

Assessment of energy content indices for exploited small pelagic fish

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Abstract – Energy content is a reliable indicator of an individual's body condition, influencing growth, reproduction, and survival with cascading effects on population dynamics and ecosystems through energy transfer. Energy density can be measured through bomb calorimetry or estimated using proxies such as morphometric indices, water content, or proximate composition. Direct methods are the most accurate but are also time-consuming and expensive, while there is a lack of proper assessment of the various existing proxies. This study, based on a large dataset of proximate composition and energy density for anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) from the Bay of Biscay and the English Channel, thoroughly compared four methods of varying complexity to identify the most accurate and practical approach for estimating energy density and total energy. Morphometric-based methods performed poorly, as they fail to distinguish variations in water, protein, and lipid content, each contributing differently to energy. While proximate composition could be reasonably well estimated from length, the accuracy of this estimation did not significantly improve energy estimations compared to morphometric indices. In contrast, water content proved to be the most reliable indicator of energy density, that can be accurately estimated either directly through its negative relationship with water content, or indirectly via proximate composition. Furthermore, incorporating three levels of individual condition states into the water content based methods, improved the accuracy of energy density estimates. This comprehensive comparison highlights the importance of standardizing water content measurements as a cost-effective alternative to calorimetry, enabling routine energy monitoring in fish surveys.

Keywords: Energy density / water content / Bay of Biscay / anchovy / sardine / proximate composition

1 Introduction

Energy content is a reliable indicator of an individual's overall condition, that directly impacts growth, reproduction, and survival rates (Molnár et al., 2009). These effects on individuals can upscale to the population dynamics (Pagano et al., 2018) and ecosystems through energy transfer from smaller prey to larger predators (Benoit-Bird, 2004; Pothoven and Fahnenstiel, 2014; Spitz and Jouma'a, 2013). In marine ecosystems, energy content reflects how individuals coped with environmental factors such as temperature and food availability over the past few months (Albo-Puigserver et al., 2017), and influences their future life trajectories (Wilson and Nussey, 2010). Energy studies have primarily focused on the

individual scale, with a focus on energy allocation throughout the fish life cycles (Jørgensen and Fiksen, 2006). Energy has been extensively used in fish bioenergetic modeling (Breck, 2008; Gatti et al., 2017) and marine ecosystem studies (Carroll et al., 2021), demonstrating that energy provides valuable insights into the changes occurring at the individual up to the ecosystem levels through energy transfer. At the individual scale, energy content is primarily expressed as energy density (ED), which reflects the amount of energy stored per unit of body mass and serves as an indicator of its condition. Tracking energy density variations over long-term datasets is critical for understanding the impacts of environmental changes, such as climate-driven shifts, on individuals, populations, and ecosystems.

Small pelagic fish (SPF) with their significant fat content are ecologically and economically important species (Rooper et al., 2024) and attractive preys for numerous marine

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predators (Ouled-Cheikh et al., 2022; Spitz et al., 2018), contributing to a major energy transfer from lower to higher trophic levels (Corrales et al., 2022; Duarte et Garcia, 2004; Lindegren et al., 2011). Worldwide, these SPF populations are subject to major fluctuations in abundance and biomass (McClatchie et al., 2017; Schwartzlose et al., 1999) as well as in size structure and length at age (Brosset et al., 2017; Canales et al., 2015; Van Beveren et al., 2014). In the Bay of Biscay, European anchovy (*Engraulis encrasicolus*, Linnaeus 1758), hereafter anchovy, and European sardine (*Sardina pilchardus*, Walbaum 1792), hereafter sardine, are the two important species of SPF supporting valuable fisheries (ICES, 2024) and predators (Spitz et al., 2018). Over the last two decades, these species have experienced substantial fluctuations in abundance between 25,000 and 175,000 tons (ICES, 2024). More recently, physiological changes have been observed in the Bay of Biscay including reduced length-at-age for sardine (Doray et al., 2018; Véron et al., 2020) and anchovy (Taboada et al., 2024) and lower body condition for sardine, as determined from Le Cren relative condition factor (Véron et al., 2020), highlighting the importance of monitoring fish condition in the context of climate change. The decrease in condition and fat content may have severe implications for the fishing sector (Beckensteiner et al., 2024; Saraux et al., 2019) as well as for energy transfer to top predators, which depend on high-quality prey in terms of size and energetic value (Golet et al., 2015; Österblom et al., 2008; Trites & Donnelly, 2003).

Monitoring fish condition requires large datasets on energy density for accurate bioenergetic and ecosystem modeling, as well as long-term assessments (Hartman and Brandt, 1995). The most straightforward way of measuring energy is through direct measurement of energy density, using bomb calorimetry (Craig et al., 1978). Calorimetry consists in measuring heat released during the combustion of a sample of dried tissues, which can be directly converted into the energy content of that sample (Campanini et al., 2021; Ciancio et al., 2007, 2020; Gatti et al., 2018; Tirelli et al., 2006). Lipid content is another widely used direct indicator of fish energy (Albo-Puigserver et al., 2020; Anthony et al., 2000; Brosset et al., 2015; Trudel et al., 2005) as lipids are the main molecules used by fish to store energy, and often the first catabolized when needed (Shulman and Love, 1999). However, fish total energy content consists in the sum of energy from lipids, proteins, and carbohydrates (Cummins and Wuycheck, 1971; Glover et al., 2010), and cannot be accurately estimated based on lipid content alone. Because accurate and reliable methods of estimating energy density are time-consuming, expensive, and impractical onboard during field surveys, indirect methods are often used as alternatives (Campanini et al., 2021).

Indirect methods for estimating fish energy density include conversion from morphometric indices (Albo-Puigserver et al., 2020), from water content measurements (Hartman and Brandt, 1995), or from proximate composition estimation (Breck, 2014). However, they are only energy proxies, which should be validated through comparison with direct measurement indices (Davidson and Marshall, 2010; McPherson et al., 2011). Morphometric indices are based on length-weight relationships, assuming that heavier fish of a given length are in better condition (higher energy density). Among morphometric indices, the relative condition index (Le Cren, 1951) is widely used in fisheries science (Gubiani et al., 2020).

Although its calculation is based on fish length and weight, the standardization procedure makes the index independent of fish length, unlike the Fulton condition factor. Numerous studies have examined the relationships between relative condition index and energy density or lipid content and revealed moderate or weak correlations between these variables (Albo-Puigserver et al., 2020; Brosset et al., 2015; Campanini et al., 2021; Sardenne et al., 2016). Water content (or dry mass content) has proven to be a good indicator of energy density for numerous fish species, with R^2 values ranging from 0.77 to 0.99 (Hartman and Brandt, 1995; Tirelli et al., 2006; Dubreuil and Petitgas, 2009; Gatti et al., 2018). Others studies went further by estimating proximate composition from water content as an intermediate step to calculate energy density (Breck, 2014; Schloesser and Fabrizio, 2015), relying on the assumption that protein mass can be accurately derived from water mass. However, Favreau et al. (2025) demonstrated that this assumption does not always hold, at least for sardine and anchovy, as these species can metabolize proteins for energy when lipid reserves are critically depleted (Campanini et al., 2021). Drawing on these studies and accounting for protein variation, we aimed to evaluate whether combining proximate composition to water content could refine energy density estimation. Additionally, we explored the feasibility of bypassing water measurements by using proximate composition to estimate energy density, potentially offering simpler and more efficient methodology.

