Short Communication

Proximate composition and energy content of forage species from the Bay of Biscay: high- or low-quality food?

Jérôme Spitz, Emeline Mourocq, Valérie Schoen, and Vincent Ridoux

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Collapses of high-energy dense concentrations of prey species induce negative effects on populations of top predators. Knowledge of prey quality appears to be crucial in ecosystem modelling and management. The aim here was to provide baseline data of forage species quality in the Bay of Biscay. Proximate composition (water, ash, protein, and lipid) and energy content have been determined to assess the quality of 78 species, including jellyfish, crustaceans, cephalopods, cartilaginous fish, and bony fish. Results show broad variations between species, with energy densities ranging from 2 to 10 kJ g^{-1}. Lipids are the most structuring component and largely determined prey quality, and prey species are not necessarily interchangeable for the fulfilment of a predator's energy and food requirements. In ecosystem models, therefore, multispecies compartments of forage organisms would ideally be constituted using prey species of equivalent quality and hence of equivalent benefit to top predators.

Keywords: ecosystem model, energy content, NE Atlantic, prey quality, proximate composition.

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J. Spitz and V. Ridoux: Littoral Environnement et Sociétés, UMR 6250, Université de La Rochelle/ CNRS, 2 rue Olympe de Gouges, 17032 La Rochelle cedex, France. J. Spitz: Parc zoologique de La Flèche, Le Tertre Rouge, 72200 La Flèche, France. E. Mourocq, V. Schoen,, and V. Ridoux: Centre de Recherche sur les Mammifères Marins, Université de La Rochelle, 17071 La Rochelle, France. Correspondence to J. Spitz: tel: +33 5 46507658; fax: +33 5 46449910; e-mail: jspitz@univ-lr.fr.

Introduction

In oceans subjected to climatic pressures and human impacts such as global warming or overfishing, the distribution and abundance of some marine resources have been and will be increasingly modified (Dulvy *et al.*, 2008; Cheung *et al.*, 2009). Subsequent shifts in prey availability could affect the fitness of predator species. Indeed, even if the overall biomass and biodiversity remain unchanged, predator fulfilments of nutritional and energy requirements could be jeopardized by a decrease in prey quality. Collapses of fat and high-energy dense concentrations of prey species coupled with an increase in lower-quality prey availability induce negative effects on top predator populations around the world (Österblom *et al.*, 2008). For example, the decline in Steller sea lions (*Eumetopias jubatus*) in Alaska was tentatively linked to a shift from high-energy density prey to low-fat fish such as walleye pollock (*Theragra chalcogramma*; Trites and Donnelly, 2003). Therefore, in addition to prey abundance, the knowledge of prey quality appears to be crucial in ecosystem modelling and management.

Ecosystems in the Bay of Biscay and adjacent northeast Atlantic Ocean are exploited by numerous fisheries and support a large diversity of top predators. The importance of fat fish for some cetaceans in this area was recently suggested by the description of their diet (Spitz *et al.*, 2006; Pusineri *et al.*, 2007). The most striking case was that of the common dolphin (*Delphinus delphis*), which maintains a large proportion of fat fish in its diet despite extensive variations in the main prey species across seasons (Meynier *et al.*, 2008). Some of these prey species, such as anchovy or herring, are commercially important and show very low levels of spawning-stock biomass (ICES, 2009a, b). At the same time, an increase in potentially low-quality prey such as snake pipefish (*Entelurus aequoreus*) was observed (Harris *et al.*, 2007). If these changes in the availability of forage species induce a reduction in food quality, i.e. a reduction in the number of calories per unit of prey biomass, the population dynamics of top predators could be affected dramatically.

Quality of food should therefore be considered in ecosystem modelling, rather than biomass alone. Indeed, considering variability in prey quality, one unit biomass of a given species is not necessarily equivalent to one unit biomass of another species sharing a similar trophic level but with a distinct body composition. As the output of such modelling strongly depends on the accuracy of foodweb structure taken into account by the model (Christensen and Walters, 2004), variation in prey quality should be examined within each box of the ecosystem.

The aim of the present study was to provide, at a large taxonomic scale, baseline data of lipid, protein, water, ash, and energy contents of forage species in the Bay of Biscay and adjacent northeast Atlantic Ocean to suggest functional groups based on prey quality for further use in ecosystem modelling.

