, prey species described in the diet of *Trachurus* spp. and *Scomber* spp., such as mysids, decapods and fish, have higher energy density than copepods that are the main prey of clupeoid species (Mintenbeck et al., 2012; Table 1).

Apart from differences in the feeding habits, older (and often larger) fishes tend to have higher energy reserves since they do not invest energy in rapid growth as juveniles (Anthony et al., 2000; Røjbek et al., 2014). Moreover, species such as mackerels have large fat reserves in their muscle to cope with the energetic requirements of the migration (Ackman and Eaton, 1971; Ben Rebah et al., 2009; Graham et al., 1983). Larger fat reserves, in combination with the diet preferences, could explain the higher energy density showed in *S. colias* and *S. scombrus* in comparison with the other species analysed in this study.

In the case of *S. pilchardus*, the mean annual energy density was higher than the other clupeoid species and similar to those of *T. mediterraneus* and *T. trachurus.* However, in terms of dietary habits *S. pilchardus* is more closely related to *E. encrasicolus* than to *Trachurus* spp. that has a migratory behaviour, larger body size and might prey on larger species (Bachiller and Irigoien 2013, 2015). Opposite to *E. encrasicolus*, *S. pilchardus* has been described as a capital breeder that accumulates large amounts of energy before spawning in winter (McBride et al., 2015). Then, if the accumulation of energy before spawning is high enough, the capital breeding behaviour could explain the high mean annual energy density of *S. pilchardus*.

4.2. Seasonal differences in relation to spawning

Temporal variations in energy density, proximate composition and feeding preferences have been reported for several fish species worldwide. Over time, different species have adapted to environmental changes and ecological processes (i.e. competition and density dependency) by developing individual life-history strategies and spawning periods, which are reflected in their whole-body energy density measure over time (Gonçalves et al., 2012; Hondolero et al., 2012).

Similar to previous studies, in our study *S. pilchardus* showed more seasonal variability in energy density than *E. encrasicolus* due to their contrasting spawning periods and breeding strategies (winter and summer spawner and capital and income breeder, respectively; Ganias et al., 2007; Pethybridge et al., 2013; Sánchez et al., 2013). As a capital breeder and winter spawner (November-March; Palomera and Olivar, 1996), *S. pilchardus* accumulates mesenteric fat before reproduction during spring and summer when zooplankton biomass is high (Sabatés et al., 2006). As a consequence, we found higher energy density in spring and summer for this species.

These results are in accordance with the dietary habits described in the Gulf of Lions for *S. pilchardus*, which in winter mainly preys on diatoms using its filter feeding capacity and in summer feeds on larger prey that are more energetic (Costalago and Palomera, 2014). In contrast, *E. encrasicolus* spawns mainly in warm waters, between 17º and 23ºC from April to August. The peak of reproduction is in spring and matches the period of high food availability (Palomera, 1992), allowing this species to use the food intake for reproduction directly. In the southwestern Mediterranean, Bacha and Amara (2009) observed that during spring and summer *E. encrasicolus* preyed on larger copepods with higher energy, probably to satisfy its reproductive needs.

In the case of *S. aurita*, the spawning period begins in late spring and has a peak during July-August because this species prefers warmer waters for spawning (Palomera et al., 2007). The high energy density in *S. aurita* in spring is probably due to the accumulation of energy just before the spawning period, following a more capital breeding strategy, while the low energy density in summer might be due to the loss of energy for reproduction. This pattern is in accordance with previous studies on lipid content of *S. aurita* in the Gulf of Gabes (South-Central Mediterranean Sea; Ben Rebah et al., 2009) and the Adriatic Sea (Mustać and Sinovčić, 2012).