In this study, we compared four indirect methods, varying in complexity, to assess the most suitable in estimating energy density and total energy in terms of accuracy and practicality. The first method used the relative condition index (Le Cren, 1951), calculated from measured length and weight. The second method relied also on measurements of length and weight, but we evaluated the added value of estimating the proximate composition based on length as an intermediate step. The third method incorporated measurements of water content, weight, and estimated proximate composition based on water mass following Breck (2014). The fourth method used the relationship between energy density and water content (Hartman and Brandt, 1995). These methods were applied to a large dataset of anchovy and sardine samples collected from the Bay of Biscay and the English Channel covering all seasons and a wide range of length, ensuring a comprehensive comparison of the four methods. Each metric was calculated, when possible, for the three condition states defined by lipid, protein and water content, and reported separately for anchovy and sardine (Favreau et al., 2025), including the poor condition state, which had been excluded in previous studies due to its higher water-to-protein ratio (Breck, 2014). By assessing these methods, we aim to facilitate the development of robust, long-term time series for energy density monitoring.

2 Material and methods

2.1 Sampling and laboratory measurements

Juvenile and adult anchovies and sardines were sampled from 2014 to 2017 in the Bay of Biscay and the English Channel (Fig. 1, data available in Huret et al., 2024). Fish were collected during scientific surveys conducted by IFREMER on the RV “Thalassa” and sampled from commercial landings

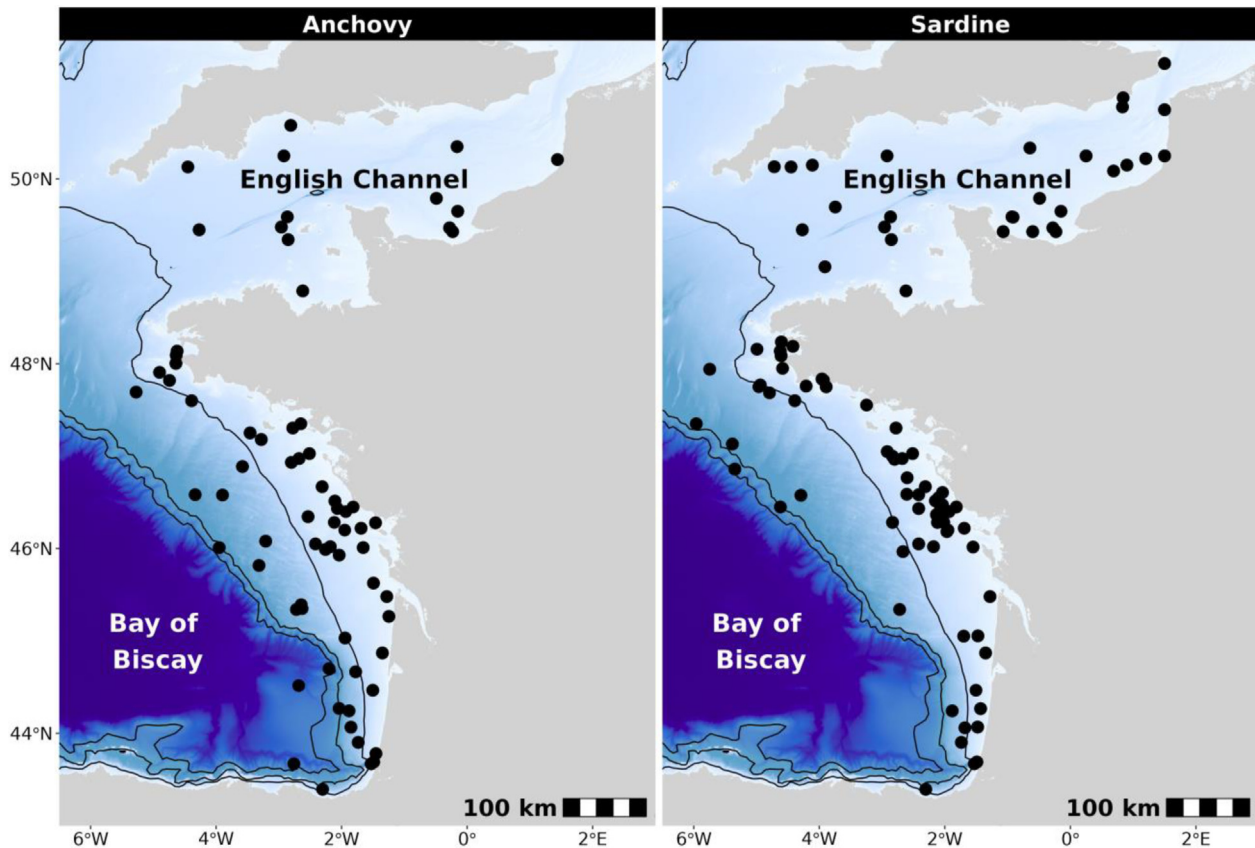


Fig. 1. Sampling locations in the Bay of Biscay and English Channel, for anchovy (left) and sardine (right) from scientific surveys and commercial landings. Black lines represent isobaths of 100, 200 and 1000 meters.

under the European Data Collection Framework (DCF) for all four seasons. This study used a total of 503 anchovies and 976 sardines collected between 2014 and 2017. The sampling sites represented the core distribution areas of these species in the Bay of Biscay and the English Channel (Fig. 1, ICES, 2024). All fish were measured to the nearest inferior tenth of a centimeter and weighed to the nearest tenth of a gram. Maturity stages were determined following ICES guidelines (ICES, 2008) based on macroscopic gonads observation and using a six-stage key. As described in Favreau et al. (2025), fishes characterized by maturity stages 3, 4 or 5 were considered as being in an active reproductive period as opposed to fishes in stages 1, 2 or 6. Fish were individually frozen at -20°C before being processed in the laboratory. In the lab, fish were thawed, ground, and freeze-dried for a minimum of 48 h. The water content of each fish (HC_{calc}) was calculated using the ratio of dry weight (DW) to wet weight (WW). Fish were then ground again to produce a fine, homogeneous dry powder for further analysis. Ash content was measured by incinerating dried tissue in a muffle furnace at 550°C for 6 h. Lipid and protein contents were analyzed by a certified laboratory (Laboce, Plouzané, France). Lipids were quantified through a hydrolysis step, followed by extraction with petroleum ether as an organic solvent. Protein content was determined using the Kjeldahl method (Sáez-Plaza et al., 2013). Carbohydrates, which make up less than 1% of fish mass, were ignored as in previous studies (Brett and Groves, 1979; Craig, 1977; Craig et al., 1978). Protein, lipid and ash contents did not exactly sum to 1

in dry weight (Favreau et al., 2025). This may arise from residual water, measurement uncertainties, or to a lesser extent the exclusion of carbohydrates. Consequently, the values were normalized by dividing each component by the sum of lipids, proteins, and ash content (Breck, 2014). In total, 104 proximate composition analyses were conducted for anchovy and 116 for sardine. Energy density was measured for 503 anchovies and 976 sardines using the protocols outlined in Dubreuil and Petitgas (2009) and Spitz and Jouma'a (2013) with an IKA C-4000 adiabatic bomb calorimeter (IKA-Werke GmbH & Co. KG). Further details on sampling, proximate composition analyses, and energy content measurements can be found in Favreau et al. (2025).

2.2 Description of the four methodologies

Four indirect methods, varying in complexity and described in Figure 2, were tested to estimate two energy indices for both species. A preliminary step was necessary for methods 2 and 3, based on lipid and protein masses to estimate energy density. To improve clarity and consistency throughout the manuscript, the term *measured* (abbreviated as *m*) refers to values directly obtained through laboratory analysis using appropriate equipment. The term *calculated* (*calc*) is used for values derived from algebraic formulas. The term *estimated* (*est*) refers to values inferred from statistical relationships between variables.