Material and methods

Almost all forage species were collected from 2002 to 2008 in the Bay of Biscay during EVHOE (EValuation des ressources Halieutiques de l'Ouest Européen) research cruises carried out from Ifremer's RV "Thalassa" in autumn each year. Some additional materials, especially for coastal or rocky species, were specifically sampled during the same period. Species were identified following published guides (e.g. Whitehead *et al.*, 1986; Quéro *et al.*, 2003). Totals of 5472 specimens from 78 different species (1 jellyfish, 7 crustaceans, 8 cephalopods, 3 cartilaginous fish, and 59 bony fish) were sampled. As far as possible, the size range was selected to match published prey sizes for top predators in the Bay of Biscay (Spitz *et al.*, 2006; Pusineri *et al.*, 2007; Meynier *et al.*, 2008). All material was stored frozen at -20°C until further analysis.

Proximate composition (water, ash, protein, and lipid) and calorific content were determined to evaluate the quality of forage species. To reduce inter-individual variability, multiple individual samples were pooled for each species. Pools of whole specimens were freeze-dried and reduced to powder.

Following the Association of Official Analytical Chemists (AOAC, 1990), total water content was determined by weighing the samples on an electronic balance before and after freeze-drying and again after final drying in an oven at 105°C. Ash was determined by heating the sample in a furnace for $\sim$12 h at 550°C (AOAC, 1990). Total protein was determined by the measurement of total nitrogen concentrations following the Kjeldahl method (AOAC, 1990). To convert total nitrogen to total protein, a conversion factor of 6.25 was applied for all forage species (Chen *et al.*, 1988). Total lipid content was determined using Soxhlet equipment with an ether-ethyl solvent (Radin, 1981). Carbohydrate content was not measured because that component is generally low in marine forage species and its contribution to total energy content is close to zero (Anthony *et al.*, 2000; Eder and Lewis, 2005). Energy contents were estimated using adiabatic bomb-calorimetry in which gross energy was determined by measuring heat of combustion.

Ash, lipid, protein, and energy contents were originally measured on dry samples. They were converted to wet mass by taking water content into account. Therefore, ash, lipid and protein contents are expressed in percentage wet total body mass and energy content in kJ g^{-1} wet total body mass. All values provided are means of duplicate determination (deviation between two assays was $<$2%). Several species were analysed in different years ($n > 1$ in Table 1).

Results

The proximate composition of the 78 forage species analysed varied largely between species (Table 1). As expected, water represented the main component, with $\sim$75% of body mass (75.1 $\pm$ 6.2%; range 60.1–92.1%). Ash represented 1.6–14.4% and was low and relatively constant across most species (Figure 1d), highest values ($>$5%) being observed in brachyuran crustaceans (7.7–14.4%), snake pipefish (6.8%), and cuttlefish (*Sepia officinalis*; 5.5%). Protein represented the second most important component after water (17.3 $\pm$ 3.3%; range 2.1–23.7%). Most values ranged from 15 to 20% (Figure 1b). A few species yielded a relatively high protein content, e.g. the swimming crab (*Necora puber*; 22.8%), the teleosts *Scomberesox saurus* (22.9%) and *Liza ramada* (23.7%). In contrast, values of protein were lowest in jellyfish (*Aurelia aurita*; 2.1%), the mesopelagic teleosts *Serrivomer beanii* (8.4%) and *Xenodermichthys copei* (9.6%), and the shrimp *Palaemon longirostris* (11.5%). Lipids were highly variable, ranging from 0.3 to 12.2% (Figure 1c). Only 15% of forage species had lipid contents $>$6% of wet body mass, and the species with greatest lipid content were the pelagic teleosts *Scomber scombrus* (10.5%) and *Sardina pilchardus* (11.7%), and the epibenthic scorpaenid *Helicolenus dactylopterus* (12.2%).

Energy density of forage species ranged from 0.7 to 10.2 kJ g^{-1} (Figure 1e). Lipid contents explained most of the variation in energy content ($r^2 = 0.761$; Figure 2), residuals being explained mainly by protein variability ($r^2 = 0.652$; Figure 3). Three classes of prey quality can be designated, therefore, according to the values of energy density (Table 2): low-quality species ($<$4 kJ g^{-1}), including *S. beanii* (2.1 kJ g^{-1}), *X. copei* (2.2 kJ g^{-1}), and *P. longirostris* (3.4 kJ g^{-1}), moderate-quality species ($4 < \mathrm{ED} < 6$ kJ g^{-1}), encompassing the majority of the species considered here, and high-quality species ($>$6 kJ g^{-1}), including species such as *Notoscopelus kroyeri* (7.9 kJ g^{-1}), *S. pilchardus* (8.7 kJ g^{-1}), and *Pagellus acarne* (9.4 kJ g^{-1}).

