
Energy density of anchovy *Engraulis encrasicolus* in the Bay of Biscay

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Abstract:

The energy density (E_D) of anchovy *Engraulis encrasicolus* in the Bay of Biscay was determined by direct calorimetry and its evolution with size, age and season was investigated. The water content and energy density varied seasonally following opposite trends. The E_D g^{-1} of wet mass (M_W) was highest at the end of the feeding season (autumn: c. 8 $kJ g^{-1}M_W$) and lowest in late winter (c. 6 $kJ g^{-1}M_W$). In winter, the fish lost mass, which was partially replaced by water, and the energy density decreased. These variations in water content and organic matter content may have implications on the buoyancy of the fish. The water content was the major driver of the energy density variations for a M_W basis. A significant linear relationship was established between E_D g^{-1} (y) and the per cent dry mass (M_D ; x): $y = -4.937 + 0.411x$. In the light of the current literature, this relationship seemed to be not only species specific but also ecosystem specific. Calibration and validation of fish bioenergetics models require energy content measurements on fish samples collected at sea. The present study provides a first reference for the energetics of *E. encrasicolus* in the Bay of Biscay.

Keywords: bioenergetics • reserves • seasonal cycle

1. Introduction

Assessing the energy content of fish species has many implications for the knowledge of marine populations and ecosystems. Population status is often estimated using population level indicators such as abundance, population structure (De Roos *et al.*, 2003), size at maturity (Olsen *et al.*, 2005), or spatial distribution (Woillez *et al.*, 2007). But individual level indicators of fish health (e.g., energy density, growth, fecundity) are key to characterise habitat suitability (McCall, 1990) or fitness in response to environmental change (ICES, 2005). Individual fish energy content is also important in the study of ecosystems. Variation in the energy density of prey species can provide essential information for predictions about the behaviour and population dynamics of top predators (Benoit-Bird, 2004). Therefore, knowledge of the energy content variations in a large range of species can highlight their role at the scale of the food web (Van de Putte *et al.*, 2006). Further, the development of bioenergetics models (e.g., dynamic energy budgets models: Kooijman, 2000), their application to fish (Van der Veer *et al.*, 2001) and their coupling to lower trophic ecosystem models to predict fish growth and reproduction (Megrey *et al.*, 2007; Maury *et al.*, 2007) implies the necessity to better understand species energetic content. Therefore sets of field data are necessary for the calibration and validation of these models.

Hartman & Brandt (1995) presented linear regressions to predict the energy density of fish given their dry mass and showed that the slopes varied between different taxa. Tirelli *et al.* (2006) argued that the practical use of such models is improved when applied at the species level. They derived a model for the anchovy *Engraulis encrasicolus* L. in the Adriatic Sea. Here a model is presented for *E. encrasicolus* in the Bay of Biscay which differs from that of Tirelli *et al.* (2006) for the Adriatic Sea. This suggests that such models may also differ within a species across eco-regions. The aim of the present paper was also to present results for the energy density of *E. encrasicolus* in the Bay of Biscay that can be used in ecosystem studies (the species being a link between zooplankton production and higher trophic levels) as well as in bioenergetics modelling. The variation of the energy density with size, age and season was investigated. To our knowledge, this is the first paper presenting data on the energy density of *E. encrasicolus* in the Bay of Biscay. The present data were obtained by direct calorimetry of total fish bodies. They complement similar data results presented by Hartman & Brandt (1995), Pedersen & Hislop (2001), Van de Putte *et al.* (2006) and Tirelli *et al.* (2006).

2. Materials and methods

2.1. The samples

In order to measure the average energy content of an individual fish as a function of size, age and season, individual fish specimens were collected across the different seasonal habitats of the life cycle as well as across different years. The life cycle pattern of *E. encrasicolus* in the Bay of Biscay has been documented (Motos, 1996; Motos *et al.*, 1996; Uriarte *et al.*, 1996; ICES, 2004). This spawning season lasts from March to August with a peak in May-June and takes place to the south of 47°N, and to the east of 5°W. All fish are mature at age-1 in spring. After spawning, most fish migrate to the north of the Bay of Biscay between 46°30'N and 48°N on the French shelf to their autumn feeding grounds. Meanwhile, juveniles are observed from the end of summer and in autumn, mostly in the southern part of the Bay of Biscay. Juveniles are first observed close to the surface off the shelf and on shelf as the result of the larvae drifts. Then they progressively colonize the coastal waters.

The specimens of *E. encrasicolus* were collected onboard the research vessel Thalassa during different surveys conducted by IFREMER in the Bay of Biscay between 2001 and 2007. Three seasons were investigated: winter (1 March to 31 March), spring (1 April to 30 April) and autumn (15 September to 15 October). The different locations of our samples covered the entire areas of the different habitats of *E. encrasicolus* according to its life cycle across the seasons (Figs 1a, 1b). Thus, the samples were used to construct an average picture of an individual fish for the years, seasons and ages investigated.

2.2. Water, ash and energy content determination

Standard procedures that have been applied on pelagic fish species were followed (Pedersen & Hislop, 2001; Tirelli *et al.*, 2006; Van de Putte *et al.*, 2006). On board, the fish were sorted by total length (L_T) classes and were placed in plastic bags. They were immediately frozen at -20°C to minimize desiccation, decomposition or body fluids loss. Only individuals that showed no apparent scratches or blood loss were retained for analysis.

In the laboratory, the fish were thawed by bag (few individuals each time). They were individually measured for total length ($L_T \pm 0.5$ mm), wet mass ($W_W \pm 0.1$ mg), age and dry mass ($W_D \pm 0.1$ mg). For each fish with $L_T > 100$ mm the otoliths were removed to determine the age as different ages could have similar length. Otolith extraction was realised without any loss of material from the individuals. In contrast, the fish with $L_T \leq 100$ mm were found in autumn only and were juveniles of age-0 as shown by juvenile age-length keys (Petitgas *et al.*, 2004). Thus here their otoliths were not extracted. The fish were then oven-dried at $70-80^{\circ}\text{C}$ to constant mass (24 to 72h). After a return to ambient temperature they were immediately weighted to avoid rehydration and their dry mass was determined.