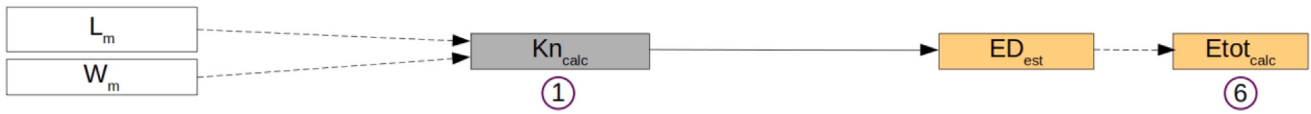
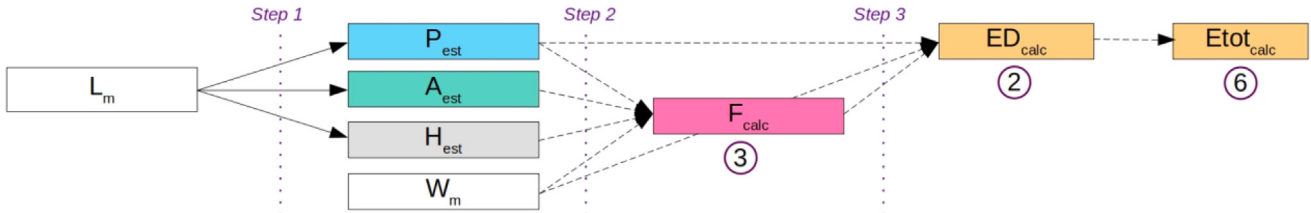
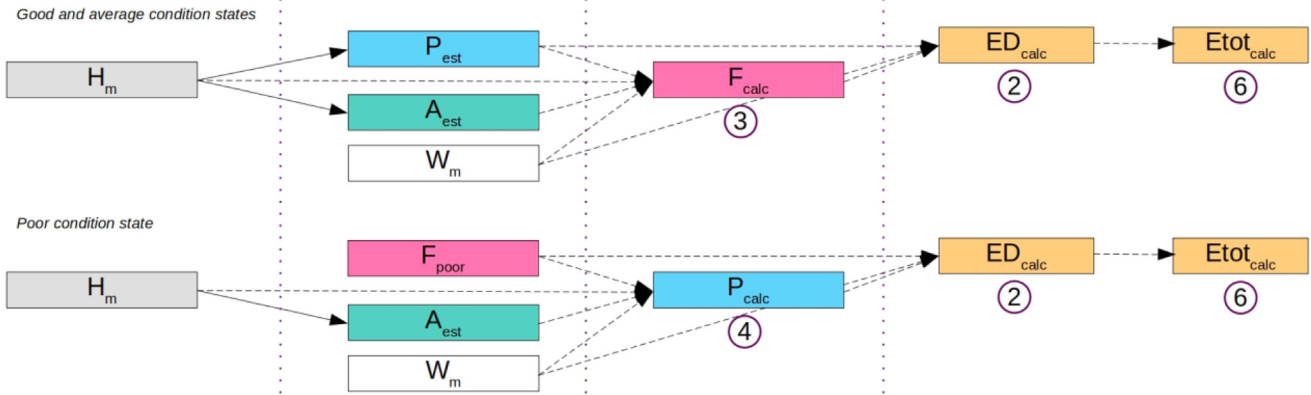
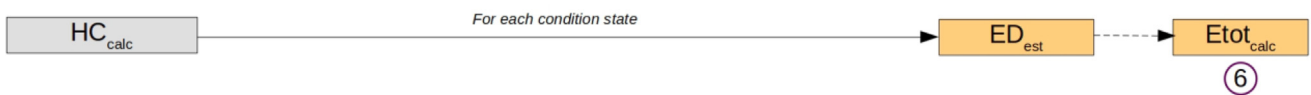
a. Method 1**b. Method 2****c. Method 3****d. Method 4**

Fig. 2. Flow chart diagram summarizing the four methods used to estimate energy indices (energy density in $\text{kJ} \cdot \text{g}^{-1} \text{ WW}$ and total energy in kJ). All estimates were compared to energy density measured by bomb calorimetry. Solid lines indicate that a linear (or log-log linear) regression was used to estimate the variables. Dashed lines indicate that an equation was used to estimate the variables. Equation number is indicated in the circles. Methods 2 and 3 are decomposed in three steps corresponding to the estimation of proximate components (step 1), calculation of lipid or protein (step 2) and calculation of energy indices (step 3). L = length, W = weight, Kn = relative condition factor, P = protein mass, F = lipid mass, A = ash mass, H = water mass, HC = water content, ED = energy density, $Etot$ = total energy. Note that m = measured, $calc$ = calculated, est = estimated.

2.2.1 Method 1: From relative condition index to energy density

The first method is based on the relationship between the relative condition index (Kn , Le Cren, 1951) and energy density (Fig. 2a). The relative condition index Kn_{calc} was calculated from measured length (L_m) and weight (W_m) for each individual using equation (1):

$$Kn_{calc} = W_m / W_{est} \quad (1)$$

with W_{est} the weight of an individual estimated from log-log relationships of the form:

$$\log(W_m) = \log(\alpha) + \beta \cdot \log(L_m) + \varepsilon$$

thus :

$$W_{est} = \alpha L_m^\beta$$

α and β coefficients were estimated for both species, based on all measurements in the dataset (anchovy: $\alpha = 0.0026$, $\beta = 3.33$; sardine: $\alpha = 0.0059$, $\beta = 3.11$, Fig. A1), ε is the residual error. We fitted a linear model linking the relative condition index (Kn_{calc}) to measured energy density (ED_m).

Table 1. Water content values used to classify anchovy and sardine into condition states (good, intermediate, poor), along with sample sizes for each state.

Condition state	Anchovy		Sardine	
	Water content	<i>n</i>	Water content	<i>n</i>
Good	$HC_{calc} \leq 68.4\%$	51	$HC_{calc} \leq 67.8\%$	283
Intermediate	$68.4\% < HC_{calc} < 75.2\%$	339	$67.8\% < HC_{calc} < 75\%$	488
Poor	$HC_{calc} \geq 75.2\%$	113	$HC_{calc} \geq 75\%$	205

$$ED_m = a + b.Kn_{calc} + \varepsilon.$$

This regression was then used to predict an energy density estimate (ED_{est}) for each individual directly from its Kn_{calc} :

$$ED_{est} = a + b.Kn_{calc}.$$

2.2.2 Preliminary assessment of lipid and protein masses to calculate energy density

Methods 2 and 3 can be decomposed in three steps, the third being the conversion of lipid (F) and protein masses (P) to calculate energy density (ED_{calc}) following equation (2):

$$ED_{calc} = \frac{F * ED_F + P * ED_P}{W_m} \quad (2)$$

with ED_F the energy density of lipids (38.5 kJ.g^{-1}) and ED_P the energy density of proteins (23.6 kJ.g^{-1}). ED_P was obtained from literature (Beamish et al., 1975; Brett and Groves, 1979; Paine, 1971) and ED_F was obtained measuring the mesenteric fat of sardine using bomb calorimetry ($n=4$, $CV=1.2\%$). We considered mesenteric fat because it consists almost entirely of lipids, and the composition of reserve lipids is assumed to be similar between mesenteric fat and other storage tissues, such as muscle. This value was within the range of values published for fish: 36.2 to 39.5 kJ.g^{-1} (Schloesser and Fabrizio, 2015). Equation (2) was first evaluated independently, using fish samples for which lipid and protein masses as well as energy density had been measured, before assessing methods 2 and 3 as a whole.

2.2.3 Method 2: From morphometry to energy density using estimated proximate composition

Method 2 requires not only morphometric data but also their relationships with fish proximate components (Fig. 2b). Step 1 involved estimating the masses (in grams) of protein (P_{est}), ash (A_{est}), and water (H_{est}) using separate log-log linear regressions with fish length. Since lipid mass is highly variable and cannot be estimated from linear regression (Favreau et al., 2025), it was calculated by subtracting estimated water, protein and ash masses to fish total weight using equation (3).

$$F_{calc} = W_m - (H_{est} + P_{est} + A_{est}). \quad (3)$$

Negative values in calculated lipid mass were set to zero. Calculated lipid masses were also compared to measured lipid

masses using linear regression. Finally, in step 3 we calculated energy density from equation (2) but using F_{calc} and P_{est} .

