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Research

Nutritional grouping of marine forage species reveals contrasted exposure of high trophic levels to essential micro-nutrients

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By transferring energy and nutrients from plankton to top predators, forage species play a major ecological role in marine food webs. While large differences in energy densities have been demonstrated among these species, other determinants of their quality remain poorly explored. We analysed 78 forage species from the Bay of Biscay, NE Atlantic, for their concentrations in various chemical elements with a documented biological role (i.e. micro-nutrients). Species encompassed jellyfish, crustaceans, cephalopods, cartilaginous and bony fish. Elements included two essential macro-minerals (nitrogen and phosphorous) and nine trace elements (arsenic (As), cobalt, copper (Cu), chromium, iron, manganese, nickel, selenium (Se), zinc). We showed a broad range of elemental composition values across forage species, partly driven by taxonomy (fish versus crustaceans/cephalopods) or their habitat (coastal versus oceanic, pelagic versus benthic). Some elements (As, Cu or Se) were more variable than others, especially in fish for Cu and Se. The 78 forage species were then classified by hierarchical clustering analysis (HCA) into different nutritional groups, based on their composition in eleven elements. Mean concentrations of each element in the diet of eight cetacean species was finally calculated, as well as the importance of each nutritional group (as defined by HCA including all elements) for each predator species. We revealed contrasting diets in terms of exposure to elements. Neritic common dolphins and harbour porpoises but also minke whales were thus mainly supplied by the Se-enriched nutritional group composed of small (pelagic) schooling fish (including sandeels, (horse) mackerel and also some Clupeids), while the diets of pilot whales or Risso's dolphins that mostly consume benthic cephalopods were clearly Cu-enriched. This study raises the issue of essential element composition as another determinant of food quality, and the risk associated with changes in forage species' availability for the proper functioning of marine food webs and ecosystems.

Keywords: cetaceans, inorganic elements, macro-minerals, matter transfer, prey, trace metals

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Introduction

Energy and matter transfers determine the functioning of food webs. Species, at both individual and population levels, are dependent on the quantity and on the quality of the available resources at each trophic level (Österblom et al. 2008). Current global changes and human pressures such as habitats' modification, natural resources' exploitation, non-native species' introduction or pollutant emissions affect the stability of ecosystems by impacting directly energy and matter fluxes between prey and predators (Albouy et al. 2014, Bartley et al. 2019, Halpern et al. 2019). Ultimately, the alteration of trophodynamics represent a major threat for ecosystem services such as food provisioning or nutrient cycling (Lafortezza and Chen 2016, Rosenblatt and Schmitz 2016).

In marine ecosystems, micronektonic species – also widely called forage species that include actively swimming organisms usually between 2 and 20 cm in size – play a crucial role by transferring energy and matter from plankton to top predators (Preciado et al. 2008, Falk-Petersen et al. 2009). Besides, while our evaluation of marine ecosystem functioning has been traditionally based on biomass quantity at each trophic level, more recent functional approaches revealed the importance of prey composition and prey quality in predators' foraging strategies and population dynamics (Spitz et al. 2014). Prey quality was indeed shown to differ among forage species for determinants of quality, including the energy density among and within various marine taxonomical groups encompassing zooplankton, crustaceans, cephalopods or fish species (Spitz et al. 2010b, Dessier et al. 2018). In a given ecosystem, the same forage fish biomass can thus bring up to four times more energy depending on the target species. As a consequence, changes in energy-rich prey availability and hence prey quality can have deleterious effects on the individual fitness of predators and, ultimately, on their population dynamics (Trites and Donnelly 2003). Marine predators are thus not only dependent on the taxonomy of their prey but on the nutritional characteristics of ingested items. Therefore, transfer of biomass alone cannot predict the efficiency of matter transfer across trophic levels.

Prey selection by marine mammals is notably shaped by prey physiological and morphological characteristics affecting the energetic profitability for predators. For instance, cetacean species characterized by high muscular performances, living in large schools and having a small body size compared to other cetaceans have been shown to preferentially select prey characterized by high lipid contents, living in schools as well, swimming actively and having an internal skeleton (Spitz et al. 2014, 2010a). The development of trait-based approaches has therefore opened the way to provide new prey guilds based on the similarities of their functional traits, going beyond the traditional taxonomic framework of dietary studies. A major benefit of such trait-based approaches is to predict responses of ecosystem changes, such as species shifts or alien species invasions (Hulot et al. 2000, Lefcheck and Duffy 2015, Pecuchet et al. 2020). The consideration of functional diversity has thus become one of the cornerstones of environmental sciences.