The energy and ash content were not measured on individual fish but on average for a group of fish. Fish were grouped by trawl haul and season, in groups of length (small: lower than 100 mm, large: greater than 140 mm and medium: between 100 and 140 mm) and age (0, 1, 2, 3 years). Each group of dried fish was mixed in a laboratory blender during 2 minutes to obtain an homogenized powder. Two samples of the homogenate (100 to 200 mg) were used for the determination of energy density with an IKA C-4000 adiabatic bomb calorimeter. If the energy density of the samples differed by more than 3%, a third sample was combusted. The average of the two or three samples was used to estimate the energy density of each group of fish. Another sample of the homogenate (about 500 mg) was placed in a muffle furnace (550°C during 24h) for the determination of the ash content. All the samples were processed at the A.R.N laboratory, IFREMER, Brest, France. A total of 43 batches representing 272 fishes were analysed for energy density determination.

The measurements resulted in a data array containing for each group of fish, the average length (L_t), the average dry mass (W_D), the average wet mass (W_W), the average water content (WC in percent of the wet mass), the average ash content (AC in percent of the dry mass), and the average energy density per gram of dry mass (E_D in $\text{kJ g}^{-1} W_D$). From these parameters, the following ones were derived: percent dry mass ($DW=100 W_D/ W_W$), organic matter content ($OM=100-AC$), energy density E_D per gram of wet mass W_W (E_D in $\text{kJ g}^{-1} W_W$). Also, Fulton's condition factor ($CF=W_W/L_T^3$: Nash *et al.* 2006) was determined on each fish and averaged in each group of fish.

2.3. Data analysis

Because the same fish could not be followed in time as for instance in a hatchery experiment and because we could not control the size classes in the samples based for instance on a monthly growth model, work was undertaken on quantities (energy density, ash content, water content) expressed relatively to the wet or the dry mass. In that

context, linear regression and ANOVA were used (analysis of variance) to evidence significant variation (i.e., linear slope) in the response of the energy density to a variation in the mass or size. Tukey's Honestly Significant Difference test (Tukey's HSD) was also used to discriminate a seasonal effect in the mean energy density for different age and size classes (Zar, 1996). For the tests to be valid, the statistical distribution of the energy density should be close to normality. This was checked by using normal scores (Q-Q plots were linear) and a Kolmogorov-Smirnov test ($P < 2.2 \cdot 10^{-16}$). Thus normality was assumed. All statistical analyses were performed using the R software (R Foundation for Statistical Computing. <http://www.R-project.org>) with a significance threshold α of 0.05.

Allometry in the energy density is a known documented feature (e.g., Burst and Conover 2003). Seasonal variation in the energy density could be ill-interpreted if due to a variation in size. Therefore and following Tirelli *et al.* (2006) those size classes that were present in all seasons were selected ($140 \text{ mm} < L_T < 180 \text{ mm}$) and seasonal variations analysed using these size classes only.

The relation of the energy density as a function of the percent dry mass expressed how the water content drove the seasonal variation in the energy density (Hartman & Brandt, 1995). A linear relationship is to be expected as the y-axis (energy density) includes wet mass in its denominator which is also included in the x-axis (percent dry mass). The interest in the regression is to construct a practical chart that allows to predict the energy density given the dry mass (which is easily measured). Least-square linear regressions were fitted by season and differences in their slopes and intercepts were tested using the F test described in Zar (1996, chapter 17). The test compares the residual sum of squares around the common regression with the residual sum of squares in each regression.

3. Results

The values of energy density and water content by size/age and season were gathered in Tables I and II. The fish total length (L_T) ranged from 45 to 195 mm and their wet mass from 0.39 to 57.36 g. Ash content decreased with increasing size. Mean \pm S.D. ash content was $3.19 \pm 0.52 \%$ W_D ($n=43$). The energy density ranged between 4.27 and 9.52 $\text{kJ}\cdot\text{g}^{-1} W_W$. Small autumn juvenile fish (age-0, $L_T < 100 \text{ mm}$) had lower energy density, higher ash content and higher water content than any other groups of larger/older fish in any season (Table I).

3.1. Energy and density

The energy density (E_D , $\text{kJ}\cdot\text{g}^{-1} W_W$) tended to increase with increasing L_T (Fig. 2). For the juvenile fish ($L_T < 100 \text{ mm}$; presence in autumn only) the increase in the energy density with length can be explained by the decrease of the ash content in the total body mass as the fish grow. For the large fish only ($L_T > 140 \text{ mm}$), there was a marked seasonal variation in the mean value of the energy density. The pattern observed here is similar to that observed by Tirelli *et al.* (2006).

The energy density on a dry and wet mass bases showed a seasonal variation, the autumn value being highest and the winter value lowest (Tables I and II, Fig. 3). The energy density did not vary with age. Tukey's HSD test showed that the mean energy density in autumn was greater than in winter or spring but that values for winter and spring could not be distinguished. The test was significant for the large fish only and the age 2 (Tables I and II). The percent difference between winter and autumn in the mean E_D on a wet mass basis was $\sim 30\%$ (Fig. 3). There was also a seasonal difference in the E_D on a dry mass basis ($\sim 12.5\%$).

3.2. Water and dry mass

The water content also varied between seasons in opposition with the energy density (Tables I and II). Significant lower water content values were recorded in autumn in comparison to spring and winter values which could not be distinguished (Tukey's HSD). Again, the test was significant for the large fish and the age 2 only.

To further investigate the respective variations in dry mass and water content, the relationships between organic matter content and water content were considered. The percent organic matter content in the dry mass was inversely proportional to the percent water in the wet mass (Fig. 4). Organic matter was thus replaced by water and vice versa across seasons.