2.2.4 Method 3: From water mass to energy density using estimated proximate composition

2.2.4.1 Identification of fish condition state

The assessment of fish condition states that were required in method 3, were based on water content (HC_{calc}) following Favreau et al. (2025). Three condition states were used (see their definition in Tab. 1).

2.2.4.2 Good and intermediate condition state

Breck (2014)'s method was used for fish in good and intermediate states. It was implemented as in method 2, except that we used measured water mass as explanatory variable to estimate protein and ash masses using log-log relationships (step 1, Fig. 2c). Lipids were also calculated using equation (3) but with measured water mass H_m instead of estimated water mass H_{est} (step 2). Negative values in estimated lipid contents were set to zero. Calculated lipid masses were also compared to measured lipid masses using linear regression. Energy density was calculated using F_{calc} and P_{est} (Eq. (2)) as in method 2 (step 3).

2.2.4.3 Poor condition state

Fish in poor condition state have exhausted their lipid reserves and draw on their proteins for their metabolism. Consequently, estimating protein mass from water mass as done for good and intermediate condition states appeared unreliable, since the water-to-protein ratio changes significantly in these individuals (Favreau et al., 2025). We therefore applied a more appropriate method, which consisted in calculating protein mass by subtracting water, ash and lipid masses from fish weight (Eq. (4), step 2 Fig. 2c). To determine lipid mass, we assumed that fish in poor condition state had exhausted all their lipid reserve, and only structural lipids remained. As Favreau et al. (2025), this proportion of structural lipid F_{poor} was determined by taking the mean of the measured lipid for poor condition fish (1.1%, $sd=0.6\%$ for anchovy and 1.0%, $sd=0.3\%$ for sardine), allowing to calculate lipid mass by multiplying the lipid content threshold by fish weight ($F_{calc} = F_{poor} * W_m$).

$$P_{calc} = W_m - (H_m + A_{est} + F_{calc}). \quad (4)$$

Calculated protein masses P_{calc} were also compared to measured proteins using linear regression. Energy density was

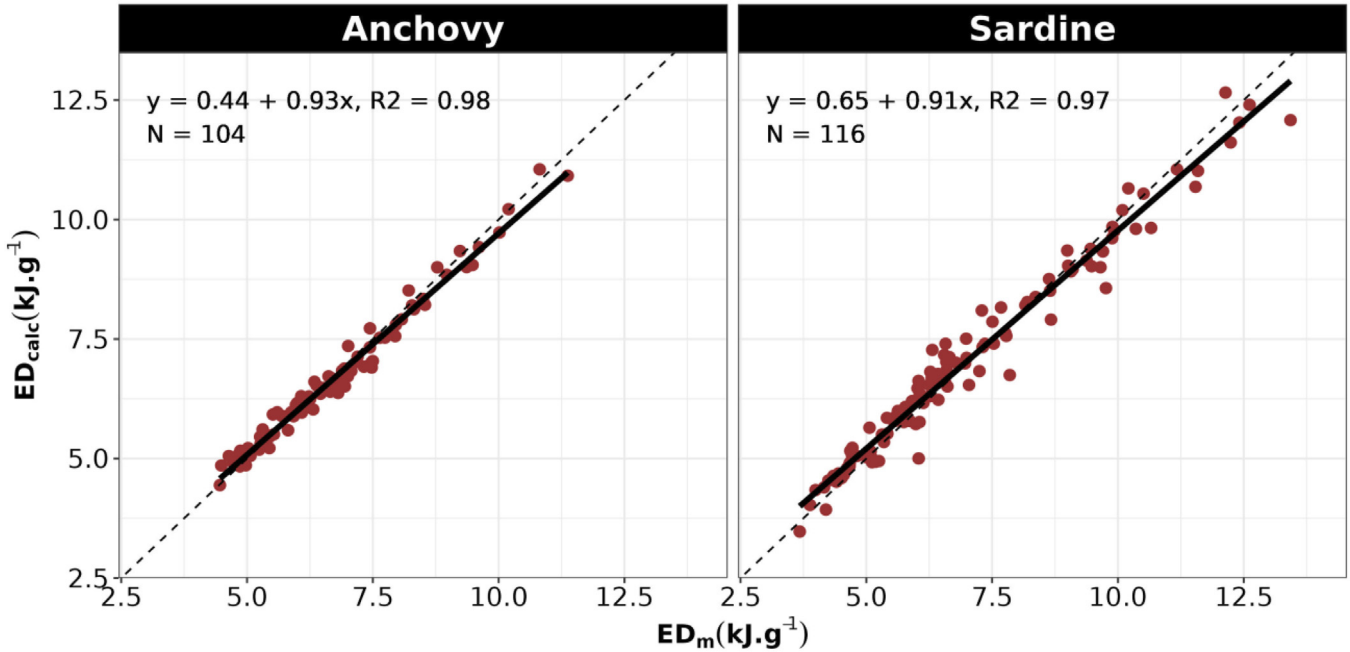


Fig. 3. Measured energy density ED_m from bomb calorimetry (kJ.g^{-1} WW) versus *calculated* energy density ED_{calc} from lipids and protein masses (g) using equation (2) for anchovy and sardine. The solid line represents the linear regression line and the dotted line corresponds to the 1:1 equation.

calculated using calculated masses of lipid F_{calc} and calculated masses of protein P_{calc} (Eq. (2)) as in method 2 (step 3).

$$Etot_{calc} = ED_{calc/est} \cdot W_m. \quad (6)$$

2.2.5 Method 4: From water content to energy density

The fourth method directly estimated the energy density from water content (%) (Fig. 2d). This relationship has been extensively studied (Gatti et al., 2018; Hartman and Brandt, 1995; Tirelli et al., 2006). However, as described in Favreau et al. (2025), this relationship varies depending on the fish condition state justifying the use of a linear model fitted separately for each condition state taking the form of :

$$\begin{aligned} ED_m &= (a_i + b_i * HC_{calc} + \varepsilon) \cdot 1HC_{calc} \in C_i \\ ED_{est} &= (a_i + b_i * HC_{calc}) \cdot 1HC_{calc} \in C_i \end{aligned} \quad (5)$$

a_i and b_i are condition-specific intercept and slope parameters and where $1HC_{calc} \in C_i$ equals 1 when the water content is consistent with fish condition state i , $i=1, 2$, or 3.

2.2.6 Calculation of total energy

While energy density provides valuable information about individual's condition and prey quality for predators, total energy ($Etot$), which integrates both weight and energy density, is another essential quantity in trophodynamics. Total energy reflects the actual energy a predator gains upon ingesting a prey item, making it particularly relevant when assessing energy transfer within the food web. Total energy (in kilojoules kJ) was calculated by multiplying estimated or calculated energy density (kJ.g^{-1}) by fish weight (g):

2.3 Quality of the linear models

Methods 1 and 4 were directly evaluated on the entire dataset ($N=503$ for anchovy, 976 for sardine). For Methods 2 and 3, relationships between proximate components and length or water mass were first fitted on 104 and 116 individuals, then applied to estimate proximate components and energy density for all fishes. The goodness of fit of the linear models was assessed using the coefficient of determination (R^2), normalized Root Mean Squared Error (nRMSE), and the slope of the regression between estimated/calculated and measured energy density. Analyses were performed using the statistical R software (R Core Team, 2023).

3 Results

3.1 Preliminary assessments to estimate energy density

3.1.1 Assessment of the conversion of lipid and protein masses to energy density

Energy density was accurately calculated ($R^2=0.98$ for anchovy and $R^2=0.97$ for sardine) from measured lipid and protein masses, although it was slightly underestimated at high energy density values (Eq. (2), Fig. 3). This confirmed that energy density can be accurately calculated from lipid and protein masses, supporting the further testing of other steps of methods 2 and 3.