These notions of nutritional quality of resources and its variability range within ecosystems are however still emergent in marine environmental studies. If energy density and total lipid content are now commonly used as key functional traits to define prey quality (Bowen et al. 1995), other determinants of the nutritional variability are rarely measured and considered in trait-based approaches. While micro-nutrients such as vitamins, amino-acids or essential major or trace elements are known to be vital for the proper physiological functioning of organisms, their importance within the fluxes of matter for marine predators and more broadly in ecosystem functioning has been poorly studied so far (Pedro et al. 2019). Specifically, trace elements in marine organisms are mostly investigated as potential contaminants or pollutants but rarely for their role of essential elements, both in living organisms and in biogeochemical cycles. Many trace elements (those called essential) are indeed known to play key roles in the physiological functioning of all living species, although with a narrow and specific range of concentrations (Hamilton and Hoffman 2003). Deficiency in these essential elements can thus significantly affect the health of organisms. For instance, zinc (Zn) deficiency reduces the enzymatic activities that control the production of hormones related to the proper functioning of the reproductive system, whereas copper (Cu) deficiency weakens the immune system (Festa and Thiele 2011, Kaur et al. 2014). Similarly, selenium (Se) is an essential element well documented for its role in the detoxification of toxic heavy metals such as mercury (Hg) in fish, seabirds and marine mammals, as well as in humans (Ralston and Raymond 2010). Selenium deficiency can thus induce a toxicological risk in reducing the demethylation of Hg, in addition to the fact that Se is involved and thus essential to many other enzymatic activities than Hg detoxification only. Such deficiencies are generally caused by changes in the dietary intakes. Several examples are known in fish from aquaculture, for instance (Prabhu et al. 2016), but also in large marine predators such as long-finned pilot whales (Caurant et al. 1996).

In addition to the nutritional risk for predators, changes in the elemental composition of forage species can affect ecosystem productivity at a larger scale. For instance, some metals such as iron (Fe) are locally limiting in oceans (Sunda and Huntsman 1995), but large vertebrates can counter the lack of such micro-nutrients in these areas by defecating. Iron intake from prey can exceed nutritional requirements for some whales and consequently, faecal Fe content has been identified as a fertilizer enhancing ecosystem productivity (Nicol et al. 2010). A decrease of Fe content in available prey, as well as other essential elements, could thus have impacts on local nutrients recycling and ultimately on ecosystem dynamics.

Here, we propose to investigate the variability of concentrations in two essential macro-minerals and nine trace elements at a large taxonomic scale in the Bay of Biscay, NE Atlantic, to evaluate the nutritional diversity or the redundancy of these

elements within the local community of 78 forage species. Considering elements individually, differences among species classified according to their taxon or habitat across the horizontal (coastal – oceanic continuum) or vertical gradient (pelagic – benthic continuum) will be first assessed. The second objective is to identify functional groups of prey species based on their elemental composition in the eleven elements. Finally, we aim to explore the differences in the mean quality of true predator diets, through the respective contribution of these prey nutritional groups in the diet of eight common cetacean species from the area. The outcome of such a nutritional typology of marine resources should reveal 1) new insights into understanding and quantification of trophic interactions within marine ecosystems and 2) contribute to the assessment of some ecological risks associated with changes in the availability of certain forage species.

Material and methods

Sampling and sample preparation

A total of 78 different forage species was collected, including 1 jellyfish, 7 crustaceans, 8 cephalopods, 3 cartilaginous fish and 59 bony fish (Table 1). Almost all species were collected in the Bay of Biscay from 2002 to 2008, during EVHOE scientific fishery surveys ('Evaluation Halieutique de l'Ouest de l'Europe') operated annually in autumn by Ifremer ('Institut Français de Recherche pour l'Exploitation de la Mer') on the R/V Thalassa. Some coastal or rocky species were additionally sampled during the same period from fishing boats. As far as possible, the size range of these forage species was selected to match published prey sizes for cetacean predators in the Bay of Biscay (Víkingsson 1997, Ringelstein et al. 2006, Pusineri et al. 2007, Windsland et al. 2007, Meynier et al. 2008, Spitz et al. 2006a, b, 2011, MacLeod et al. 2014; Table 2). All the material was frozen on board and kept at −20°C until being processed. In the laboratory, whole organisms were briefly thawed. To reduce inter-individual variability, few to hundreds of individuals (depending on the size of species) were grouped for each species (i.e. constitution of pools) and homogenized using a stainless-steel knife mill, carefully rinsed with ultrapure water between each sample. These pools of whole specimens (corresponding to analytical samples) were frozen again −20°C, freeze-dried and reduced into fine powder until further analyses. A total of 115 samples was finally analysed. The process of organisms and samples (brief thawing, homogenization, freeze-dried and reduction into powder) was done within a maximum of two years after at-sea collection, and the samples (powders) were stored in a clean and dry place until analyses. Total element analyses on samples were then all conducted at the same date (in 2016).