The high energy density observed during the spawning period (winter) for *T. trachurus* indicates that the energy used for reproduction is mainly derived from the current feeding intake (van Damme et al., 2014). This result differs from previous studies on feeding intensity in the Adriatic Sea (Jardas et al., 2004; Šantić et al., 2005), where it was suggested that this species accumulates energy to use it later for reproduction in winter. On the contrary, in the NE Atlantic *T. trachurus* was defined as an income breeder, similar to our results (Bonnet et al., 1998; Ndjaula et al., 2009). In the case of *T. mediterraneus*, our results show that it accumulates energy prior to spawning. Previous studies in the Adriatic and Aegean Sea reported low feeding intensity and low lipid content during the spawning period (Santic et al., 2004; Tzikas et al., 2007). Therefore, *T. mediterraneu*s follows a breeding strategy more similar to a capital breeder. It is interesting to note that the two congeneric species of *Trachurus* spp. studied here utilize different breeding strategies that could play an important role in the resource partitioning that has been observed between these species in the northwestern Mediterranean Sea (Albo-Puigserver et al., 2016). However, given the single annual period sampled, further studies on the energy and feeding dynamics are needed to confirm these results.

Regarding the two *Scomber* species, both had low seasonal variability in energy density. The energy density of *S. scombrus* slightly decreased in winter, probably due to the energy investment in reproduction, while *S. colias* maintained similar energy density levels across all seasons, a characteristic of an income breeding species. Both species, besides preying on copepods, also have an active predation on larger prey such as euphasiids, decapods and fish larvae that are more energetic (Batchiller et al., 2015; Table 1). Moreover, opposite to small pelagic fishes, the migratory behavior of the larger *Scomber* spp. influences their energy requirements, resulting in higher demands.

Our results contrast with previous studies that proposed larger and more long-lived fish (i.e. mackerels) are more likely to use capital sources, and shorter-lived fish (i.e. sardine and anchovy) are more likely to use income sources for breeding (McBride et al., 2015; Somarakis et al., 2000). Instead, we suggest that the breeding strategy used in short and long-lived fish depends mainly if the spawning period is closely coupled with seasonal plankton blooms or not, a hypothesis that has been also suggested by others (Pethybridge et al., 2014; Røjbek et al. 2014). Furthermore, in long-lived fish other energetic requirements such as the large migratory movements might influence their life-history breeding strategy.

In general, we observed higher energy density in spring for all species, regardless of their breeding strategy. This result is in agreement with the higher energy input in the pelagic photic-zone during this period due to the late-winter phytoplankton bloom, when in the surface-water layers there is higher plankton food availability (Álvarez et al., 2012; Estrada, 1996). In other areas, it has been described that the composition of the phytoplankton drives the seasonal changes in energy reserves (i.e. lipids) of zooplankton (Peters et al., 2007; Røjbek et al., 2014). The greater food availability and its higher energy content explain the higher energy density of the small and medium pelagic fishes in spring.

We would like to highlight that this study only covers one year of sampling. Therefore, the capital -income breeding strategies identified for the studied species need to be confirmed with long-term (interannual) studies since food availability or zooplankton composition may vary from one year to another depending on environmental variability. Moreover, other aspects such as sex ratio might affect energy density during the reproduction period, since it has been observed that in some species the hydrated gonads of females are more energetic than the male gonads. In future studies, an interannual analysis of energy density on the different sexes is recommended.

4.3. Quality as prey

The pelagic fish species analysed in the present study are important components of the diet of different marine predators, including seabirds, marine mammals, elasmobranchs and large commercially fish such as tuna (see Table 1). These predators vary their own fitness not only by maximising quantity of prey, but also by prey selection (Österblom et al., 2008). In the case of the three small pelagic fish, only *S. pilchardus* was classified as a high quality prey. Previous studies in the Gulf of Lions and Bay of Biscay also measured high energy density in *S. pilchardus* (Vivien et al., 2012; Spitz and Jouma'a, 2013; Table 4). However, as pointed out by Spitz and Jouma'a (2013), depending on the season, predators feeding on *S. pilchardus* will obtain more or less energy per unit of food. The energy densities observed in our study area for *E. encrasicolus* were lower than those reported in the Gulf of Lions, northwestern Mediterranean Sea (Table 4; Vivien et al., 2012) but similar to those reported in the Bay of Biscay (Atlantic Sea) and Adriatic Sea (Table 4).