Method 2

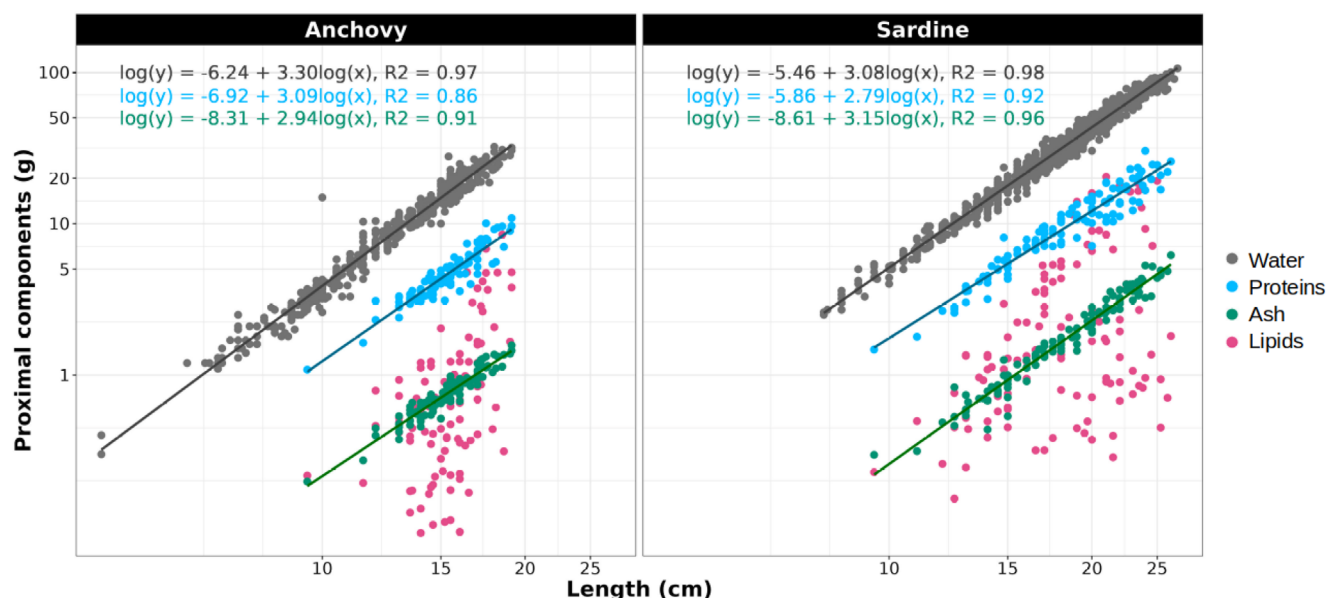


Fig. 4. Log-log relationships between length and water mass, length and protein mass and length and ash mass (method 2) for anchovy and sardine. The solid line represents the log-log regression line.

3.1.2 Assessment of the estimation of proximate components for methods 2 and 3

The first step of method 2 was to estimate protein, ash and water masses from fish length as explanatory variable and from log-log linear relationships, for anchovy and sardine (Fig. 4). Strong log-log relationships between length and water ($R^2 > 0.97$), length and protein ($R^2 > 0.86$) and length and ash ($R^2 > 0.91$) were found, for both species. For method 3, Figure 4 from Favreau et al. (2025) showed strong log-log relationships between water mass and protein mass ($R^2 > 0.96$) and water mass and ash mass ($R^2 > 0.87$), for both species. Significant differences were observed in the intercepts of the log-log linear models between protein and water masses for good and average condition states (ANCOVA P -values < 0.001 for sardine and anchovy). This indicates that fish in better condition have systematically higher protein content for a given water mass. In contrast, no significant differences were detected in the intercepts of the ash-to-water mass relationships (ANCOVA P -values = 0.50 for anchovy and 0.88 for sardine), suggesting that ash content is not affected by fish condition. Additionally, a significant interaction between condition state and water mass was found for protein content (ANCOVA interaction P -values < 0.05 for both species), indicating that the slope of the protein-water relationship changes with fish condition. No such interaction effect was observed for ash content (ANCOVA interaction P -values = 0.29 for anchovy and 0.81 for sardine), implying a stable ash-to-water relationship regardless of condition. Lipid mass as a function of length or water mass was highly variable (Fig. 4), supporting the need to estimate lipids in a different way.

3.1.3 Calculation of the lipid mass for methods 2 and 3

Lipid mass was calculated by subtracting the combined estimated masses of water, ash, and protein from the total fish

weight in method 2, while in method 3, it was calculated by subtracting the combined measured mass of water and estimated masses of ash and protein for fish in good and intermediate condition states (Eq. (3)). Calculated and measured lipid masses were compared in Figure 5. Calculated of lipid mass using method 2 was better for sardine ($R^2 = 0.79$) than for anchovy ($R^2 = 0.61$, Fig. 5a) despite a global overestimation of lipid mass (slopes > 1). Estimation of lipid mass using method 3 was better for fish in good condition state ($R^2 = 0.89$ for sardine and $R^2 = 0.95$ for anchovy) than for average condition state ($R^2 = 0.71$ for sardine and $R^2 = 0.72$ for anchovy, Fig. 5b).

3.1.4 Calculation of protein mass for fish in poor condition for method 3

In method 3, protein mass of poor condition fish was calculated based on fish mass, estimated ash mass, measured water mass and the lipid threshold value (Eq. (4), Fig. 6). Calculated values were very close to measured protein mass for both species ($R^2 = 0.98$ for anchovy and $R^2 = 0.99$ for sardine, Fig. 6).

3.2 Estimation of energy indices from the four methods

Energy density was directly estimated from the relative condition index in method 1 and from water content (%) in method 4 (Figs. 7a and 7d, Tab. 2). The relationships between the relative condition index and energy density, as well as between water content and energy density, are shown in Figures A2 and A3, respectively. For methods 2 and 3, energy density was calculated based on estimated or calculated lipids and proteins masses using equation (2) (Figs. 7b and 7c, Tab. 2). Morphometry-based method (methods 1 and 2)