Discussion

With 78 species analysed, the present study is the first to examine proximate composition and quality of forage species in the NE Atlantic across such a broad variety of taxa, including jellyfish, crustaceans, cephalopods, and cartilaginous and bony fish. Among fish species, all habitats were covered; benthic, demersal, neritic pelagic, and oceanic pelagic. The results showed broad variations in proximate composition and quality between species. Lipids were the most structuring component and were determined largely by prey quality. Therefore, with energy densities ranging from 2 to 10 kJ g^{-1}, the quality of forage species was heterogeneous, and we propose three classes of quality of species; low ($<$4 kJ g^{-1}), moderate ($4 < \mathrm{ED} < 6$ kJ g^{-1}), and high quality ($>$6 kJ g^{-1}). Across the taxa studied, some 20% were classified as low-quality species, 50% as species of moderate quality, and 30% as species of high quality. Only a few species had an energy value $>$8 kJ g^{-1}.

Within-species variations in proximate composition and energy content could not be investigated in full. Parameters such as year, season, maturity, and age could influence energy values (Anthony *et al.*, 2000; Van de Putte *et al.*, 2006). In this study, up to several hundred specimens per species were pooled (Table 1) to smooth intraspecific variability, and almost all specimens were sampled in the same season. Therefore, the hierarchy proposed was consistent with previous results worldwide, with some fat and high-energy density families such as clupeids or myctophids opposite to lean and low-to-moderate-energy density families, such as gadids or squids (Anthony *et al.*, 2000; Eder and Lewis, 2005). However, more samples are needed to document intraspecific variations in proximate composition and energy content, especially for fat species which could have notable seasonal variations (Dubreuil and Petitgas, 2009). Moreover, it must be acknowledged that forage species body composition and energy content are not the only variables required to describe prey profitability intrinsically. For example, prey swimming speed, dispersion, encounter rate, and non-energy-related nutritional aspects of the diet need to be taken into account for a full evaluation of the profitability of a given prey to a given predator.

Despite these reservations, it is clear that in the NE Atlantic, prey profitability for a predator assessed from energy densities can differ largely between species. All forage species, even when morphologically or taxonomically similar, cannot be considered as equivalent and interchangeable for the fulfilments of predator energy and food requirements. In the context of low-quality prey expansion

Table 1. Average proximate composition (water, protein, lipid, ash as % of wet total body mass), length (cm), and energy content (kJ g^{-1}) of 78 forage species taken from the NE Atlantic.