Regarding medium pelagic fish species, *T. trachurus*, *S. scombrus* and *S. colias* were classified as high quality prey according to their energy density ranges. Similarly, in the Bay of Biscay these species were also classified as high quality prey mainly (Table 4). From a predator viewpoint, feeding on a species classified as high quality, such as, *S. pilchardus*, *T. trachurus*, *S. scombrus* and *S. colias*, results in more energy per unite of food intake than preying on *E. encrasicolus* or *S. aurita*. Therefore, for pelagic predators that prey mainly on small pelagic fish, such as Atlantic bonito, *Sarda sarda* and Bluefin tuna, *Thunnus thynnus*, it could be advantageous to prey on *S. pilchardus* during spring and summer when they are energetically better prey than *E. encrasicolus* (Navarro et al., 2016; Røjbek et al., 2014). However, other aspects such as the catchability of prey, time of searching, size of prey will also influence prey profitability (Bowen et al., 2002).

4.4. *Concluding remarks*

This study reports reference values of the energy density of seven key pelagic fish species in an important fishing area of the western Mediterranean Sea for the first time. Results revealed clear differences in energy density between species and between seasons that are related to species life-history and energy allocation strategies in addition to their feeding ecology. These results highlight that when evaluating the energy intake by forage fish and the consequences of changes in population levels, attention should be paid to species and seasonal variability. The information derived from this study will enhance the accuracy of input data for bioenergetics-based population and food web models that are increasingly used as resource management assessment tools.

While this study shows that energy storage of small and medium pelagic fishes differs over time, the implications of long-term environmental changes (global warming and decreased primary productivity) on ecological energetics remains unknown. In the Mediterranean Sea an increase of the sea temperature and a decrease in plankton productivity have been already observed (Calvo et al., 2011; Mozetic et al., 2010; Vargas-Yáñez et al., 2008). These changes could impact the energy fluxes of marine food webs. In fact, recent studies have proposed that the main reason of the drastically decline in the biomass and in the mean size of *S. pilchardus* and *E. encrasicolus* in the western Mediterranean is a decrease in zooplankton quality and quantity due to environmental factors (Brosset et al., 2015; Saraux et al., 2014; Van Beveren et al., 2014, 2016). Moreover, an increase in the sea surface temperature during winter might cause a reduction in the reproduction window of *S. pilchardus* (winter spawner) (Palomera et al., 2007). Therefore, we could expect a change in the diet of marine predators from a diet dominated by *S. pilchardus* to one dominated by other species with lower nutritional quality, such as *S. aurita* that have been shown to expand its range northwards with the increase of temperature (Sabatés et al., 2006). Food web models that incorporate the energy density data provided in this study will assist in testing this, and other environmental hypotheses.

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Species	Spawning period	Capital/ Income	Diet	Predator species	References

Figure legends

Figure 1. (A) Map of the study area where small and medium sized pelagic fishes were collected. The sampling area is indicated with a dashed line and black dots are the harbours where samples were landed (Torredembarra, Tarragona and Cambrils). (B) Position of the study area in the Mediterranean Basin.

Figure 2. Annual energy density (kJ g-1 of wet weight) of seven species of small and medium sized pelagic fishes from the western Mediterranean Sea. Box length represents interquartile range, bar length represents range and horizontal lines represent median values. Black dots are outliers. Pairs of means differing significantly (P <0.05) by pairwise tests between species are indicated by the letters - species with the same letter were not significantly different.

Figure 3. Seasonal variation in the energy density (kJ g-1of wet weight) of seven species of small and medium sized pelagic fishes from the western Mediterranean Sea. Box length represents interquartile range, bar length represents range and horizontal lines represent median values. Black dots are outliers.

Table legends

Table 1. Species sampled in this study and information on their typical spawning period, breeding strategy (Capital – Income), main diet and known predators in the Mediterranean Sea.