The condition factor of *E. encrasicolus* varied across seasons and reached its lowest level in winter (Fig. 5). Tukey's HSD test showed that the mean condition factor in winter was lower than in spring or autumn but that values for autumn and spring could not be distinguished. As the fish was not expected to grow in winter, the result was that it significantly lost mass in winter. The replacement of organic matter by water (Fig. 4) was thus partial.

3.3. Energy density and dry mass

The energy density on a wet mass basis was linearly related to the percent dry mass (Fig. 6). The slopes fitted by season could be considered equal ($P > 0.05$) as well as the intercepts ($P > 0.05$). A linear regression model was thus fitted for all the samples and was highly significant (intercept=-4.94; slope=0.41; $r^2 = 0.96$, $n = 43$, $P < 0.001$). The slope of this regression model for the Bay of Biscay was greater than that for the Adriatic sea obtained by Tirelli *et al.* (2006) (intercept=-3.32; slope=0.32; $r^2 = 0.82$, $n = 161$, $P < 0.001$).

4. Discussion

4.1. Range of values

The range of values in energy density observed here for *E. encrasicolus* in the Bay of Biscay (6.04-8.44 kJ.g⁻¹ W_w) are in accordance but higher than that in other studies on engraulid species, e.g., *Anchoa mitchilli*: 2.41-4.29 kJ.g⁻¹ W_w (Hartman & Brandt, 1995), *Engraulis japonicus*: 5.25-7.34 kJ.g⁻¹ W_w (Takahashi *et al.*, 2001), *Engraulis australis*: ~5.2 kJ.g⁻¹ W_w (Bunce, 2001) or *E. encrasicolus* in the Adriatic sea: 2.66-7.02 kJ.g⁻¹ W_w (Tirelli *et al.*, 2006). *Anchoa Mitchilli* in Chesapeake Bay and *E. encrasicolus* in the Adriatic Sea were sampled during different seasons and in all size classes (<100 mm and 40 – 140 mm respectively) as in the present study but their size classes were smaller than for *E. encrasicolus* in Biscay (60 –180 mm). *Anchoa Mitchilli* was the smallest anchovy (<100 mm) and showed the lowest energy density values. *Engraulis japonicus* and *E. australis* were investigated during one season only when preyed by birds. Differences in fish sizes, seasons investigated and ecosystems could thus explain the variability between these values.

4.2. Seasonal variations

The seasonal variations in the energy density that were observed agreed with other works on different fish species: Norway pout *Trisopterus esmarkii* and herring *Clupea harengus* (Pedersen & Hislop, 2001); lesser sandeel *Ammodytes marinus* (Hislop *et al.*, 1991); *E. encrasicolus* (Tirelli *et al.*, 2006). The seasonal variations in E_D have been related to the reproductive cycle but also to changes in the food consumption and diet (Hislop *et al.*,

1991; Pedersen & Hislop, 2001). These authors report that fish will in general undergo a period of energy storage in autumn prior to wintering and spawning in spring. Food consumption is low in winter yet followed by spawning. In our case, energy storage in autumn resulted from an increase in the dry mass (increase in the condition factor) as well as an increase in the energy density of the dry mass, which is indicative of a change in the biomolecules of the reserves. Change in the diet and separate biochemical analyses of different tissues (e.g., viscera, muscle, gonads) as in Wang & Houde (1994) would be required to explain precisely the change in energy density of the dry mass.

It is noteworthy that the one outlier point showing a lower than expected energy density value (Figs. 2 and 6) corresponds to juvenile fish in autumn. The E_D measurement was repeated for that group of fish and it is our understanding that a biological reason should explain the low value. Variability in the E_D between juvenile fish groups was high in autumn. The energy density in the subsequent spring was similar to the medium and high values of the autumn juveniles, but there was no very low value in spring. Thus it is possible that autumn juveniles with too low energy content do not survive winter. In effect, a required minimum level of energy to survive winter has already been reported for juvenile rainbow trout *Oncorhynchus mykiss* (Biro *et al.*, 2004), Atlantic salmon *Salmo salar* (Finstad *et al.*, 2004) or lake herring *Coregonus artedii* (Pangle *et al.*, 2004).

4.3. Feeding behaviour

Several studies across the world report that anchovies feed during their spawning season with no separation between feeding and reproduction: *Engraulis mordax* in the California current (Hunter & Leong, 1981), *A. mitchilli* in Chesapeake Bay (Wang & Houde, 1994), *E. encrasicolus* in the Black sea (Lisovenko & Andrianov, 1996), the Bay of Cadiz (Millan, 1999) and the Bay of Biscay (Plounevez & Champalbert, 1999). Here, there was no significant decrease in the energy density in spring in comparison to winter, which supports the idea that *E. encrasicolus* continued feeding during its spawning period. Moreover the high condition factor observed in spring here supports the idea of continued feeding during the spawning season. Millan (1999) also reported a similar observation on the condition factor and Wang & Houde (1994) measured an increase in fish mass during the spawning season. The energy requirement for spawning would then be satisfied by food intake, which would result in total fecundity to vary with fish condition and zooplankton availability, a situation already documented by Somarakis *et al.* (2004) in northern Aegean sea.

4.4. Replacement of organic matter by water

From our results, the seasonal pattern in the fish energy density could be schematically described as follows. In autumn during the feeding season, water in the fish body was replaced by organic matter and the energy density of the dry mass increased. In winter, the fish lost organic matter, the energy density of the dry mass decreased and water replaced organic matter. In spring during the spawning season, food intake allowed to maintain the winter values of energy density and dry mass. This scheme agrees with other works. Biochemical analyses revealed that the interchange between organic matter and water concerns the lipids (Hardy & Keay, 1972; Wallace & Hulme, 1977) but also the proteins (Geiger *et al.*, 2000). Loss of mass in the storage organs (muscle, liver or guts depending on the species) associated with periods of starvation or overwintering have already been reported for *S. salar* (Einen *et al.*, 1998) or cod *Gadus morhua* (Schwalme & Chouinard, 1999).