Group	Order	Family	Species	N	n	Length	Water	Proteins	Lipids	Ash	Energy
Jellyfish	Semaeostomeae	Ulmaridae	*Aurelia aurita*	30	1	[8–12]	92.1	2.1	0.3	4.2	0.7
Crustaceans	Eucaria	Euphausiidae	*Meganyctiphanes norvegica*	704	1	[2–3]	77.8	15.8	1.2	3.8	3.9
4.8 [3.4–6.9]*	Decapoda (macrurans)	Oplophoridae	*Acanthephyra purpurea*	480	1	[3–6]	88.4	16	4.3	4.5	5.3
	4.3 [3.4–5.3]	Palaemonidae	*Palaemon longirostris*	612	1	[1–2]	82.4	11.5	1.5	2.9	3.4
		Pasiphaeidae	*Pasiphaea sivado*	342	1	[4–9]	78.1	17.6	0.5	3.4	4.1
	Decapoda (brachyurans)	Grapsidae	*Pachygrapsus marmoratus*	25	1	[23–40]	60.1	19.9	1	14.4	5.8
	5.6 [4.2–6.9]	Portunidae	*Polybius henslowii*	37	1	[4–5]	72.4	14.1	1.4	8.8	4.2
		5.5 [4.2–6.9]	*Necora puber*	8	1	[4–7]	62.8	22.8	2	7.7	6.9
Cephalopods	Teuthoidea	Loliginidae	*Allotheutis* spp.	221	4	[3–8]	78.9 [78.1–80.8]	16.4 [14.5–16.7]	1.3 [0.8–1.8]	1.7 [1.6–2.0]	3.9 [3.6–4.2]
4.4 [3.8–4.8]	4.4 [3.9–4.8]	4.4 [3.9–4.8]	*Loligo forbesi*	4	1	[10–21]	76.5	17.9	2.2	2	4.6
			Loligo vulgaris	15	5	[12–25]	76.2 [75.4–77.0]	18.9 [18.1–19.6]	1.5 [0.7–2.2]	1.7 [1.6–1.9]	4.8 [4.4–5.3]
		Ommastrephidae	*Illex coindeti*	9	3	[14–17]	77.8 [77.0–79.2]	17.3 [15.2–18.7]	1.9 [1.5–2.2]	1.6 [1.5–1.8]	4.3 [4.1–4.4]
		4.4 [4.3–4.4]	*Todaropsis eblanae*	9	3	[12–15]	77.8 [77.7–78.0]	18 [16.0–19.4]	2.4 [2.3–2.6]	1.8 [1.7–1.9]	4.4 [4.3–4.5]
	Sepiolida	Sepiolidae	*Sepiola* spp.	77	1	[1–2]	77.4	16	2	2.6	4.8
	Sepioidea	Sepiidae	*Sepia officinalis*	10	2	[6–10]	75.8 [75.7–75.9]	15.8 [15.3–16.4]	1.2 [1.0–1.4]	5.5 [5.2–5.8]	3.8 [3.6–3.9]
	Octopoda	Octopodidae	*Eledone cirrhosa*	3	1	[10–11]	76	16.2	2.8	2.2	4.7
Cartilaginous	Carcharhiniformes	Scyliorhinidae	*Scyliorhinus canicula*	3	1	[48–51]	72.1	22.6	5.1	2.3	6.4
fish	Rajiformes	Rajidae	*Leucoraja naevus*	3	1	[40–51]	75.5	20.7	4.1	1.6	5.7
5.3 [3.9–6.4]	Chimaeriformes	Chimaeridae	*Chimaera monstrosa*	6	1	[9–10]	81.3	16.4	2.2	2	3.9
Bony fish	Anguilliformes	Congridae	*Conger conger*	3	1	[53–60]	72.8	18.8	5.2	1.7	6.9
5.7 [2.1–10.2]	4.5 [2.1–6.9]	Serrivomeridae	*Serrivomer beanii*	26	1	[21–65]	78.1	8.4	1.1	2.3	2.1