Element analyses

Total nitrogen (N) concentrations were determined following the Kjeldahl method (AOAC 1990). Briefly, this method consists in digesting the samples with sulfuric acid to transform all N present into ammonium sulfate. The solution is then alkalized and the resulting ammonia is determined by distillation into a known volume of boric acid, the excess of which (corresponding to the amount of nitrogen in samples) is finally determined by titration.

For all other elements, aliquots of samples (~200 mg dry weight of homogenised powder) were digested using a 6:2 (v/v) mixture with nitric acid (HNO_3 69%) and hydrochloric acid (HCl 34%). Acidic digestion of the samples was performed overnight at room temperature and then in a microwave oven. Total concentrations of the micro-mineral phosphorus (P) and of the essential trace elements arsenic (As), cobalt (Co), chromium (Cr), copper (Cu), iron (Fe), manganese (Mn), nickel (Ni), selenium (Se) and zinc (Zn) were determined by inductively coupled plasma atomic emission spectrometry (ICP-OES, Vista-Pro Varian) and/or mass spectrometry (ICP-MS, X Series 2 Thermofisher Scientific). The quality assurance of these elemental analyses relied on blank and internal standard controls, and on the accuracy and reproducibility of data relative to the certified reference materials (CRMs) used in each analytical run. The CRMs used were TORT-3 (lobster hepatopancreas, National Research Council of Canada/NRCC) and DOLT-4 (dogfish liver, NRCC). Blank values were systematically below the detection limits and CRM values concurred with certified concentrations, with recovery rates ranging between 83% and 116% depending on the elements and on the CRM. Limits of quantification (LOQ) were calculated for each sample, depending on the mass of the aliquot analysed. Minimum and maximum values are reported in the Supporting information.

Data treatment and formatting before statistical analyses

The few concentrations below LOQ were first replaced by half of the LOQ for each sample of concern. Specifically, this concerned 19 and 2 samples out of the 115 analysed for Cr and Ni respectively, corresponding to about 15% of values (for Cr) or much less than 15% (for Ni), in which cases this method of replacing non-detects by half the LOQ may be applied for data analysis (U.S. Environmental Protection Agency 2000). For subsequent link with predators (cetaceans) that consume whole and fresh prey, all the concentrations obtained on a dry weight (dw) basis were then converted on a wet weight (ww) basis. This conversion was done using the specific moisture percentage determined for each sample after freeze-drying (averaged at species level in Table 1). Finally, to focus on the variability of elements among species, only the average concentrations calculated per species (i.e. n = 78) were used in further data treatment and statistics. In the case of *Palamemon longirostris* for Ni and of *Hyperoplus lanceolatus* for Se, the exceptionally high values measured for these species and elements (Supporting information) were respectively replaced by the quantiles 99 of the Ni and Se distribution (with quantiles calculated on n = 78) to conduct proper data analyses (except for the calculation of coefficients of variation). All statistical analyses were performed under the

Table 1. Characteristics of the 78 forage species considered from the NE Atlantic, also partly reported in Spitz et al. (2010b), with indication of 1) the species code used in the hierarchical clustering analysis (Fig. 4) and 2) the habitats documented for each species across horizontal or vertical gradient (i.e. horizontal gradient: Coastal/Shelf – C/S, Shelf/Upper Slope – S/US or Upper Slope/Deep Sea – US/DS; vertical gradient: Benthic – B, Benthopelagic – BP or Pelagic – P). N = total number of individuals, n = number of samples (pools of individuals) constituted for elemental analyses, average size (cm) of individuals [minimum-maximum], moisture percentage (%) of samples (mean ± standard deviation). Taxa and species are ordered according to taxonomic criteria.