Engraulis encrasicolus	Apr-Oct	Income	Copepods, cladocerans	*Etmopterus spina, Hexanchus griseu, Larus audouinii, Merluccius merluccius, Prionace glauca, Puffinus mauretanicus, P. yelkouan, Sarda sarda, Seriola dumerili, Thunnus thynnus, Tursiops truncates, Xiphias glaudius*	Barría et al., 2015; Blanco et al., 2001; Bourgeois et al., 2011; Costalago et al., 2012; Kabasakal, 2004; Matallanas et al., 1995; McBride et al., 2015; Navarro et al., 2009; Navarro et al., 2016; Oro et al., 1997 ; Palomera, 1992; Stergiou and Karpouzi, 2002
Sardina pilchardus	Oct-Apr	Capital	Copepods, cladocerans, diatoms	*Larus audouinii, Merluccius merluccius, Mustelus mustelus, Prionace glauca, P.yelkouan, Puffinus mauretanicus, Puffinus yelkouan, Sarda sarda, Scomber scombrus, Seriola dumerili, Thunnus thynnus, Xiphias glaudius*	Barría et al., 2015; Bourgeois et al., 2011; Costalago and Palomera, 2014; Kabasakal, 2004; McBride et al., 2015; Navarro et al., 2009; Nikolioudakis et al., 2012; Stergiou and Karpouzi, 2002
Sardinella aurita	Jul-Sep	Capital*	Copepods, decapods larvae, fish larvae	*Coryphaena hippurus, Larus audouinii, Sarda sarda, Tetrapturus belone, Xiphias glaudius*	Campo et al., 2006; Castriota et al., 2008; Freón et al., 1997; Karachle and Stergiou, 2014; Lomiri et al., 2008; Stergiou and Karpouzi, 2002
Trachurus trachurus	Nov-May	Income	Copepods, euphasiids, fish	*Coryphaena hippurus, Euthynnus alleteratus, Hexanchus griseu, Seriola dumerili*	Andaloro and Pipitone, 1997; Ivan Jardas et al., 2004; Massutí et al., 1998; Šantić et al., 2005; van Damme et al., 2014
Trachurus mediterraneus	May-Aug	Capital*	Copepods, euphasiids, fish	*Coryphaena hippurus, Euthynnus alleteratus, Hexanchus griseus, Seriola dumerili*	Andaloro and Pipitone, 1997; Bayhan et al., 2013; Šantić et al., 2004; Tsikliras et al., 2010; Viette et al., 1997; Yankova et al., 2008
Scomber scombrus	Jan-Mar	-	Euphasiids, decapod larvae, fish	*Coryphaena hippurus, Euthynnus alleteratus, Puffinus yelkouan, Thunnus thynnus*	Bourgeois et al., 2011; Massutí et al., 1998; Olaso et al., 2005; Stergiou and Karpouzi, 2002
Scomber colias	May-Jul	-	Copepods, mysids, decapod larvae, fish	*Coryphaena hippurus, Euthynnus alleteratus, Puffinus yelkouan,*	Bourgeois et al., 2011; Castro, 1993; Keč et al., 2012; Massutí et al., 1998; Stergiou and Karpouzi, 2002

* The breeding strategy has not been described using capital- income terminology. However, from published data on conditional and lipid indices, these species have been classified in this study.

Table 2. Annual mean and standard deviation of Energy Density (ED; kJ · g-1 of wet weight), weight (g) body length (cm), % of dry weight of individuals used for analyze the ED of the seven small and medium sized pelagic fishes sampled in the western Mediterranean Sea. Species are classified according to their mean ED values following Spitz et al. (2010) as Moderate Quality (4 < ED < 6 kJ g−1) and High Quality species (ED > 6 kJ g−1).

Species	*Engraulis encrasicolus*	*Sardina pilchardus*	*Sardinella aurita*	*Trachurus trachurus*	*Trachurus mediterraneus*	*Scomber scombrus*	*Scomber colias*
ED (kJ·g^{-1})	5.35±0.61	6.03±1.17	5.64±1.03	6.03±0.61	5.82±1.02	7.17±1.30	6.93±0.87
Length (cm)	13.03±1.55	14.33±1.38	20.63±3.48	23.89±3.81	29.72±4.37	28.72±2.82	31.96±5.80
Weight (g)	14.65±5.75	22.90±7.78	73.14±33.70	125.41±61.31	217.41±94.62	200.70±67.44	344.41±157.24
%Dry weight	26.01±1.74	27.25±3.14	27.33±2.93	28.25±1.77	27.26±2.69	30.10±3.14	30.29±2.11
Quality type	Moderate	High	Moderate	High	Moderate	High	High