	Clupeiformes	Clupeidae	*Sprattus sprattus*	246	4	[7–13]	70.9 [69.1–75.4]	17.2 [16.4–18.2]	8.2 [3.4–11.2]	2.5 [2.3–2.7]	6.5 [4.8–7.3]
	7.8 [5.8–10.1]	8.5 [6.5–10.1]	*Sardina pilchardus*	15	3	[14–22]	65.3 [63.2–67.4]	17.8 [16.7–19.1]	11.7 [8.4–17.1]	2.4 [1.8–3.3]	8.7 [7.5–10.1]
			Clupea harengus	3	1	[20–20]	62.8	18.6	10.7	3.6	10.2
		Engraulidae	*Engraulis encrasicolus*	208	4	[9–13]	72.0 [69.0–76.0]	19.6 [18.2–20.3]	3.4 [1.7–5.2]	2.8 [1.9–3.2]	5.8 [4.9–6.7]
	Osmeriformes	Alepocephalidae	*Xenodermichtys copei*	173	1	[4–12]	87.5	9.6	0.4	2.4	2.2
	3.6 [2.6–6.1]	Argentinidae	*Argentina sphyraena*	22	2	[11–16]	72.2 [71.5–72.2]	17.8 [16.5–19.0]	5.7 [5.2–6.1]	2.5 [2.5–2.5]	6.1 [6.0–6.2]
		Platytroctidae	*Normichthys operosa*	53	1	[7–16]	77.2	11	0.8	2.5	2.6
	Stomiiformes	Sternoptychidae	*Argyropelecus olfersii*	138	1	[1–10]	69.2	14.8	1.3	5.3	3.5
	3.5 [2.8–4.2]	3.9 [3.5–4.2]	*Maurolicus muelleri*	201	1	[3–5]	76.3	13.5	5.2	3.7	4.2
		Stomiidae	*Stomias boa ferox*	28	1	[8–31]	88.4	11.5	1.2	3.1	2.8
	Aulopiformes	Paralepididae	*Arctozenus risso*	124	1	[9–20]	88.4	15.8	2.5	3.4	4.3
	Myctophiformes	Myctophidae	*Lampanyctus crocodilus*	63	1	[7–15]	74.7	16.1	1.6	2.9	4.1
	6.6 [4.1–8.6]	6.6 [4.1–8.6]	*Benthosema glaciale*	697	1	[2–6]	85.5	13.9	7.5	3.4	5.9
			Notoscopelus kroyeri	60	1	[3–13]	87.5	16.6	11.9	2.3	7.9
			Lobianchia gemellari	30	1	[7–9]	67.1	18.8	8.6	2.1	8.6
	Gadiformes	Macrouridae	*Coelorinchus coelorinchus*	5	1	[8–10]	77.6	16.2	2.6	3	5.1
	4.7 [3.7–5.5]	Gadidae	*Merlangius merlangus*	24	4	[17–22]	79.5 [79.3–79.7]	16.7 [16.6–16.9]	0.7 [0.3–1.0]	2.9 [2.3–3.5]	3.9 [3.8–3.9]
		4.5 [3.9–5.5]	*Pollachius pollachius*	2	1	[29–30]	79	17.2	0.7	2.8	4.2
			Micromesistius poutassou	40	4	[14–20]	77.9 [77.0–78.3]	17.4 [16.1–18.1]	1.5 [1.1–1.7]	3.1 [2.2–4.0]	4.4 [4.0–4.7]
			Trisopterus luscus	9	3	[22–26]	77.3 [76.9–78.2]	17.7 [16.8–19.2]	1.8 [1.2–2.3]	2.9 [1.7–4.2]	4.7 [4.6–5.0]
			Gadiculus argenteus	23	1	[8–11]	75.5	16.2	3.7	3.4	5
			Trisopterus minutus	21	3	[14–18]	73.8 [71.5–75.3]	18.8 [17.9–20.3]	2.8 [2.4–3.3]	3.5 [2.3–4.7]	5.1 [5.0–5.2]
			Gaidropsarus spp.	5	1	[14–23]	76.8	17.2	2.6	1.9	5.5