Taxon/family	Species	Species code	Horizontal habitat[a]	Vertical habitat[a]	N	n	Average size of individuals [min–max][b]	Moisture %
Jellyfish								
Umaridae	*Aurelia aurita*	Aaur	C/S	P	30	1	[8–12]	92.1
Crustaceans								
Euphausiidae	*Meganyctiphanes norvegica*	Mnor	S/US	P	704	1	[2–3]	78.1
Oplophoridae	*Acanthephyra purpurea*	Apur	S/US	P	480	2	[3–6]	73.7 ± 0.0
Palaemonidae	*Palaemon longirostris*	Plon	C/S	BP	612	1	[1–2]	82.4
Pasiphaeidae	*Pasiphaea sivado*	Psiv	S/US	P	342	1	[4–9]	77.2
Grapsidae	*Pachygrapsus marmoratus*	Pmar	C/S	B	25	1	[2–4]	60.1
Portunidae	*Polybius henslowii*	Phen	C/S	B	37	1	[4–5]	72.4
	Necora puber	Npub	C/S	B	8	1	[4–7]	62.8
Cephalopods								
Loliginidae	*Allotheutis* spp.	Aspp	C/S	BP	221	3	[3–8]	79.4 ± 1.4
	Loligo forbesi	Lfor	S/US	BP	4	1	[10–20]	76.5
	Loligo vulgaris	Lvul	C/S	BP	15	3	[12–25]	76.2 ± 0.8
Ommastrephidae	*Illex coindeti*	Icoi	S/US	BP	9	2	[14–17]	78.2 ± 1.5
	Todaropsis eblanae	Tebl	S/US	BP	9	2	[12–15]	77.9 ± 0.2
Sepiolidae	*Sepiola* spp.	Sepiol	C/S	BP	77	1	[1–2]	77.4
Sepiidae	*Sepia officinalis*	Soff	C/S	BP	10	2	[6–10]	75.8 ± 0.1
Octopodidae	*Eledone cirrhosa*	Ecir	C/S	B	3	1	[10–11]	76.0
Fish								
Cartilaginous fish								
Scyliorhinidae	*Scyliorhinus canicula*	Sccan	C/S	BP	3	2	[48–51]	73.7 ± 2.3
Rajidae	*Leucoraja naevus*	Rnae	C/S	B	3	1	[40–51]	75.5
Chimaeridae	*Chimaera monstrosa*	Cmon	S/US	BP	6	1	[9–10]	81.3
Bony fish								
Congridae	*Conger conger*	Ccon	C/S	BP	3	2	[53–60]	74.7 ± 2.6
Serrivomeridae	*Serrivomer beanii*	Sbea	US/DS	P	26	1	[21–65]	88.4
Clupeidae	*Sprattus sprattus*	Sspr	C/S	P	246	4	[7–13]	70.9 ± 3.0
	Sardina pilchardus	Spil	C/S	P	15	2	[14–22]	66.4 ± 1.4
	Clupea harengus	Char	C/S	P	3	1	[20–20]	62.8
Engraulidae	*Engraulis encrasicolus*	Eenc	C/S	P	208	3	[9–13]	73.1 ± 3.6
Alepocephalidae	*Xenodermichtys copei*	Xcop	US/DS	P	173	1	[4–12]	87.5
Argentinidae	*Argentina sphyraena*	Asph	C/S	BP	22	2	[11–16]	72.2 ± 1.0
Platytroctidae	*Normichthys operosa*	Nope	US/DS	BP	53	1	[7–16]	85.5
Sternoptychidae	*Argyropelecus olfersii*	Aolf	US/DS	P	138	1	[1–10]	78.8
	Maurolicus muelleri	Mmue	S/US	P	201	1	[3–5]	77.2
Stomiidae	*Stomias boa*	Sboa	US/DS	P	28	1	[8–31]	84.1
Paralepididae	*Arctozenus risso*	Aris	US/DS	P	124	1	[9–20]	77.9
Myctophidae	*Lampanyctus crocodilus*	Lcro	US/DS	P	63	1	[7–15]	79.6
	Benthosema glaciale	Bgla	US/DS	P	697	2	[2–6]	74.7 ± 0.0
	Notoscopelus kroyeri	Nkro	US/DS	P	60	1	[3–13]	68.6
	Lobianchia gemellari	Lgem	US/DS	P	30	1	[7–9]	67.1
Macrouridae	*Coelorinchus coelorinchus*	Ccoe	S/US	BP	5	1	[8–10]	77.6
Gadidae	*Merlangius merlangus*	Mmng	C/S	BP	24	3	[17–22]	78.1 ± 2.1
	Pollachius pollachius	Ppol	C/S	BP	2	2	[29–30]	78.6 ± 0.6
	Micromesistius poutassou	Mpou	S/US	BP	40	3	[14–20]	77.8 ± 0.7
	Trisopterus luscus	Tlus	C/S	BP	9	2	[22–26]	77.6 ± 0.9
	Gadiculus argenteus	Garg	S/US	BP	23	1	[8–11]	75.5
	Trisopterus minutus	Tmin	C/S	BP	21	2	[14–18]	74.9 ± 0.6
Lotidae	*Gaidropsarus* spp.	Gspp	US/DS	B	5	1	[14–23]	76.8
Phycidae	*Phycis blennoides*	Pble	S/US	BP	3	1	[26–28]	77.5
Merluccidae	*Merluccius merluccius*	Mmcc	S/US	BP	9	2	[22–29]	80.9 ± 0.4
Atherinidae	*Atherina presbyter*	Apre	C/S	P	129	2	[5–12]	67.4 ± 2.1
Belonidae	*Belone belone*	Bbel	C/S	P	3	1	[55–59]	74.0
Scomberesocidae	*Scomberesox saurus*	Ssau	C/S	P	5	1	[25–30]	71.6