During winter mass is lost, organic matter is partially replaced by water while total length remains constant. This is expected to cause variation in the fish buoyancy (Maes *et al.*, 2006), which may or not be compensated for by a variation in the swimbladder or active swimming. It is noteworthy to mention here that seasonal changes in the fat content of pelagic fish have been related to variations in their swimbladder characteristics (Ona,

1990; Jørgensen, 2003; Jacobsen *et al.*, 2003) leading to seasonal changes in their acoustic target strength. These findings support the need for buoyancy compensation in pelagic fish due to the seasonal changes in their body fat content and energy density. Fage (1911) described *E. encrasicolus* as being demersal in winter and pelagic in spring, which is consistent with the hypothesis of a variation in buoyancy due to a loss in flesh not enough compensated by water replacement.

4.5. Relationship between energy density and percent dry mass

Hartman & Brandt (1995) evidenced linear relationships between the percent dry mass and the energy density on a wet mass basis for many fish species in the low salinity estuary of Chesapeake Bay and argued that the linear regression parameters were species-specific. But the regression model fitted to our data was different from that reported for *E. encrasicolus* in the Adriatic sea (Tirelli *et al.*, 2006). Moreover, our relationship for *E. encrasicolus* in Biscay was closer to that for herring *C. harengus* in the North Sea (slope=0.417, intercept=-4.64: Pedersen & Hislop, 2001) than to that for *E. encrasicolus* in the Adriatic sea. Our result would thus suggest that the relationships are not only species-specific but also ecosystem-specific. Differences in the seasonal dynamics of ecosystems could over-ride the species-specific component in the relationship. Hartman & Brandt (1995) concluded that species-specific differences in intercept and slope were due to differences in the ash content and lipid level. Ash content was high for *E. encrasicolus* in the Adriatic sea (4.5%), low for *C. harengus* in the North Sea (~2.5%) and intermediate for *E. encrasicolus* in Biscay (~3%). Here, ash content varied with size and was highest for the small *E. encrasicolus* (3.8%, L<100 mm: Table 1), which could explain the high value for the Adriatic sea. Thus differences in ash content cannot be considered as species-specific only as they could also result from differences in fish growth and condition depending on ecosystem specific temperature and food availability. The lipid level in the reserve and the seasonal variation in the dry mass for a given species could also be ecosystem-specific and vary depending on the type of seasonal variation in plankton production and temperature. Thus, *E. encrasicolus* in the Bay of Biscay could store a higher energy content to overwinter and reproduce than in the Adriatic sea, where the species could be more directly responsive to the environment, a behaviour already suggested by Somarakis *et al.* (2004). Hartman & Brandt (1995) suggested to use the linear relationship as a chart to rapidly derive the energy content of the fish knowing its percent dry mass only. It seems that a reference study in each eco-region would be necessary before using the relationship in that way.

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Tables

Table I. Mean values by size classes and seasons for the ash content (AC), water content (WC), energy density on a wet mass basis ($E_D W_W$) and dry mass basis ($E_D W_D$).

Size classes	AC (%)	WC (%)	$E_D W_W$ (kJ.g ⁻¹)	$E_D W_D$ (kJ.g ⁻¹)
<i>Small</i> Autumn (11) ($L_t < 100$ mm)	3.84 (0.53)	75.04 (1.01)	5.27 (0.58)	21.07 (1.83)
<i>Medium</i> ($100 < L_t < 140$ mm)				
<i>Winter</i> (2)	3.39 (0.07)	72.91 (0.37)	6.01 (0.16)	22.174 (0.20)
<i>Spring</i> (1)	2.86	73.57	6.27	23.74
<i>Autumn</i> (2)	3.35 (0.18)	71.85 (2.20)	6.70 (0.93)	23.75 (1.46)
<i>Large</i> ($L_t > 140$ mm)				
<i>Winter</i> (9)	2.98 (0.26)	72.75 (1.67)	6.28 (0.74)	22.97 (1.41)
<i>Spring</i> (8)	2.84 (0.19)	72.46 (1.79)	6.50 (0.71)	23.53 (1.15)
<i>Autumn</i> (10)	2.90 (0.26)	67.62 (1.97)*	8.38 (0.78)*	25.84 (0.93)*

n: number of batches.

Standard deviation in parenthesis.

* values significantly different from other values for the same size class and other seasons (Tukey's HSD).

Table II. Mean values (sd in parenthesis) of mature fish ($140 < L_T < 180$ mm) by ages and seasons for water content (WC), energy density on a wet mass basis ($E_D W_W$) and dry mass basis ($E_D W_D$).

Age classes	WC (%)	$E_D W_W$ (kJ.g ⁻¹)	$E_D W_D$ (kJ.g ⁻¹)
<i>1</i> <i>Winter</i> (2)	73.17 (2.55)	6.11 (1.35)	22.62 (2.88)
<i>Spring</i> (2)	72.31 (3.30)	6.48 (1.36)	23.29 (2.13)
<i>Autumn</i> (4)	68.11 (2.43)	8.17 (0.93)	25.57 (1.02)
<i>2</i> <i>Winter</i> (4)	72.98 (2.11)	6.20 (0.83)	22.87 (1.42)
<i>Spring</i> (4)	72.35 (1.55)	6.58 (0.53)	23.76 (0.79)
<i>Autumn</i> (5)	67.53 (1.86)*	8.44 (0.76)*	25.97 (1.00)*

n: number of batches.

Standard deviation in parenthesis.

* values significantly different from other values for the same age and other seasons (Tukey's HSD).