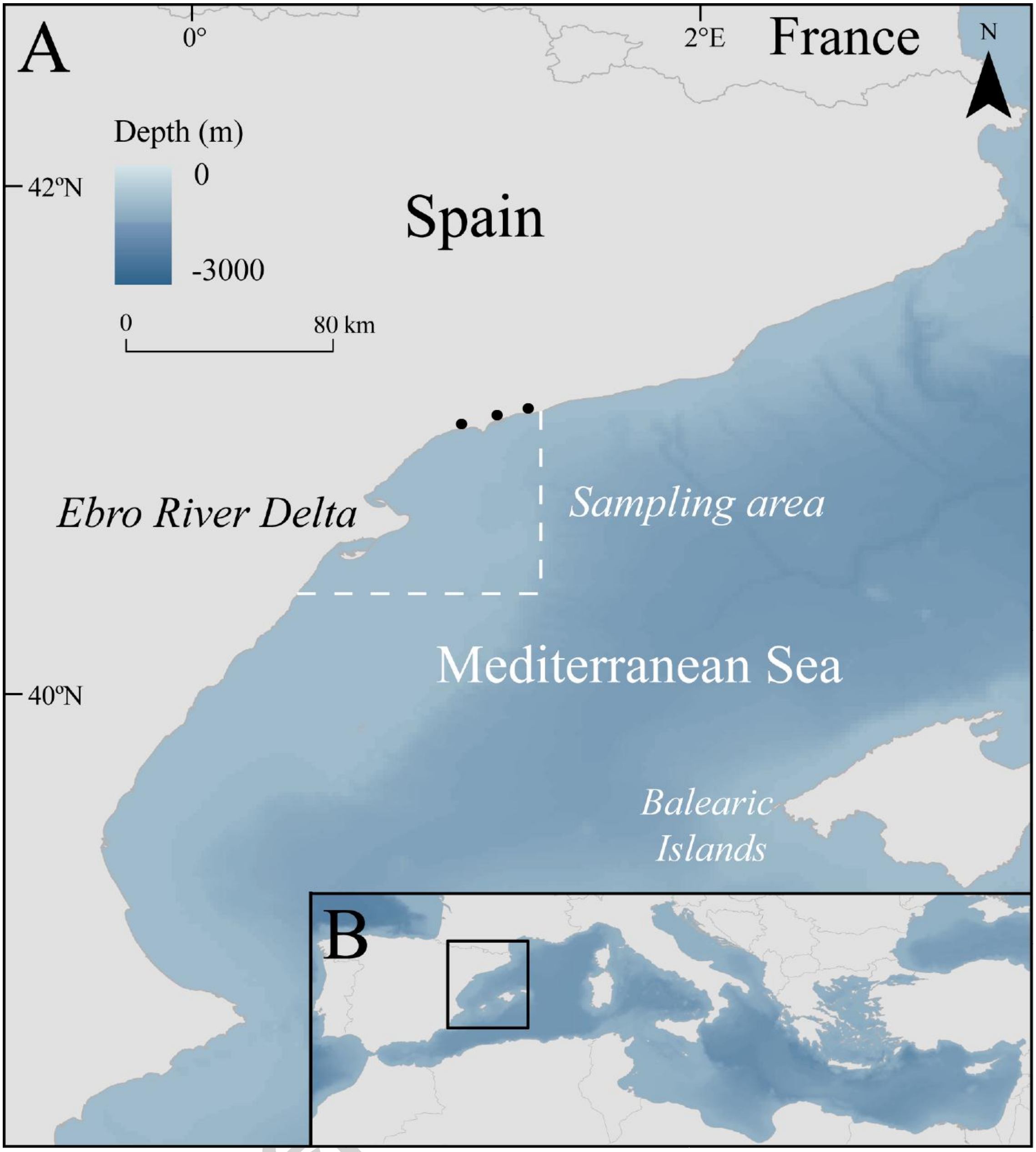
Table 3. Mean and standard deviation of energy density (kJ · g^{-1} of wet weight) and number of individuals analyzed (n) of seven small and medium sized pelagic fishes species sampled in the western Mediterranean Sea during spring-2012, summer-2012, fall-2012 and winter 2013. Results of the PERMANOVA tests (Pseudo-F values) between seasons for each species separately are shown. Pairs of means differing significantly (P <0.05) by pairwise tests are indicated by the letters - seasons with the same letter were not significantly different.