Continued

Table 1. *Continued*

Group	Order	Family	Species	*N*	*n*	Length	Water	Proteins	Lipids	Ash	Energy
		Phycidae	*Phycis blennoides*	3	1	[26–28]	77.5	17.4	2.5	2.7	5
		Merlucciidae	*Merluccius merluccius*	9	3	[22–29]	80.4 [79.5–81.2]	16 [15.1–16.9]	0.7 [0.3–1.1]	2.7 [2.2–3.2]	3.7 [3.4–3.9]
	Atheriniformes	Atherinidae	*Atherina presbyter*	129	3	[5–12]	67.8 [65.9–68.8]	19.8 [18.9–21.2]	7.3 [6.6–8.1]	3 [2.1–3.7]	7.3 [7.1–7.5]
	Beloniformes	Belonidae	*Belone belone*	3	1	[55–59]	74	20.1	2.9	2.7	6.2
	6.0 [5.8–6.2]	Scomberesocidae	*Scomberesox saurus*	5	1	[25–30]	71.6	22.9	2.1	2.4	5.8
	Beryciformes	Trachichthyidae	*Hoplostethus mediterraneus*	17	1	[4–7]	75.9	15.9	2.3	4.9	4.7
	Zeiformes	Caproidae	*Capros aper*	36	1	[6–7]	71.3	17.2	4.8	4.6	6.2
	Syngnathiformes	Syngnathinae	*Entelurus aequoreus*	128	1	[25–34]	73.5	14.7	1.9	6.8	4.7
	Scorpaeniformes	Sebastinae	*Helicolenus dactylopterus*	3	1	[15–17]	65.7	18.2	12.2	2.6	9.2
	7.5 [5.1–9.2]	Scorpaenidae	*Scorpaena loppei*	3	1	[91–98]	73.2	20.2	1.4	4.1	5.1
		Triglidae	*Chelidonichthys cuculus*	7	2	[17–20]	69.0 [66.9–71.1]	19.8 [18.9–20.6]	6.9 [5.5–8.2]	2.9 [2.3–3.5]	8.2 [7.8–8.5]
	Perciformes	Moronidae	*Dicentrarchus labrax*	3	1	[44–48]	84.1	20.2	4.5	2	6
	6.2 [4.8–9.4]	Carangidae	*Trachurus trachurus*	30	5	[14–30]	72.4 [71.1–74.0]	18.2 [17.3–19.0]	5 [3.6–6.2]	3.1 [2.4–4.5]	6 [5.6–6.5]
		Sparidae	*Spondyliosoma cantharus*	6	2	[17–23]	69.9 [68.5–71.3]	18.3 [18.0–18.6]	6.8 [5.0–8.7]	2.5 [2.2–2.8]	6.9 [6.4–7.4]
		8.1 [6.9–9.4]	*Boops boops*	9	1	[14–25]	67	19.8	5.8	2.3	8
			Pagellus acarne	4	1	[15–17]	65.1	19.7	10.9	2.4	9.4
		Mullidae	*Mullus surmuletus*	15	2	[11–14]	71.7 [71.4–71.9]	18.7 [18.2–19.1]	4.5 [4.1–4.9]	2.7 [2.5–2.9]	6.4 [6.3–6.4]
		Cepolidae	*Cepola macrophthalma*	6	1	[38–53]	80.2	14.2	1.1	4.1	3.9
		Mugilidae	*Liza ramada*	3	1	[33–42]	67.6	23.7	3.4	3.6	6.5
		Labridae	*Labrus bergylta*	2	1	[28–32]	75.8	20	1.6	1.9	5.4
		Ammodytidae	*Hyperoplus lanceolatus*	6	1	[30–37]	75.1	18.1	0.9	3.2	4.8
		5.3 [4.8–5.8]	*Ammodytes tobianus*	9	2	[27–31]	73.5 [73.5–73.6]	18.9 [18.9–18.9]	4.1 [3.8–4.4]	2 [1.9–2.1]	5.8 [5.7–5.8]
		Trachinidae	*Trachinus draco*	5	1	[18–23]	74.6	18.2	1.4	3.9	5.3
		Blenniidae	*Paralipophrys trigloides*	16	1	[7–12]	73.1	19.1	2	3.5	5.5
		Callionymidae	*Callionymus lyra*	5	1	[15–19]	75.4	17.1	2	3.6	5.2
		Gobiidae	*Lesueurigobius friesii*	143	1	[4–6]	72.4	16.5	4.1	4.8	5.6
		Scombridae	*Scomber scombrus*	12	4	[25–29]	67.3 [66.4–69.9]	17.5 [17.3–17.8]	10.5 [7.9–13.6]	2.1 [1.8–2.4]	7.9 [7.1–8.5]
	Pleuronectiformes	Scophthalmidae	*Lepidorhombus whiffiagonis*	3	1	[21–26]	73.9	18.1	3.1	2.3	6.1
	5.7 [5.0–6.5]	Bothidae	*Arnoglossus imperialis*	19	1	[8–14]	74	18.8	1.8	3.6	5.4
		Pleuronectidae	*Glyptocephalus cynoglossus*	2	1	[29–34]	76.6	17.4	3.4	2.1	5.6
		5.7 [5.6–5.8]	*Microstomus kitt*	2	1	[28–29]	73.9	19.8	2.8	2.2	5.8
			Pleuronectes platessa	2	1	[27–34]	74.3	17.9	3.1	3	5.8
		Soleidae	*Solea solea*	3	1	[28–31]	77.0	18.9	1.5	2.1	5
		5,8 [5–6.5]	*Dicologlossa cuneata*	7	1	[12–20]	69.2	21.9	3.7	3	6.5

N, number of individuals; *n*, number of analysed pool. Square brackets indicate the ranges of values. When several species are documented for a family, an order, or a group, mean and range of energy content are provided.