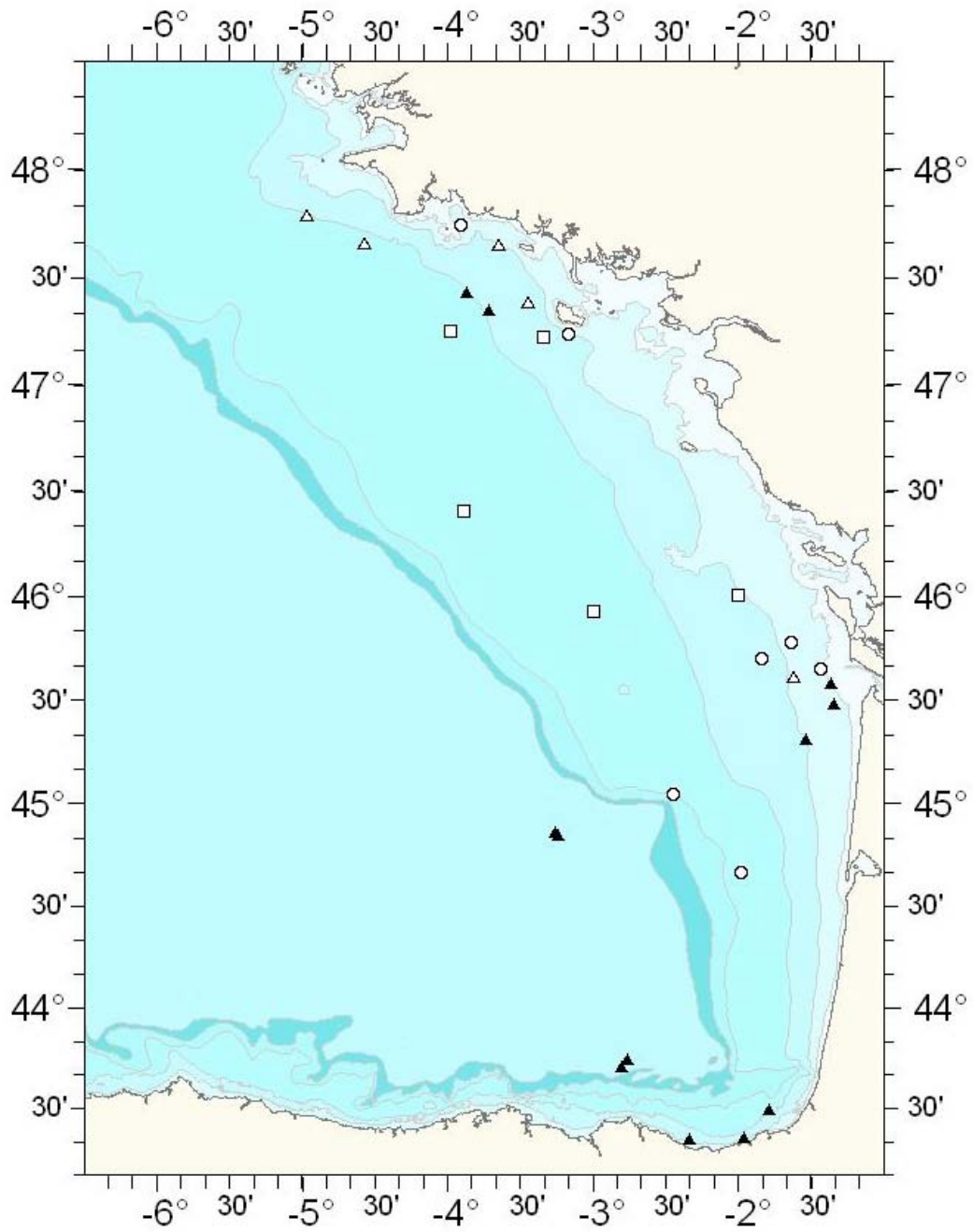


Fig.1.

Figs. 1. Location of the samples in the Bay of Biscay for adults in winter (□), spring (○) and autumn (△) and juveniles in autumn (▲).