Species	**Pseudo-F (p-value)**	**n**	**Spring**	**n**	**Summer**	**n**	**Fall**	**n**	**Winter**
E. encrasicolus	8.96 (<0.01)	20	5.80±0.57 ^{a}	20	5.39±0.57 ^{b}	20	4.93±0.28 ^{c}	20	5.30±0.66 ^{b}
S. pilchardus	22.69 (<0.01)	20	7.11±1.03 ^{a}	20	6.56±1.23 ^{a}	20	5.40±0.55 ^{b}	23	5.21±0.45 ^{b}
S. aurita	10.55 (<0.01)	10	6.56±0.75 ^{a}	10	5.16±0.59 ^{b}	10	6.04±1.10 ^{a}	10	4.80±0.54 ^{b}
T. trachurus	5.33 (0.01)	10	5.83±0.58 ^{a}	-	-	10	5.79±0.47 ^{a}	10	6.48±0.54 ^{b}
T. mediterraneus	6.54 (<0.01)	10	6.58±0.55 ^{a}	10	5.08±0.51 ^{b}	11	5.44±0.72 ^{b,c}	10	6.23±1.36 ^{a,c}
S. scombrus	5.31 (<0.01)	9	8.05±0.92 ^{a}	11	7.02±1.53 ^{a,b}	10	7.56±0.81 ^{a}	10	6.14±1.09 ^{b}
S. colias	2.82 (0.05)	10	6.88±0.66	10	7.57±0.76	10	6.64±0.98	10	6.66±0.82

Table 4. Publish data on energy density (kJ · g-1 of wet weight) for species of forage fish included in this study. Species are classified according to their ED content following Spitz et al. (2013) as Moderate Quality (4 < ED < 6 kJ g−1) and High Quality species (ED > 6 kJ g−1).

Species / Area	Year	Season	Energy density	References	Quality type
E. encrasicolus					
Gulf of Lions	2002-2003	Spring	12.81±0.66	Vivien et al., 2012	High
Bay of Biscay	2002-2010	Spring	5.5±0.5	Spitz and Jouma'a, 2013	Moderate
Bay of Biscay	2002-2010	Fall	6.4±1.2	Spitz and Jouma'a, 2013	High
Bay of Biscay	2002-2010	Year mean	5.8±0.9	Spitz and Jouma'a, 2013	Moderate
Bay of Biscay	2001-2007	Winter	6.11±1.35	Dubreuil and Petitgas, 2009	High
Bay of Biscay	2001-2007	Spring	6.48±1.36	Dubreuil and Petitgas, 2009	High
Bay of Biscay	2001-2007	Fall	8.17±0.93	Dubreuil and Petitgas, 2009	High
Adriatic Sea	2002	Fall	5.56*	Tirelli et al., 2006	Moderate
Adriatic Sea	2003	Spring	4.51*	Tirelli et al., 2006	Moderate
S. pilchardus					
Gulf of Lions	2002-2003	Spring	14.14±1.49	Vivien et al., 2012	High
Bay of Biscay	2002-2010	Spring	5.8±0.8	Spitz and Jouma'a, 2013	Moderate
Bay of Biscay	2002-2010	Fall	8.8±1.6	Spitz and Jouma'a, 2013	High
Bay of Biscay	2002-2010	Year mean	7.5±2.0	Spitz and Jouma'a, 2013	High
T. trachurus					
Bay of Biscay	2002-2010	Spring	7.9±1.5	Spitz and Jouma'a, 2013	High
Bay of Biscay	2002-2010	Fall	6.5±1.0	Spitz and Jouma'a, 2013	High
Bay of Biscay	2002-2010	Year mean	7.0±1.3	Spitz and Jouma'a, 2013	High
S. scombrus					
Bay of Biscay	2002-2010	Spring	5.9±0.8	Spitz and Jouma'a, 2013	Moderate
Bay of Biscay	2002-2010	Fall	8.3±1.0	Spitz and Jouma'a, 2013	High
Bay of Biscay	2002-2010	Year mean	7.5±1.5	Spitz and Jouma'a, 2013	High

* Mean of two size class categories (110-119 mm and 120-129 mm).


