Journal of FISH BIOLOGY
Published for the Fisheries Society of the British Isles

Journal of Fish Biology (2013) **82**, 2147–2152
doi:10.1111/jfb.12142, available online at wileyonlinelibrary.com

Variability in energy density of forage fishes from the Bay of Biscay (north-east Atlantic Ocean): reliability of functional grouping based on prey quality

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(Received 28 September 2012, Accepted 29 March 2013)

Energy densities of 670 fishes belonging to nine species were measured to evaluate intraspecific variability. Functional groups based on energy density appeared to be sufficiently robust to individual variability to provide a classification of forage fish quality applicable in a variety of ecological fields including ecosystem modelling.

Key words: calorific value; ecological groups; functional ecology; prey profitability.

Rather than biomass alone, prey quality is a critical determinant of ecosystem functioning (Spitz *et al*., 2012). Variation in forage species quality can have important consequences for reproductive success and population dynamics of predators. Collapses or declines of high energy density (ED) prey have already been shown to affect several marine mammal and seabird populations (Österblom *et al*., 2008). A decrease in ED can occur at the species level by a reduction in individual fat storage due to changes in oceanographic and foraging conditions, or at the ecosystem level by shifts from high quality species to low quality species caused by climatic or human pressures. Therefore, knowledge and monitoring of forage species quality are crucial aspects in ecosystem modelling and management (Trites & Donnelly, 2003; Van De Putte *et al*., 2006; Spitz *et al*., 2010*a*).

The Bay of Biscay on the continental shelf of the north-east Atlantic Ocean is exploited by numerous fisheries and supports a large diversity of top predators (Kiszka *et al*., 2007; Certain *et al*., 2008; Lorance *et al*., 2009). The importance of forage fish quality appeared to be critical for several marine top predators living in this area. For instance, common dolphins *Delphinus delphis* select high quality prey to fulfil their high energy requirements (Meynier *et al*., 2008; Spitz *et al*.,

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2010*b*). Avian breeding success and chick survival also suffer from an increase in low-quality prey in the diet (Wanless *et al*., 2005; Harris *et al*., 2007). At a large taxonomic scale, a first study provided baseline data of ED for *c*. 80 forage species from the Bay of Biscay and the adjacent north-east Atlantic Ocean (Spitz *et al*., 2010*a*). This study proposed three functional groups based on ED: low ($\text{ED} < 4$ kJ g^{-1}), moderate ($4 < \text{ED} < 6$ kJ g^{-1}) and high quality species ($\text{ED} > 6$ kJ g^{-1}). Typically, among the main forage fish species of the continental shelf, the families Clupeidae, Scombridae and Carangidae were high quality fishes, whereas the families Gadidae and Ammodytidae exhibited moderate quality and the Merluccidae were lower quality. Functional groups of species allow the development of generalized approaches to understand ecosystem functioning (Blaum *et al*., 2011). Functional groups defined on the basis of prey quality to predators (quality groups, QGs) could clarify some prey–predator relationships, improve the relevance of ecosystem models and contribute to predicting consequences of environmental changes. ED can vary among seasons or among years, as a result of reproductive cycles and variations in food availability and composition (Anthony *et al*., 2000; Van De Putte *et al*., 2006). Hence, the established hierarchy and the use of QGs in the Bay of Biscay based on a temporally limited sample set could be weakened by natural intraspecific variability. If interspecific variability was lower than intraspecific variability, the use of functional groups based on ED mean values would become unreliable.

The aim of this study was to explore the range of ED variability in major forage fishes from the Bay of Biscay to test whether temporal changes can undermine the reliability of species-specific ED values as a criterion for assigning species to functional groups of prey quality.

Nine of the main forage fish species for top predators in the Bay of Biscay (Spitz *et al*., 2006*a*, 2006*b*, 2013; Meynier *et al*., 2008) were collected from 2002 to 2010 in the Bay of Biscay during annual research surveys carried out from the Ifremer R/V *Thalassa* in spring and in autumn. A total of 670 specimens were sampled (Table I) including hake *Merluccius merluccius* (L. 1758), small pout *Trisopterus minutus* (Lacépède 1800), blue whiting *Micromesistius poutassou* (Risso 1826), scad *Trachurus trachurus* (L. 1758), sandeels (Ammodytidae), sardine *Sardina pilchardus* (Walbaum 1792), sprat *Sprattus sprattus* (L. 1758), anchovy *Engraulis encrasicolus* (L. 1758) and mackerel *Scomber scombrus* L. 1758. All fish species were sampled during the two seasons and during at least four different years. As far as possible, size ranges were selected to match published prey-size distributions for top predators (Spitz *et al*., 2006*a*, 2006*b*, 2013; Meynier *et al*., 2008) and also to incorporate ontogenetic variability to an extent consistent with known prey-size distributions. Samples were stored frozen at -20° C on board until further analyses. Then, whole specimens were freeze dried and reduced to powder. Total water content was determined by weighing the samples on an electronic balance before and after freeze drying. ED values were estimated on dry samples by using adiabatic bomb-calorimetry in which gross energy was determined by measuring heat of combustion. Gross energy values were converted to wet-mass values by taking water content into account. Thus, ED values are expressed in kJ g^{-1} of total wet body mass. ED values are means of duplicate determinations (s.d. between two assays was $<2\%$).