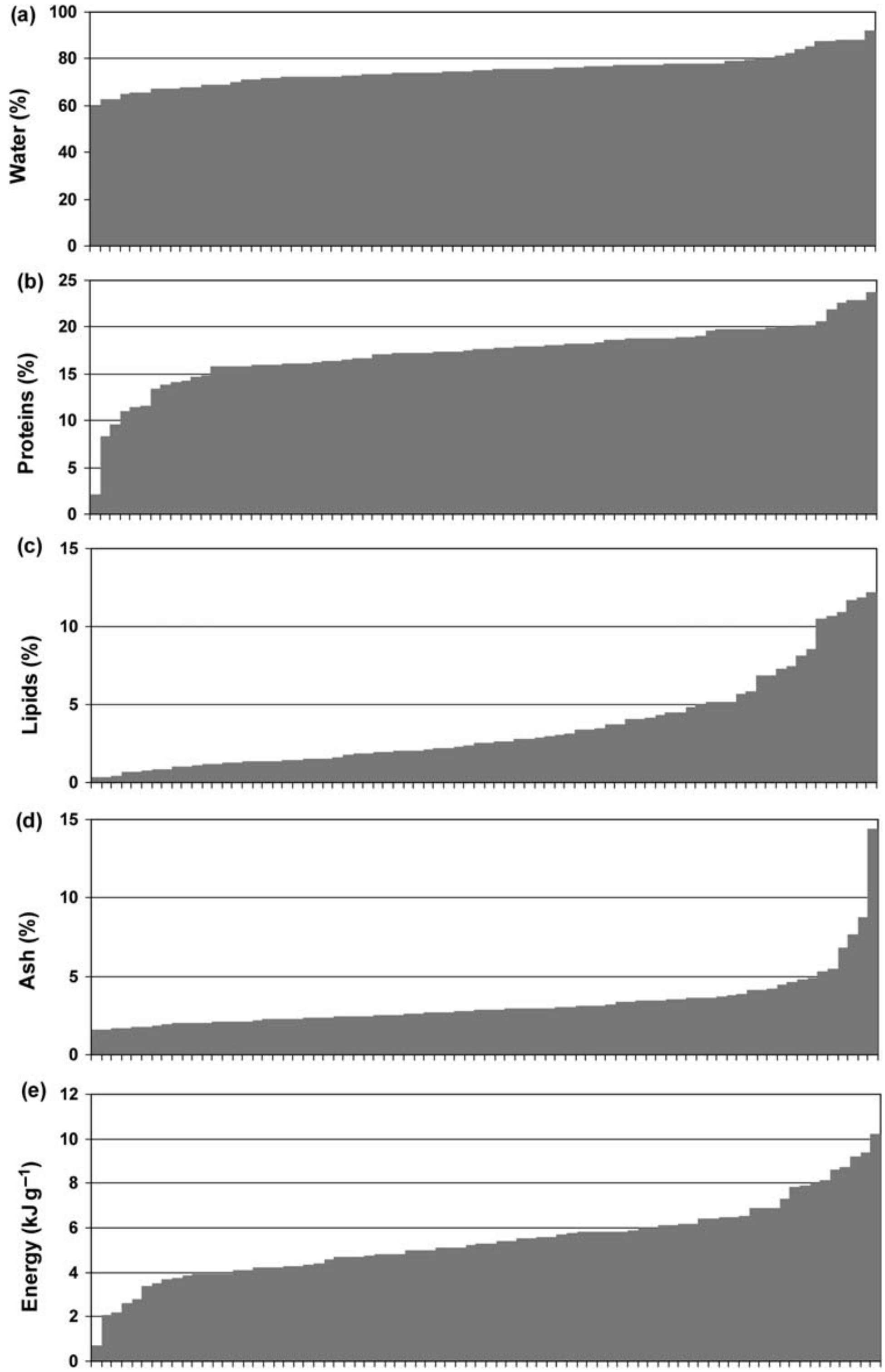

Figure 1. Component variability spectra for 78 forage species taken from the NE Atlantic, expressed as a percentage of wet total body weight: (a) water, (b) protein, (c) lipid, (d) ash, and (e) energy. For each component, species were classified hierarchically.

in marine ecosystems (Österblom *et al*., 2008), this study provides baseline data for evaluating any possible effects of regime shifts associated with changes in forage species availability.

Finally, the heterogeneity of forage-species quality needs to be considered in ecosystem modelling. Intermediate and lower trophic levels are often represented by multispecies boxes within models defined merely by size and general ecological profile, e.g. mesopelagic fish, small demersal fish, or large oceanic squid (Morissette *et al*., 2006; Chen *et al*., 2008). The results here highlight the fact that some combination of species within the same