A
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France
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Depth (m)
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Spain
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80 km
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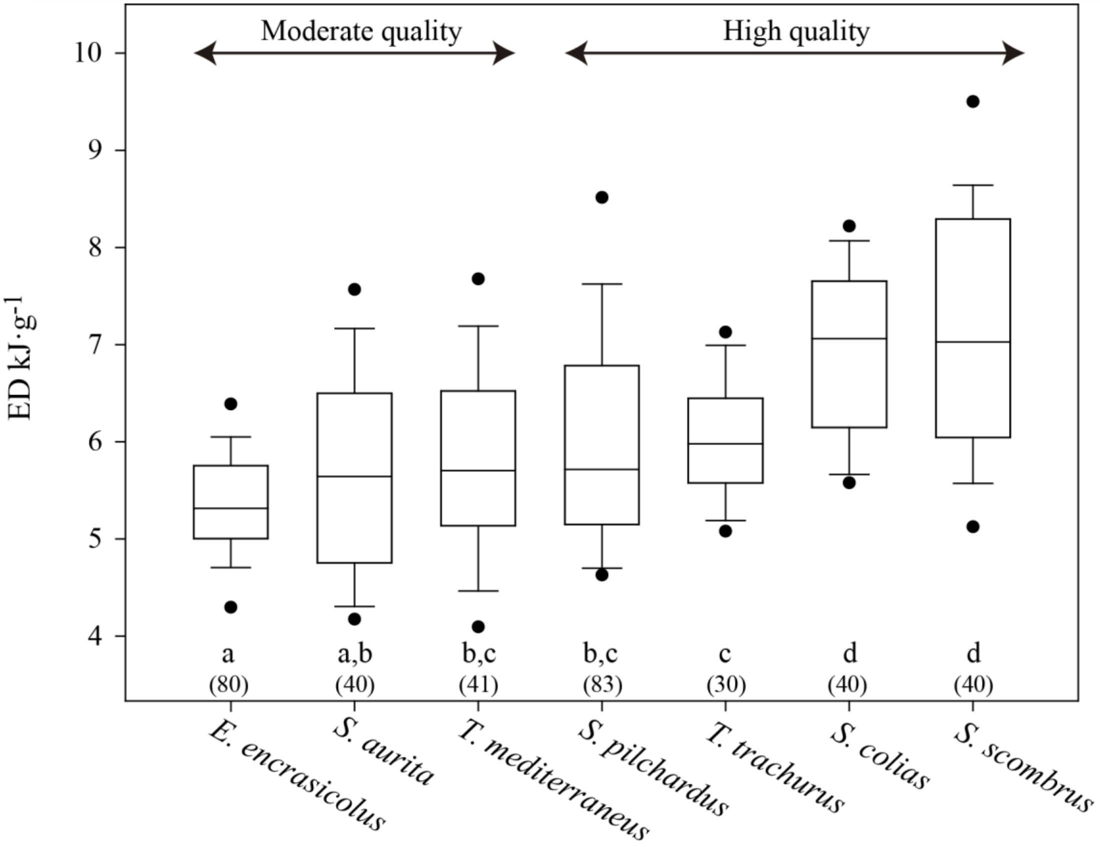
40ºN
Mediterranean Sea
Balearic
Islands
B