The range of ED variability differed among forage fish species of the Bay of Biscay (Fig. 1). *Merluccius merluccius* showed the lowest variability with ED values

TABLE I. Mean ± S.D. energy density (ED) and rate of assignment of individuals to quality groups (QGs) for each of the nine fish species: low ($ED < 4$ kJ g^{-1}), moderate ($4 < ED < 6$ kJ g^{-1}) and high quality species ($ED > 6$ kJ g^{-1})

	L_s (mm)		ED (kJ g^{-1})			Assignment of individuals to QGs (%)		
Species	*n*	Range	Annual	Spring	Autumn	Low	Moderate	High
Merluccius merluccius	31	190–325	4·0 ± 0·4 [3·4–4·5]	4·1 ± 0·2 [3·9–4·3]	4·0 ± 0·4 [3·4–4·5]	57·1	42·9	0·0
Micromesistius poutassou	74	120–235	4·9 ± 0·8 [3·8–6·2]	4·6 ± 0·9 [3·8–6·0]	5·0 ± 0·7 [4·0–6·2]	5·3	84·2	10·5
Trisopterus minutus	59	125–210	4·9 ± 0·6 [3·8–5·8]	4·2 ± 0·3 [3·8–4·5]	5·1 ± 0·6 [4·2–5·8]	6·7	93·3	0·0
Ammodytidae	30	145–255	5·7 ± 0·6 [4·8–6·5]	5·7 ± 1·0 [5·0–6·5]	5·6 ± 0·6 [4·8–6·2]	0·0	66·7	33·3
Engraulis encrasicolus	139	100–155	5·8 ± 0·9 [4·3–8·3]	5·5 ± 0·5 [4·5–7·1]	6·4 ± 1·2 [4·3–8·3]	0·0	70·6	29·4
Trachurus trachurus	63	140–195	7·0 ± 1·3 [5·6–9·7]	7·9 ± 1·5 [6·4–9·7]	6·5 ± 1·0 [5·6–8·2]	0·0	28·6	71·4
Sprattus sprattus	78	75–105	7·2 ± 1·3 [5·2–9·4]	7·2 ± 1·3 [5·3–8·6]	7·2 ± 1·5 [5·2–9·4]	0·0	18·2	81·8
Scomber scombrus	49	175–300	7·5 ± 1·5 [5·1–9·7]	5·9 ± 0·8 [5·1–7·3]	8·3 ± 1·0 [6·7–9·7]	0·0	29·4	70·6
Sardina pilchardus	147	120–215	7·5 ± 2·0 [4·5–12·1]	5·8 ± 0·8 [4·5–7·5]	8·8 ± 1·6 [5·7–12·1]	0·0	28·9	71·1

n, number of individuals; L_S, standard length.

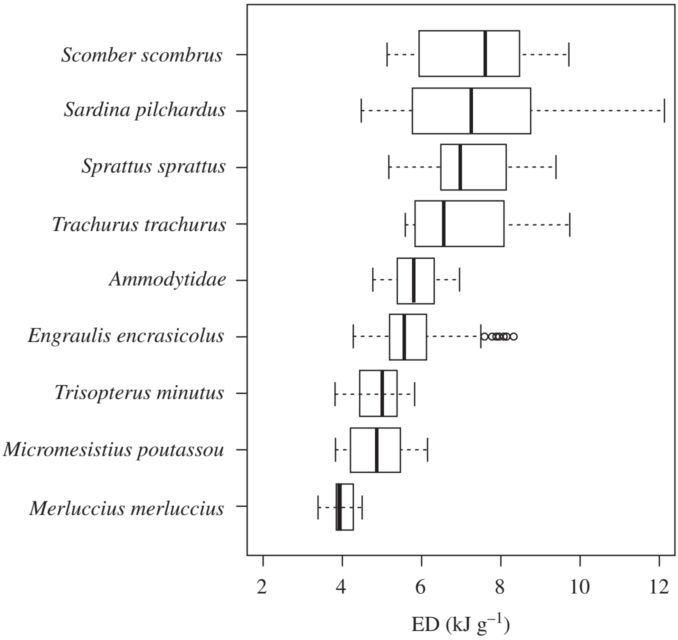

FIG. 1. Boxplot comparing energy density (ED) of nine major forage fish in the Bay of Biscay. The bold solid line within each box is the median, the bottom and top of each box represent the 25th and 75th percentiles, the whiskers represent the 10th and 90th percentiles and values outside this range are plotted as individual outliers.