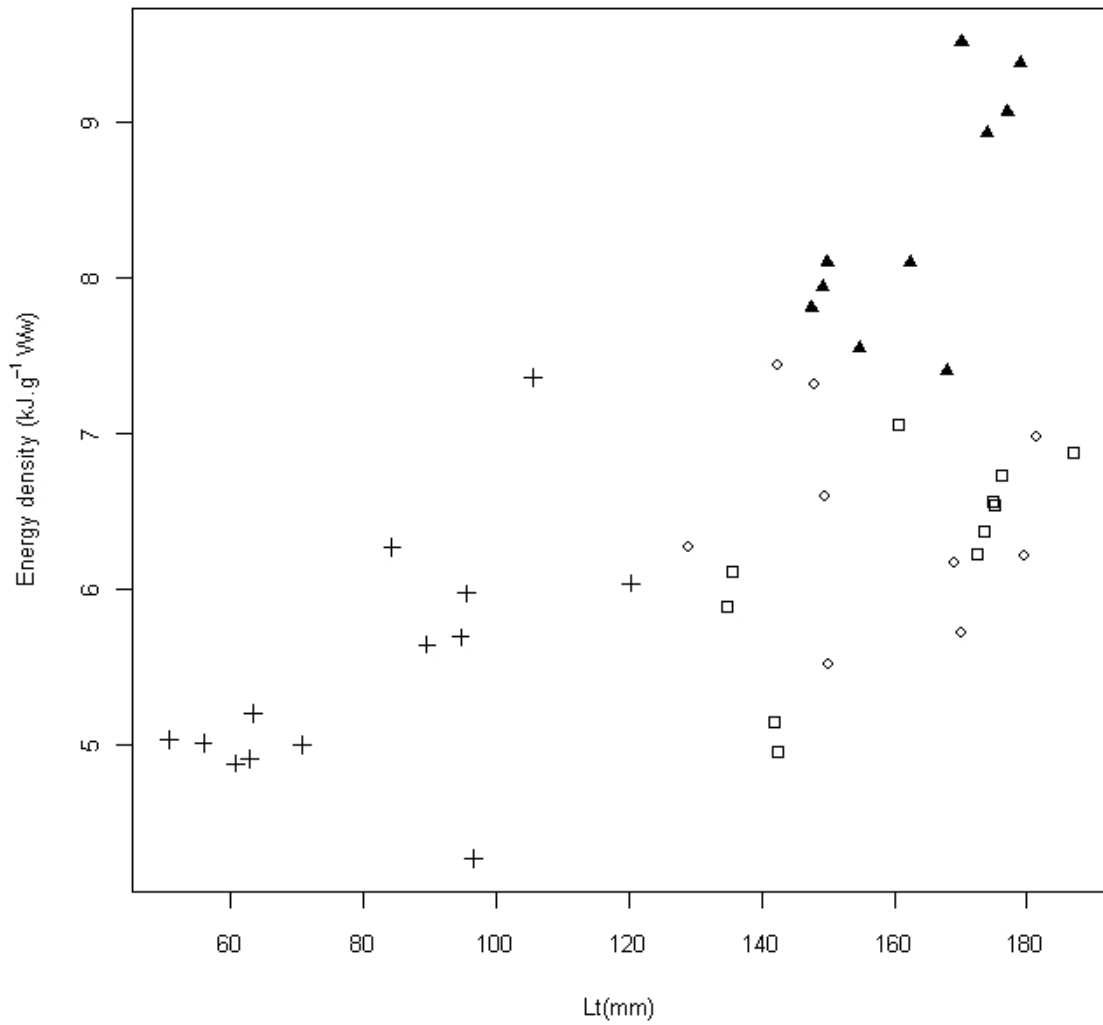


Fig. 2.

Fig. 2. Relationship between total body length (L_t) and wet mass energy density E_D ($\text{kJ}\cdot\text{g}^{-1} W_w$) for *Engraulis encrasicolus* adults in winter (\square), spring (\circ) and autumn (\blacktriangle) and juveniles (+).

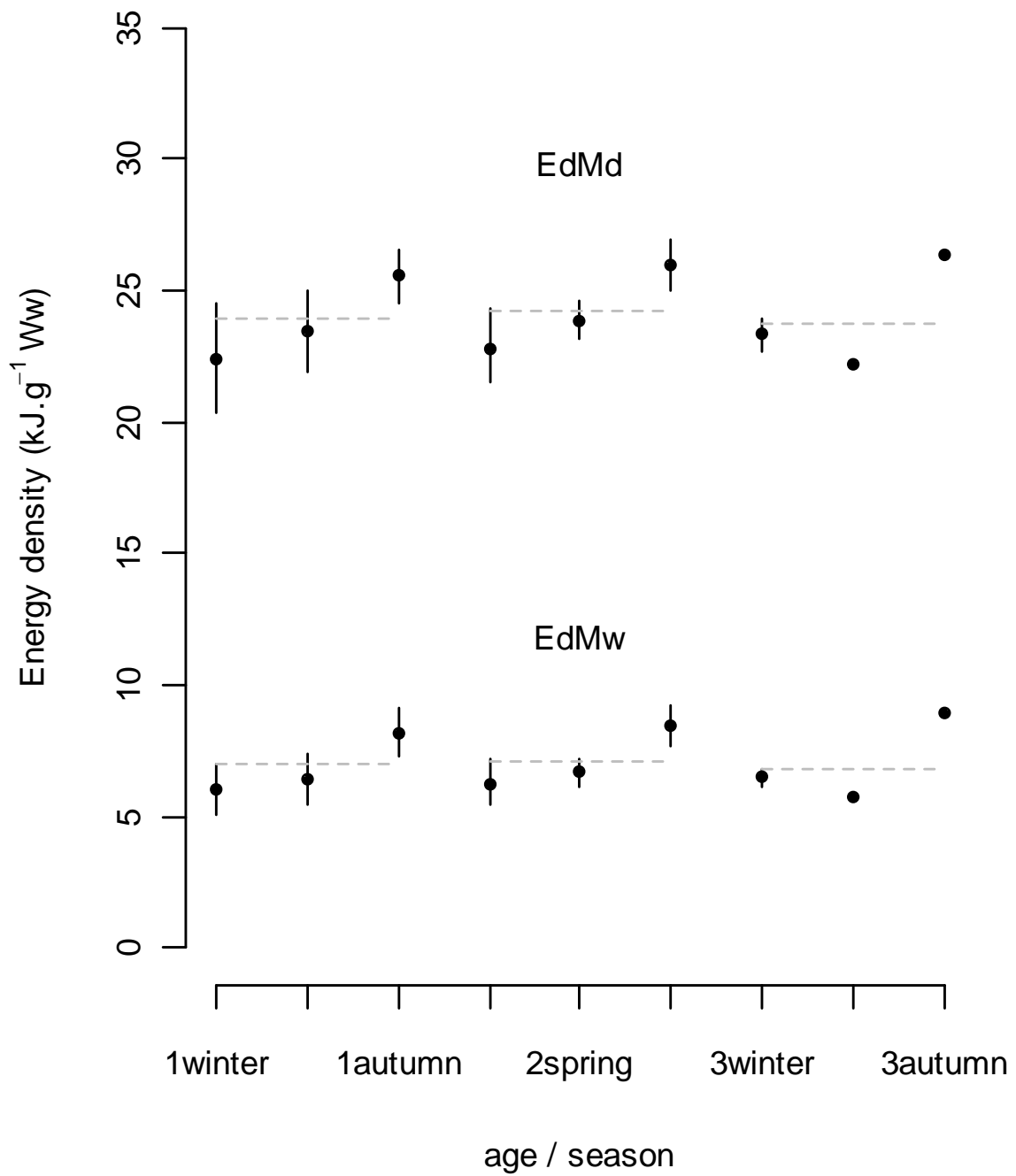


Fig. 3.

Fig. 3. Mean dry mass and wet mass energy density ($E_D W_D$ and $E_D W_W$) by age group and by season (black points) for individuals with total length 140 -180 mm. Error bars indicate +/- one standard deviation. Grey dotted lines indicate mean energy density for each age class.