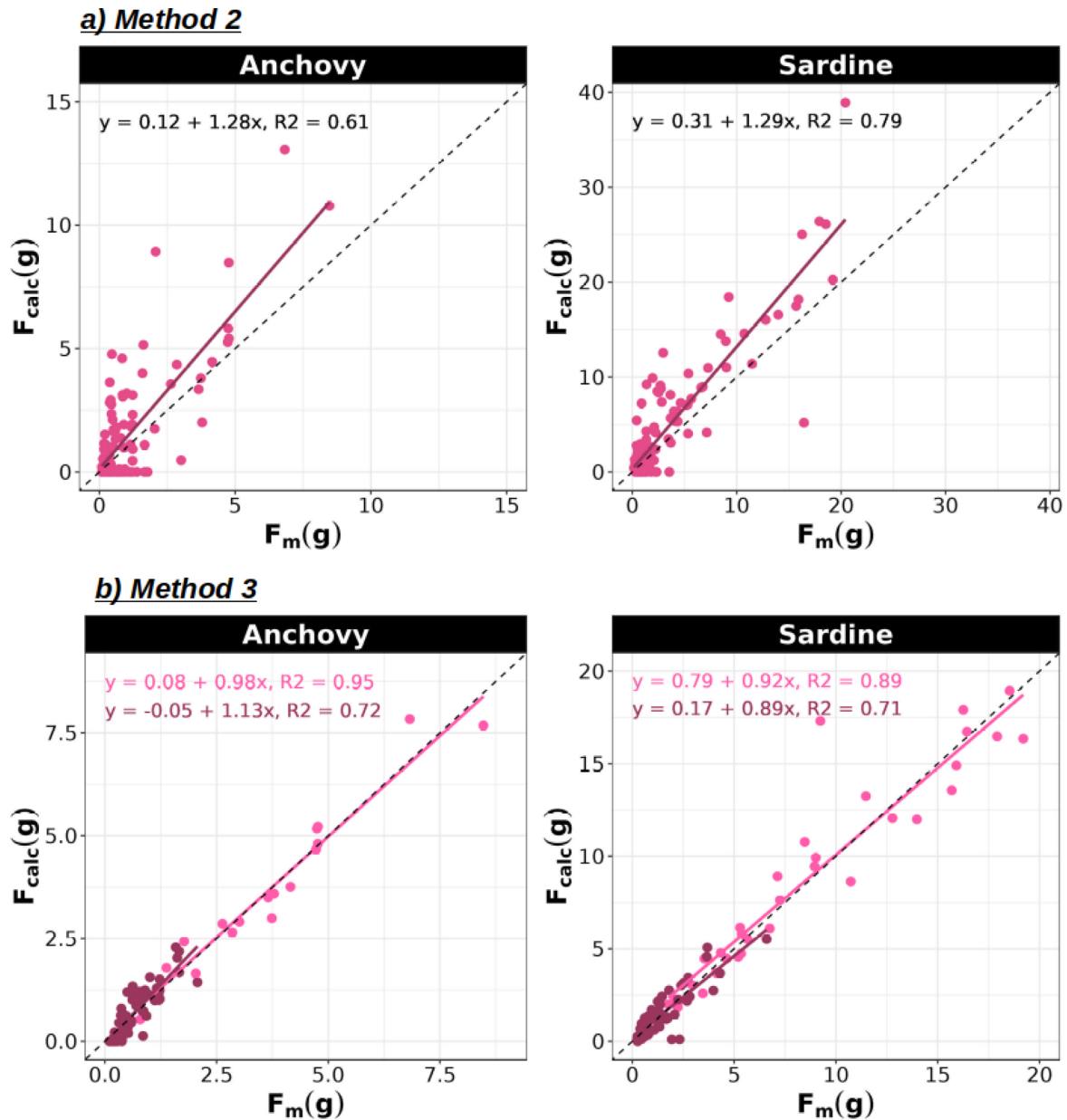


Fig. 5. Measured lipid mass F_m (g) versus calculated lipid mass F_{calc} (g) obtained from equation (3) for anchovy (left) and sardine (right) and for method 2 (a) and 3 (b). For method 3, light and dark pink dots represent fish in intermediate and strong condition states, respectively. The solid line represents the linear regression line and the dotted line corresponds to the 1:1 equation.

showed poor quality in the energy density estimations for anchovy but slightly more accurate for sardine (Tab. 2). Water content-based methods, (methods 3 and 4) distinguishing fish condition states, provided energy density estimations that fitted well with measured values for anchovy and sardine (Tab. 2) with similar R^2 and nRMSE values for both methods. Differentiating condition states for methods 3 and 4 improved considerably the energy density estimation, especially for individuals in poor condition state (Fig. A3). Total energy was calculated using equation (6) for the four methods (Fig. A4). Differences between methods were smaller for total energy than for energy density, with morphometry-based methods showing R^2 above 0.77 and water content-based methods above 0.99.

4 Discussion

Using a unique dataset of energy density and proximate composition measured on a large number of anchovy and sardine sampled across different seasons and regions, we compared four indirect methods to identify the most appropriate in estimating the energy density and total energy, considering both accuracy and practicality. The four methods evaluated included method 1 based on the relative condition index, method 2 using length and weight as measured input, together with the estimated proximate composition from length, method 3 incorporating water content and weight as measured inputs, and estimated proximate composition from

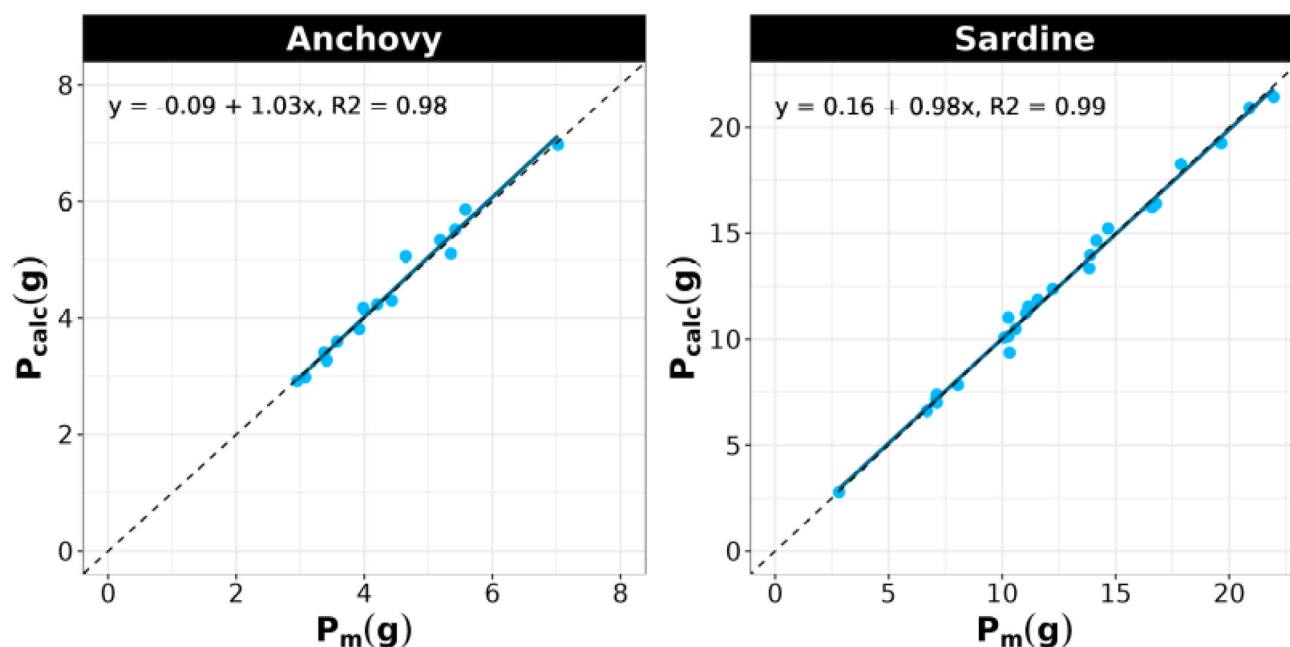
Method 3

Fig. 6. Measured protein mass P_m (g) versus calculated protein mass P_{calc} (g) obtained from equation (5) for anchovy and sardine in poor condition state (method 3). The solid line represents the linear regression line and the dotted line corresponds to the 1:1 equation.