from 3·4 to 4·5 kJ g^{-1} (S.D. $<$ 0·4 kJ g^{-1}). In contrast, *S. pilchardus* exhibited the highest variability, with ED values from 4·5 to 12·1 kJ g^{-1} (S.D. $>$ 2 kJg^{-1}; Table I). Within forage fishes, variability in specific ED increased with mean ED [Fig. 2(a); $r^2 = 0{\cdot}865$]; the higher a fish species' mean ED, the higher its variability. Irrespective of years and seasons, 72·6% of individuals in this study were accurately assigned to the QGs previously defined. The rate of accurate assignment varied from 57·1 to 93·3% according to species (Table I). No correlation existed between this rate and the specific ED variability [Fig. 2(b); $r^2 < 0{\cdot}001$], but as expected, this rate appeared lower for species with ED mean values closer to group limits (4 and 6 kJ g^{-1}). Thus, the present work shows that QGs are relatively robust to intraspecific ED variability. Indeed, a great majority of individual EDs matched the expected QGs, and in most cases, intraspecific ED variation induced limited overlap between two QGs.

This study did not investigate factors influencing intraspecific ED variations. Interannual differences are probably related to environmental conditions that influence feeding behaviour and availability and quality of zooplankton prey (Anthony *et al.*, 2000). At seasonal scales, ED differences generally reflect variations of stored energy reserves for reproduction (Anthony *et al.*, 2000; Van De Putte *et al.*, 2006; Dubreuil & Petitgas, 2009). Seasonal variations determine larger ED variations than interannual variations, particularly for fatty fishes (*e.g. S. pilchardus, S. scombrus* and *T. trachurus*). These high energy fishes exhibited an important increase in their lipid reserves before spawning. In this case, the broad ED variation did not affect the

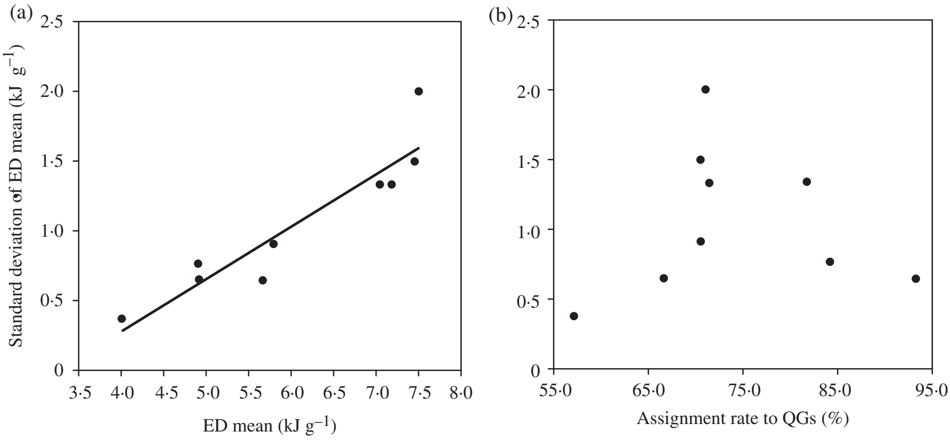

FIG. 2. Relationships between S.D. of energy density (ED) mean and (a) ED mean or (b) assignment rate to quality groups (QGs) for each of the nine fish species. (a) The curve was fitted by $y = 0{\cdot}374x - 1{\cdot}2125$ ($r^2 = 0{\cdot}865$).

coherence of QGs because these fish species already belonged to the highest-quality group. Nevertheless, seasonal ED changes could have important implications for piscivorous predators in temporally modifying energy intake per unit of food mass eaten. Consequently, it is recommended that assigning a new species to QGs should be based on individual ED measurements from at least two years and two seasons.

In conclusion, functional groups based on ED appeared to be sufficiently robust for classifying forage species quality. Hence, the use of prey quality groups can lead to fundamental insights into functional ecology or ecosystem modelling, and also contribute to conservation or management strategies. Nevertheless, such approaches do not replace in-depth investigations of factors influencing intraspecific variation in ED that have important implications at a smaller scale.

The work was part of a larger research programme on the forage species–top predators' interactions in the Bay of Biscay and adjacent Atlantic Ocean areas. We are particularly grateful to J. Massé, P. Petitgas, J. C. Mahé, R. Bellail, J. C. Poulard, J. P. Leaute (Ifremer) and the staff of the R/V *Thalassa* for their help during EVHOE and PELGAS scientific cruises. This research has been supported by the European projects REPRODUCE (ERAC-CT-2006-025989, FP7) and FACTS (no. 244966, FP7).

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