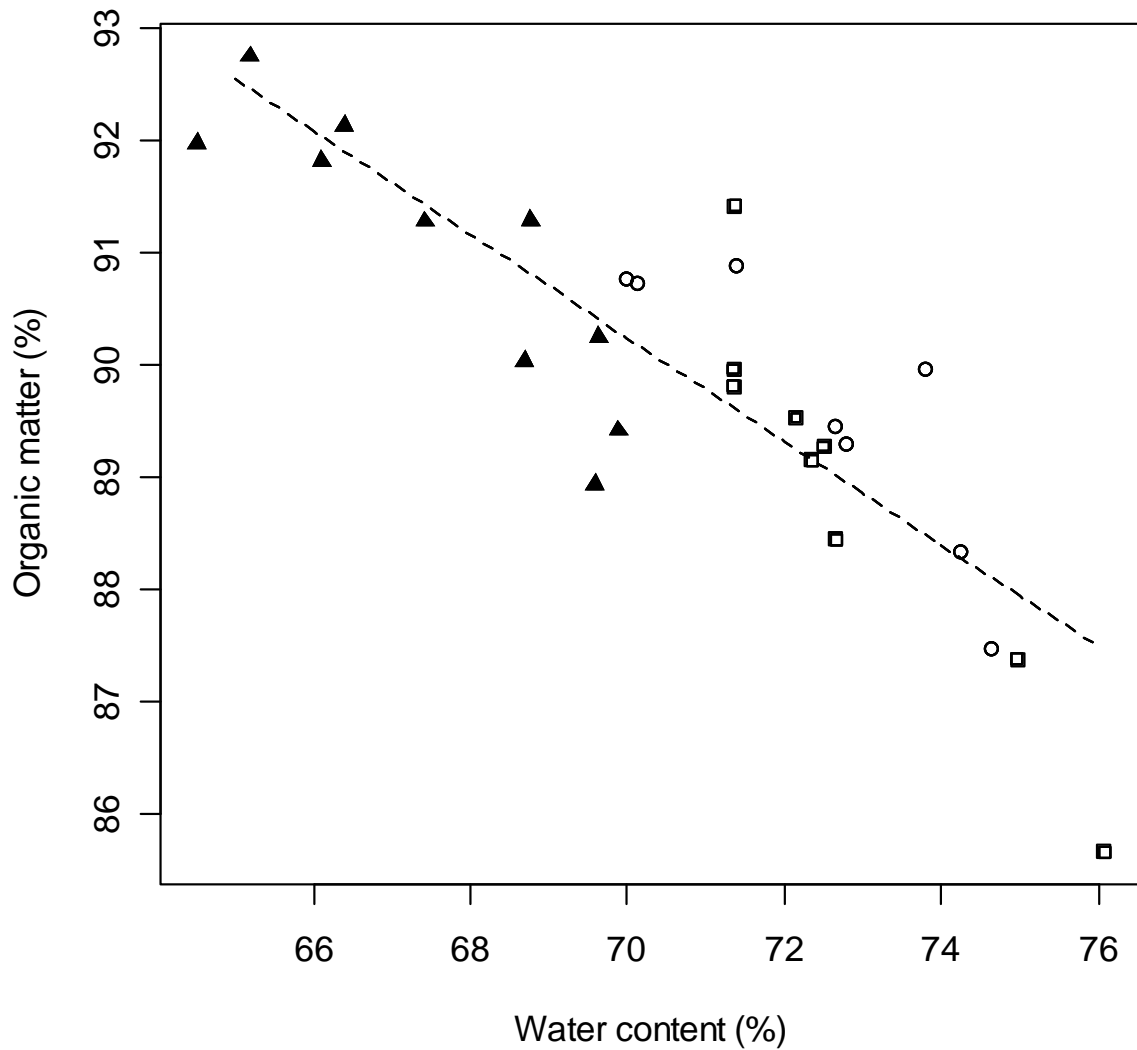


Fig. 4.

Fig. 4. Relationship between water content WC (%) and organic matter content in the dry mass (% OM) for individuals with total length 140 -180 mm collected in winter (◻), spring (○) and autumn (▲). The dotted line was fitted for the total sample (intercept = 122.45, slope = -0.46 , $r^2 = 0.73$, $n = 27$, $P < 0.001$).