Moderate quality
High quality
ED kJ·g-1
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(41)
b,c
(83)
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(30)
d
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d
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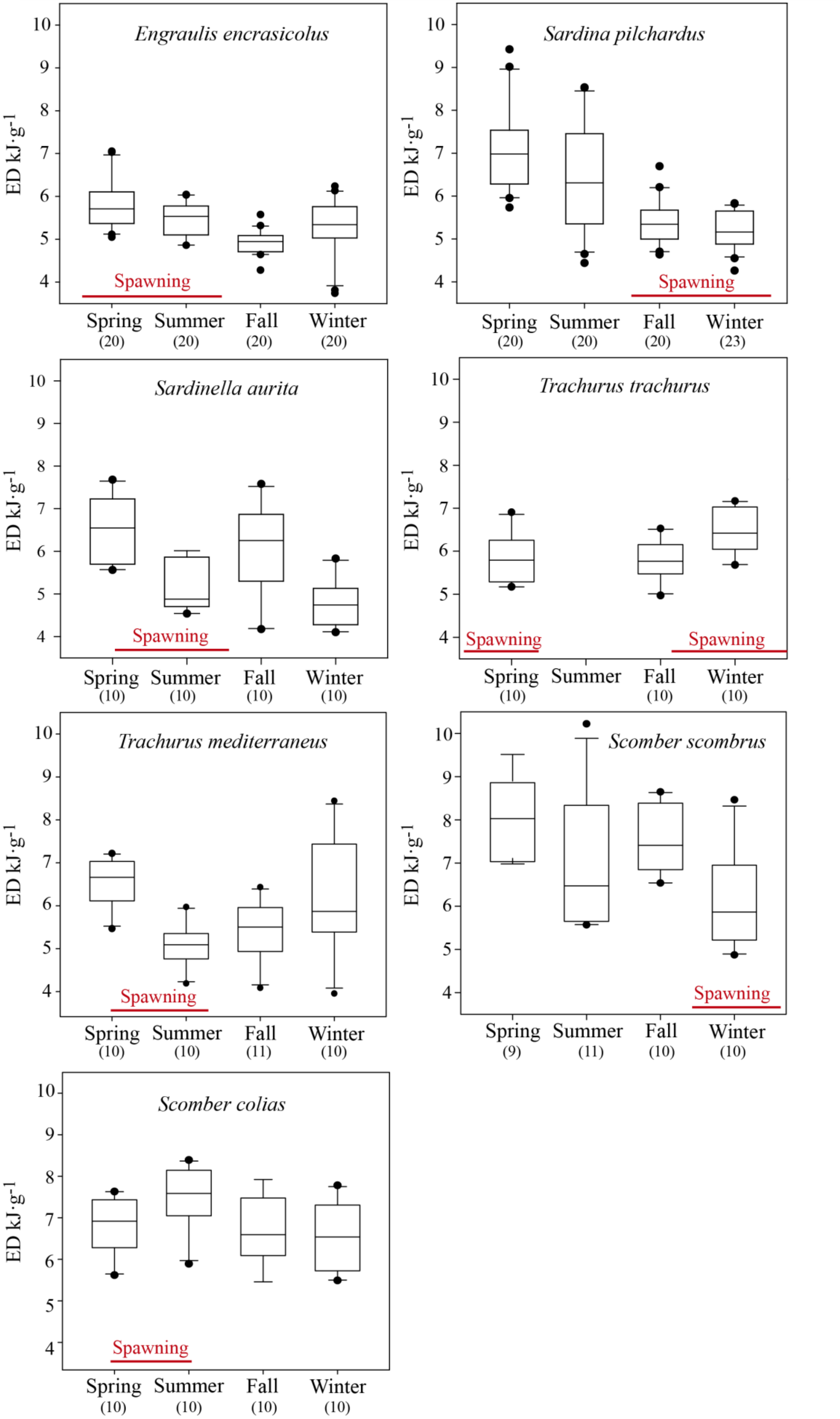
E. encrasicolus
S. aurita
T. mediterraneus
S. pilchardus
T. trachurus
S. colias
S. scombrus


Engraulis encrasicolus
Sardina pilchardus
Sardinella aurita
Trachurus trachurus
Trachurus mediterraneus
Scomber scombrus
Scomber colias
ED kJ·g-1
4
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Spawning
Spring (20) Summer (20) Fall (20) Winter (20)
Spring (20) Summer (20) Fall (20) Winter (23)
Spring (10) Summer (10) Fall (10) Winter (10)
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Spring (10) Summer (10) Fall (10) Winter (10)