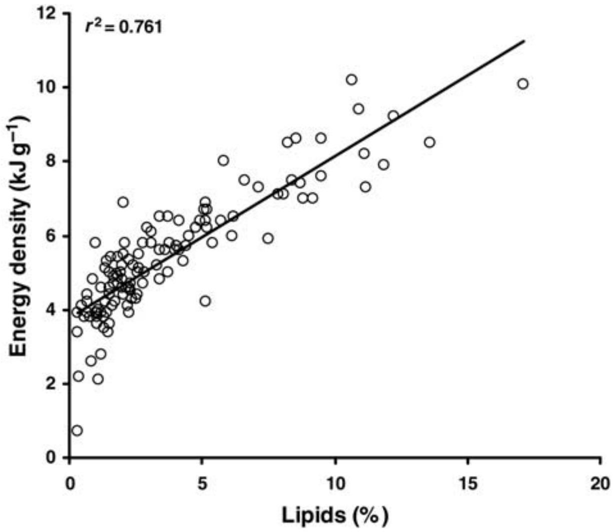

Figure 2. Fish energy content of 78 forage species from the NE Atlantic as a function of fish lipid content.

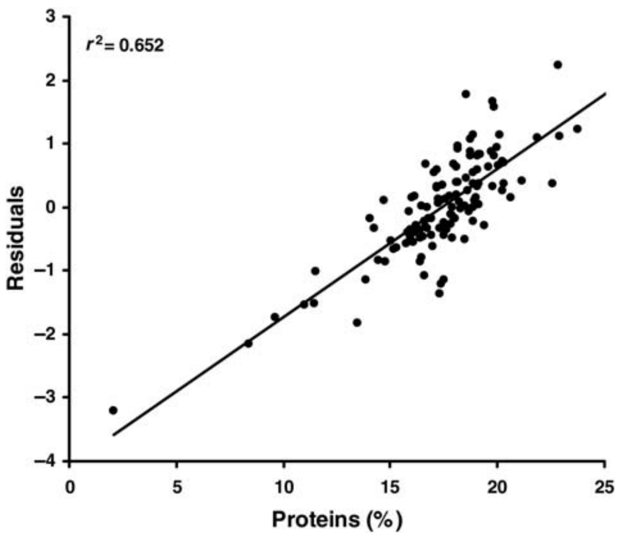

Figure 3. Residuals of the relationship between energy and lipid contents (Figure 2) of 78 forage species from the NE Atlantic as a function of fish protein content.

Table 2. Classification of 78 forage species from the NE Atlantic based on quality: low (<4 kJ g^{-1}), moderate (4 < ED < 6 kJ g^{-1}), and high (>6 kJ g^{-1}).

Low-quality species	Moderate-quality species	High-quality species
Jellyfish	Crustaceans	Crustaceans
Crustaceans	Oplophoridae	Some Portunidae
Euphausiidae	Pasiphaeidae	*Necora*
Palaemonidae	Some Portunidae	Cartilaginous fish
Cephalopods	*Polybius*	Scyliorhinidae
Sepiidae	Grapsidae	Bony fish
Cartilaginous fish	Cephalopods	Argentinidae
Chimaeridae	Loliginidae	Atherinidae
Bony fish	Ommastrephidae	Belonidae
Alepocephalidae	Sepiolidae	Caproidae
Cepolidae	Octopodidae	Carangidae
Merlucciidae	Cartilaginous fish	Clupeidae
Platytroctidae	Rajidae	Engraulidae
Serrivomeridae	Bony fish	Moronidae
Some Sternoptychidae	Ammodytidae	Mugilidae
Argyropelecus	Blenniidae	Mullidae
Stomiidae	Bothidae	Some Myctophidae
	Callionymidae	*Notoscopelus*
	Gadidae	*Lobianchia*
	Labridae	Scombridae
	Macrouridae	Scophthalmidae
	Some Myctophidae	Sebastinae
	Lampanyctus	Some Soleidae
	Benthosema	*Dicologlossa*
	Paralepididae	Sparidae
	Phycidae	Triglidae
	Pleuronectidae	
	Scomberesocidae	
	Scorpaenidae	
	Some Soleidae	
	Solea	
	Some Sternoptychidae	
	Maurolicus	
	Syngnathinae	
	Trachichthyidae	
	Trachinidae	

box in a model can be inconsistent when defined solely on habitat and size similarity. For instance, mesopelagic fish including myctophids and alepocephalids, or demersal fish including triglids and phycids are heterogeneous groupings in terms of body composition and energy content. Such species types are not equally valuable to, or even looked for by, top predators. It is therefore proposed that in models of pelagic ecosystems, multispecific compartments of forage organisms be defined with the aim of maximizing within-compartment homogeneity in body composition, energy content, and ultimately profitability to top predators.

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