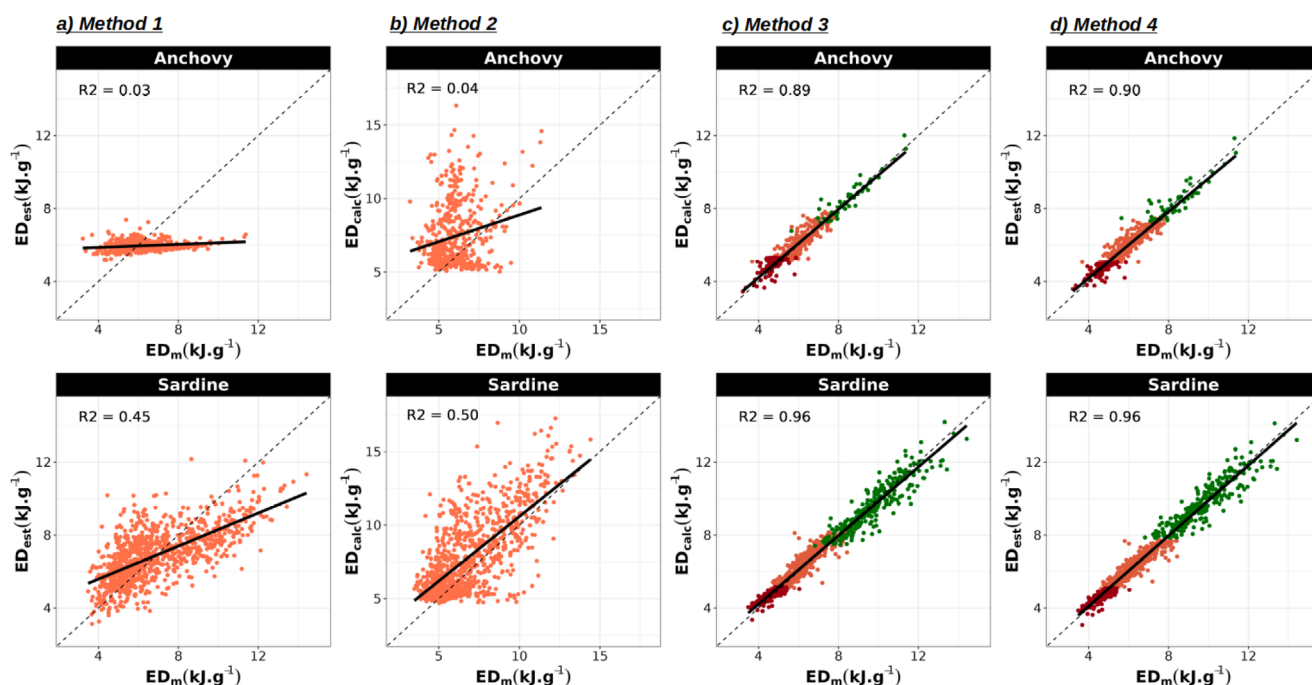


Fig. 7. Measured energy density ED_m (kJ.g^{-1} WW) versus estimated/calculated energy density ED_{est}/ED_{calc} (kJ.g^{-1} WW) for anchovy and sardine obtained with four different methods. For methods 3 and 4, energy density calculations /estimations were conducted separately for poor (red dots), intermediate (orange dots) and good (green dots) condition states. The solid line represents the linear regression line and the dotted line corresponds to the 1:1 equation.

water mass, and method 4 using only water content. Taking into account fish condition states identified by Favreau et al. (2025) improved energy density estimation for methods 3 and 4. The study's main outcomes are : (i) morphometry-based

methods provide weak estimates of energy density; (ii) only protein and ash content can be accurately estimated from fish length while lipid content cannot, as previously demonstrated for water mass in Favreau et al. (2025) ; (iii) using proximate

Table 2. Summary of the goodness of fit of the 4 methods to estimate fish energy density. The coefficient of determination (R^2) measures the proportion of variance in the response variable that is explained by the explanatory variable with values between 0 and 1 and the higher the values the better is the fit of the model. The normalized root mean square error (nRMSE) quantifies the average magnitude of the estimation error with lower values indicating more accurate estimations. The slope of the regression allows us to assess potential biases across the range of values: a slope lower than 1 indicates that large values are underestimated and small values are overestimated, while a slope greater than 1 indicates the opposite.

	Anchovy			Sardine		
	R^2	nRMSE	Slope	R^2	nRMSE	Slope
Method 1	0.03	0.206	0.04	0.45	0.228	0.45
Method 2	0.04	0.465	0.36	0.50	0.303	0.88
Method 3	0.89	0.062	0.92	0.96	0.062	0.96
Method 4	0.90	0.062	0.91	0.96	0.058	0.96

composition as an intermediate step does not improve the accuracy of energy indices estimates; and (iv) water content is still the most reliable indicator of fish energy.

4.1 Morphometry is inaccurate to estimate energy density

Method based on the relative condition index (method 1) showed limitations to estimate energy density as previously reported (Albo-Puigserver et al., 2020; Brosset et al., 2015; Ciancio et al., 2020; Campanini et al., 2021). This aligns with the long-standing debate on the usefulness of morphometric indices for estimating body condition (Jakob et al., 1996; Kotiaho, 1999; Labocha et al., 2014; Peig & Green, 2009; Stevenson & Woods, 2006). Morphometric indices assume that changes in an organism's body mass or volume primarily reflect variations in lipid content. However, protein content can also fluctuate, especially for fish in poor condition, and morphometric indices cannot distinguish whether changes in body mass are due to lipid or protein. Additionally, since lipids, despite being energy-dense, are present in smaller quantities compared to components like protein or water, significant changes in energy content may not be accurately captured by morphometric indices. It is illustrated in Figure A2 where the relationship between ED and the relative condition index depends of the condition state and thus the relative contribution of protein and lipid to energy (Favreau et al., 2025). The relationship is weak for fish in weak and intermediate condition states (low lipid content) and better for fish in good condition state (high lipid content). Moreover, factors such as gut content, reproductive status, or parasite load can influence body weight without reflecting changes in energy reserves (Wilder et al., 2016), further complicating the estimation of energy density. Reproduction, for example, significantly affects fish weight as gonads can occupy up to two-thirds of the abdominal cavity and 10% of the fish's weight (Nunes et al., 2011). Since gonads are less energy-dense (Huang and Zhu, 2023) than fat, they increase the fish's weight without a corresponding increase in energy density, affecting the reliability of these indices (Brosset et al., 2015; Campanini et al., 2021). However, this does not appear to be the case in our study, at least for sardine (Fig. A2). Attempts to reduce this bias, like using gutted weight (Albo-Puigserver et al., 2020), yielded only minimal improvements. Overall, morphometric

indices are more effective at tracking changes in fish “shape” than at estimating energy content, and their use in energy density estimation remains problematic unless validated by additional data on body composition (McPherson et al., 2011; Peig & Green, 2009).

Morphometry-based method incorporating proximate composition estimation (method 2) confirmed the difficulty to estimate energy density from morphometry (Campanini et al., 2021; Sardenne et al., 2016) despite this additional step. The reasons for poor energy density estimation may stem from inaccuracies in water content estimation from fish length. Despite a strong relationship between fish length and water mass ($R^2 > 0.95$), the dominance of water (60–80%) over lipids (1–20%) means that even small inaccuracies in estimating water mass can significantly distort lipid estimates. This is especially critical since our method estimated lipid content by subtracting the sum of water and other components from the fish's total weight. Since lipids are a key driver of energy density, errors in estimating their mass can lead to poor energy density estimations.

While morphometry-based methods failed to provide accurate estimates of energy density, they were relatively effective in estimating total energy (kJ), likely because total energy is largely driven by fish size rather than proximate composition. However, variability is still observed, especially for Methods 1 and 2. For Method 1, this likely reflects underestimation of total energy in larger fish, which tend to have higher energy density. For Method 2, variability may arise from overestimations in lipid mass, leading to overestimated energy content when lipid levels are high.

4.2 Water content is the best indicator of energy indices

Water content-based methods (methods 3 and 4), provided highly accurate estimates of energy density, confirming that the inaccuracies observed in method 2 were due to errors in water mass estimation. These findings also confirmed that water content is a reliable proxy for energy density, consistent with previous studies (Dubreuil and Petitgas, 2009; Hartman and Brandt, 1995; Schloesser and Fabrizio, 2015; Tirelli et al., 2006). Moreover, incorporating fish condition states (Favreau et al., 2025) further improved the precision of energy density estimates in both methods, especially for fish in poor condition

state. This adjustment allowed us to account for poor condition state fish in method 3, which are often excluded from studies due to their high water content distorting proximate composition relationships, particularly due to protein mobilization (Breck, 2014). For method 4, explicitly considering condition states enhanced the accuracy of energy density estimations for fish in both poor and good conditions by addressing the non-linear relationship between water content and energy density, driven by the varying contributions of lipids and proteins depending on the fish's condition (Favreau et al., 2025).