(Continued)

Table 1. Continued.

Taxon/family	Species	Species code	Horizontal habitat[a]	Vertical habitat[a]	N	n	Average size of individuals [min–max][b]	Moisture %
Trachichthyidae	*Hoplostethus mediterraneus*	Hmed	US/DS	BP	17	1	[4–7]	75.9
Caproidae	*Capros aper*	Cape	C/S	BP	36	2	[6–7]	73.4 ± 2.9
Syngnathinae	*Entelurus aequoreus*	Eaeq	C/S	BP	128	1	[25–34]	73.5
Sebastidae	*Helicolenus dactylopterus*	Hdac	S/US	BP	3	1	[15–17]	65.7
Scorpaenidae	*Scorpaena loppei*	Slop	S/US	BP	3	1	[9–10]	73.2
Triglidae	*Chelidonichthys cuculus*	Acuc	C/S	BP	7	2	[17–20]	69.0 ± 3.0
Moronidae	*Dicentrarchus labrax*	Dlab	C/S	BP	3	1	[44–48]	72.6
Carangidae	*Trachurus trachurus*	Ttru	C/S	P	30	3	[14–30]	73.3 ± 0.7
Sparidae	*Spondyliosoma cantharus*	Spcan	C/S	BP	6	2	[17–23]	69.9 ± 2.0
	Boops boops	Bboo	C/S	BP	9	1	[14–25]	67.0
	Pagellus acarne	Paca	C/S	BP	4	1	[15–17]	65.1
Mullidae	*Mullus surmuletus*	Msur	C/S	BP	15	2	[11–14]	71.7 ± 0.4
Cepolidae	*Cepola macrophthalma*	Crub	C/S	BP	6	1	[38–53]	80.2
Mugilidae	*Liza ramada*	Lram	C/S	BP	3	1	[33–42]	67.6
Labridae	*Labrus bergylta*	Lber	C/S	BP	2	1	[28–32]	75.8
Ammodytidae	*Hyperoplus lanceolatus*	Hlan	C/S	P	6	1	[30–37]	75.1
	Ammodytes tobianus	Atob	C/S	P	9	2	[27–31]	73.6 ± 0.1
Trachinidae	*Trachinus draco*	Tdra	C/S	BP	5	1	[18–23]	74.6
Blenniidae	*Paralipophrys trigloides*	Ptri	C/S	B	16	1	[7–12]	73.1
Callionymidae	*Callionymus lyra*	Clyr	C/S	BP	5	1	[15–19]	75.4
Gobiidae	*Lesueurigobius friesii*	Lfri	C/S	BP	143	1	[4–6]	72.4
Scombridae	*Scomber scombrus*	Ssco	C/S	P	12	3	[25–29]	67.6 ± 2.0
Scophthalmidae	*Lepidorhombus whiffiagonis*	Lwhi	S/US	B	3	1	[21–26]	73.9
Bothidae	*Arnoglossus imperialis*	Aimp	C/S	B	19	1	[8–14]	74.0
Pleuronectidae	*Glyptocephalus cynoglossus*	Gcyn	C/S	B	2	1	[29–34]	76.6
	Microstomus kitt	Mkit	C/S	B	2	1	[28–29]	73.9
	Pleuronectes platessa	Ppla	C/S	B	2	1	[27–34]	74.3
Soleidae	*Solea solea*	Svul	C/S	B	3	2	[28–31]	73.7 ± 4.7
	Dicologlossa cuneata	Dcun	C/S	B	7	1	[12–20]	69.2