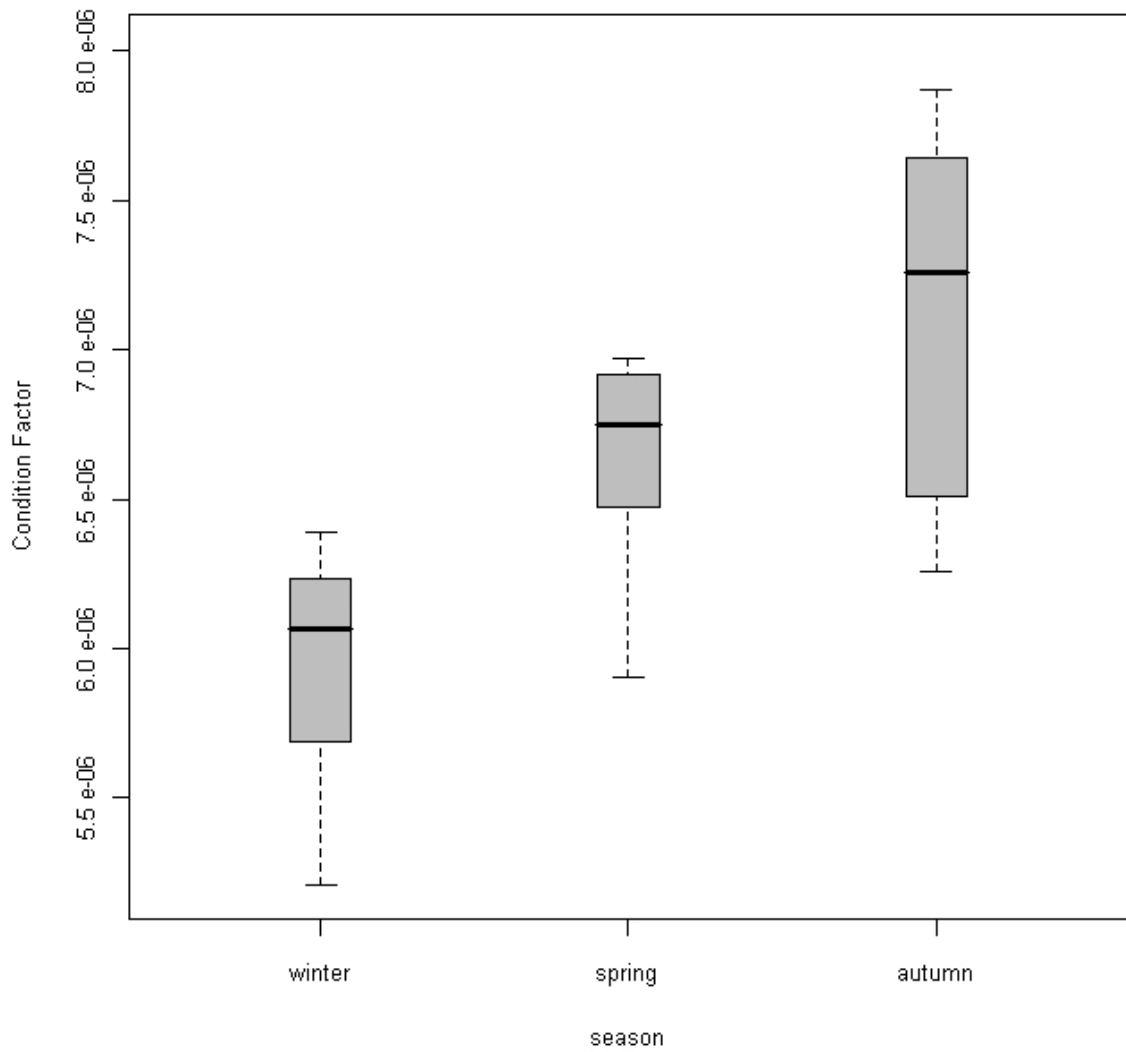


Fig. 5.

Fig. 5. Boxplots of Fulton's Condition Factor for individuals with total length 140 -180 mm collected in winter, spring and autumn.

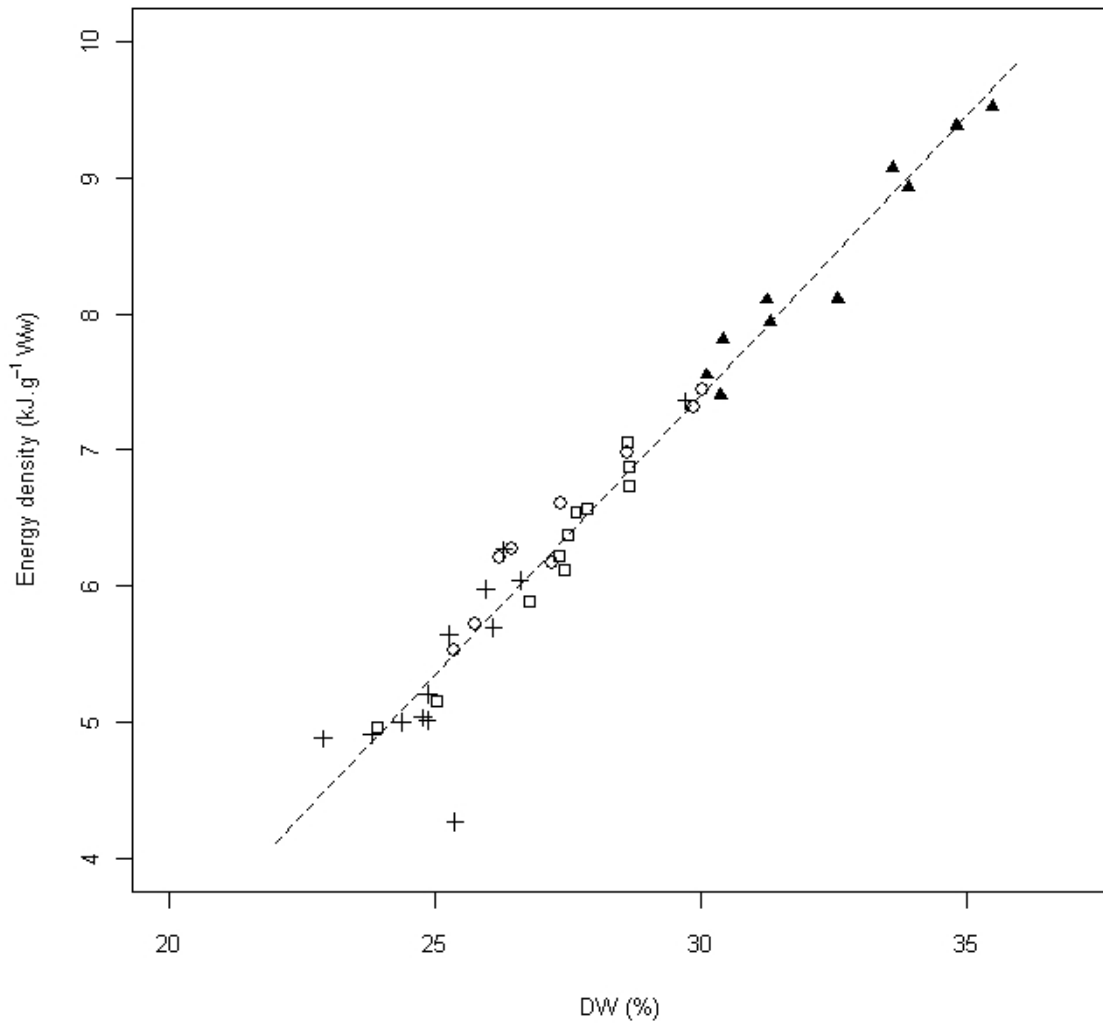


Fig. 6.

Fig. 6. Relationship between percent dry mass DW (%) and wet mass energy density E_D ($\text{kJ.g}^{-1} W_W$) for *Engraulis encrasicolus* adults collected in winter (□), spring (○) and autumn (▲) and juveniles (+). The dotted line was fitted for the total sample (intercept = -4.937, slope = 0.411, $r^2 = 0.957$, $n = 43$, $P < 0.001$).