Similarly to morphometry-based methods, estimating proximate components did not improve energy density estimation for water content-based methods (methods 3 vs. method 4). While using both water content and proximate components to estimate energy density has been explored in previous research (Breck, 2014; Groves, 1970), our findings suggest that estimating proximate composition from length or water mass data does not significantly enhance the accuracy of energy density estimations (Schloesser and Fabrizio, 2015). However, proximate composition data remain valuable for defining the condition states of the fish species (Favreau et al., 2025). Once these condition states are defined, they can be reliably identified using water content alone. Therefore, when the objective is solely to estimate energy density, using the direct relationship with water content (method 4) offers a simpler and often more robust alternative (Dubreuil and Petitgas, 2009; Hartman and Brandt, 1995; James et al., 2012; Tirelli et al., 2006).

Both water-based methods for estimating total energy closely match the measured values for both species ($R^2 > 0.99$), a promising result for trophic studies as it allows accurate estimation of the actual energy a predator ingests from a given prey based on its water content and weight.

Given the critical role of water content as a primary indicator of energy density, it is crucial to develop efficient and standardized measurement methods. Since measuring water content onboard vessels is often impractical, samples are typically frozen for later analysis. However, freezing can alter fish length and weight, especially for smallest fishes (Crane et al., 2016) as well as water content estimates due to thawing. Therefore, it is important to test the best storage and transportation methods to ensure optimal preservation of samples, as these methods may vary depending on the characteristics of the fish (Baltasar et al., 2021; Crane et al., 2016; Wessels et al., 2010).

4.3 Differences between anchovy and sardine

Our results showed that energy estimation was generally more accurate for sardine than for anchovy, with the largest discrepancies observed in morphometry-based methods, and to a lesser extent, in water content-based methods. Morphometry-based methods failed to precisely estimate energy density for anchovy ($R^2 < 0.05$) whereas the estimation was better for sardine ($R^2 > 0.45$). These differences likely arose from species-specific morphometric and physiological traits: anchovy is smaller, shows less variation in energy density (due to limited lipid reserves), and have higher water content, making it difficult to assess lipid fluctuations based on body shape alone. Additionally, the high water content and low lipid

reserves of anchovy make it particularly challenging to estimate lipid and energy content from proximate components, as small errors in water mass estimation can significantly impact lipid calculations.

In Figure A2, the relationship between ED and the relative condition index varied with reproductive status for anchovy but not for sardine. However, this observation for anchovy is not due to the reproductive status but to the season effect (Fig. A2), as sardine can reproduce in autumn and spring and does not show any difference in the relationship between the relative condition index and ED. Although some studies have demonstrated an effect of reproduction on this relationship in the Mediterranean sea (Brosset et al., 2015; Campanini et al., 2021), we did not observe this effect in the Bay of Biscay. Studies in the Mediterranean Sea, such as Albo-Puigserver et al. (2020), found no difference in the relationship between ED and the relative condition index for sardine and anchovy. We attribute this discrepancy to the narrower range of fish size and energy density in Mediterranean individuals compared to our Bay of Biscay study, which could mask differences between species in the ED estimation from the relative condition index. Applying our methodology to other SPF species with varying lengths and fat content would help clarify the extent to which body size or energy reserves influence the accuracy of energy density estimates.

4.4 Is the fatmeter a solution to estimate water content?

Since drying the fish is a necessary step for bomb calorimetry, directly measuring water content using traditional methods such as oven drying or freeze-drying is inherently faster and still provides reliable estimates (Schloesser and Fabrizio, 2015). However it is not feasible for on-board processing. Non-invasive instruments like the fatmeter (Distell Fish Fatmeter; Kent, 1990) have gained popularity for assessing fish condition by estimating fat content in a few seconds (Brosset et al., 2015; Davidson and Marshall, 2010; McPherson et al., 2011). The fatmeter measures the water content using a microstrip sensor and convert it to lipid content from standard relationships. However, the accuracy of fatmeter measurements varies significantly across species and studies. For example, the goodness of fit between fatmeter measurements and lipid content can range from $R^2 = 0.02$ for striped bass (Schloesser and Fabrizio, 2015) to $R^2 = 0.72$ for American shad (Bayse et al., 2018). Results can also strongly differ even for a single species, e.g. sardine, where R^2 values varied from 0.48 (Brosset et al., 2015) to 0.81 (Campanini et al., 2020). One of the main reasons for the large variability in fatmeter-based estimations is that the device only measures water content at the surface of the fish, primarily within muscle tissue, and cannot account for variations in water content throughout the entire body. While many studies focus on specific tissues, such as muscle, to assess fish body condition or lipid content (Brosset et al., 2023), we argue that evaluating such metrics at the whole-fish level is more appropriate, when estimating energy density (ED). This is particularly important for SPF, which are known to store mesenteric fat that cannot be detected in muscle tissue alone, explaining the fatmeter bias (McPherson et al., 2011). We acknowledge, however, that

tissue-specific analyses may be more relevant for other research objectives or for larger species where whole-fish analysis is not feasible. Although the fatmeter may provide better energy estimates than morphometric indices, it is still less reliable than direct water content measurements. Further research into the relationship between fatmeter-derived water content and energy density would help improve its accuracy.

5 Conclusion

Our findings confirm that morphometric-based methods are suboptimal proxies for estimating energy density and proximate composition, compared to water content-based methods. Morphometry-based methods failed to reliably estimate energy density because they do not adequately capture variations in lipid and protein levels, which are key contributors to fish energy. Water content was found to be the most reliable indicator of energy density, making methods based on water content more accurate and practical. Although morphometric body condition indices are non-invasive, this benefit is less relevant in fisheries surveys, where fish are generally dead when measurements are made. Conducting routine water content measurements during fisheries surveys would provide reliable and operational estimates of fish energy density. This method is efficient and cost-effective. It would allow for the collection of a larger dataset and the establishment of long-term time series, facilitating annual monitoring. While onboard water content measurements may not be feasible, collecting samples for later laboratory analysis using an oven or a freeze-dryer can be a practical alternative. As a result, we tested the implementation of water content monitoring on 2024 and 2025 PELGAS surveys for sardine and anchovy. Approximately 200 individual per species, covering a range of sizes and different areas were collected at sea. Fish were frozen immediately onboard and water content was measured in the laboratory as soon as possible after returning to shore, to minimize potential bias from prolonged storage. Provided that energy density has been previously measured to establish robust regressions, measuring water content can offer precise information on the condition of individual fish. This approach is particularly relevant in the context of global change, which can affect the condition of individuals, populations, and ecosystems.

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Conflicts of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability statement

Data are available online on *SEANOE* in Huret et al., 2024.

Author contribution statement

A.F. and M.H. designed the methodology. A.F. ran the analysis. M.H. raised fundings. A.F. wrote the original manuscript. A.F, M.H, J.S, and M.D. contributed to revising and editing the manuscript.

Supplementary material

Figure A1: Length-weight relationships of sardine and anchovy in (a) the log-scale and in (b) the natural scale.

Figure A2: Relationships between energy density and the relative condition index (Le Cren index) for anchovy (left) and sardine (right) with regard to reproduction, season and condition state.

Figure A3: Relationships between energy density and water content (%) for anchovy (left) and sardine (right) for poor (red dots), intermediate (orange dots) and good (green dots) condition states.

Figure A4: Measured total energy E_{totm} (kJ) versus calculated total energy $E_{totcalc}$ (kJ) for anchovy and sardine. Total energy was calculated from energy density (kJ.g⁻¹ WW) and fish mass (g) using equation 6. For methods 3 and 4, colors indicate condition states: poor (red), intermediate (orange), and good (green). The solid line represents the linear regression line and the dotted line corresponds to the 1:1 equation.

The Supplementary Material is available at <https://www.alr-journal.org/10.1051/alr/2025018/olm>.

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