[a] Habitats of species across horizontal or vertical gradients (assumed to correspond to their physical distribution in the marine environment and/or to their feeding zone) were defined following general published literature (Quéro et al. 2003, Froese and Pauly 2021) and were refined following survey data in the area, for fish species in particular (Trenkel et al. 2009).
[b] Sizes correspond to the bell diameter for jellyfish, to the cephalothorax width for crab-like crustaceans (i.e. Grapsidae and Portunidae), to the total length for shrimp-like crustaceans and all fish (except *Chimera monstrosa*: pre-anal fin length), and to the dorsal mantle length for cephalopods.

software R ver. 4.0.3 (<www.r-project.org>). The R packages fpc, ggplot2, ggthemes, plyr, readxl, tidyverse, vegan, wesanderson and writexl (in alphabetical order) were used.

Assessment of elemental variability among forage species

To assess elemental variability among forage species, coefficients of variation (CV, in %) were first calculated for each element (using concentration data in ww). This relative index of data dispersion (i.e. ratio between an absolute dispersion index – the standard deviation – and a central value – the mean of data) indeed allows comparing elements with different orders of magnitude. Coefficients of variation were calculated within each taxon (except jellyfish, with n = 1) and also considering all species together (Table 3). Density plots of concentrations were then performed for each element, on concentrations normalized between 0 and 1, to visualize the different profiles of elements in terms of distribution of values: distribution towards a majority of low values (i.e. in the first and/or second quartile of the distribution) or high values (i.e. in the third and/or fourth quartile of the distribution).

Assessment of elemental variability across taxa and habitats

Boxplots of concentrations were performed, with species classified according to their taxon or according to their habitat across the horizontal and vertical gradients (Table 1), using centered-reduced concentrations for each element. This data representation allows 1) comparing the concentrations of elements of different orders of magnitude among the different groups defined a priori (i.e. according to the taxon or the habitat of species), while 2) maintaining intra-elemental variability and setting the mean of concentrations to zero for each element, and thus 3) visualizing groups with different elemental profiles and high or low concentrations in certain elements. Specifically, the habitats of species across horizontal or vertical gradients (which we assume to correspond to their physical distribution in the marine environment and/

Table 2. Brief description of the predator data (cetacean community from the Bay of the Biscay) used for the calculation of elemental composition of predators' diet.

Cetacean group[a]	Species	Reference	No. of stomachs
Baleen whales	*Balaenoptera acutorostrata*	Windsland et al. 2007	37
	Balaenoptera physalus	Víkingsson 1997	1524
Small delphinids from neritic waters	*Delphinus delphis* (neritic)	Meynier et al. 2008	71
	Stenella coeruleoalba (neritic)	Spitz et al. 2006a	32
	Phocoena phocoena	Spitz et al. 2006b	29
	Tursiops truncatus	Spitz et al. 2006b	25
Small delphinids from oceanic waters	*Delphinus delphis* (oceanic)	Pusineri et al. 2007	63
	Stenella coeruleoalba (oceanic)	Ringelstein et al. 2006	60
Deep diving delphinids	*Grampus griseus*	MacLeod et al. 2014	11
	Globicephala melas	Spitz et al. 2011	11

[a] Grouping following both taxonomic and habitat criteria.

or to their feeding zone; Table 1) were defined following general published literature (Quéro et al. 2003, Froese and Pauly 2021) and was refined following survey data in the area, for fish species in particular (Trenkel et al. 2009). For each element, statistical differences among the groups a priori defined (corresponding to differences among taxa or habitats) were finally tested through non-parametric Kruskal–Wallis (KW) tests followed by post hoc multiple comparison tests with Holm's adjustment method, after verification of data normality (through Shapiro–Wilks tests) and homoscedasticity (through Bartlett tests) precluding any use of parametric tests. The level of significance for these statistical analyses was always set at $\alpha = 0.05$ and the results of KW tests in particular are detailed in the Supporting information.

Definition of nutritional groups of forage species

Based on the eleven elements, groups of forage species that had similar patterns in terms of elemental composition were identified by hierarchical clustering analysis (HCA) using Ward's minimum variance method (Ward 1963). This method is based on the linear model criterion of least squares and allows to define groups that minimize the within-group sum of squares (the computation of within-group sums of squares being based on a Euclidean model). After clustering, the optimal number of groups (seven groups) was first assessed by visual inspection of the resulting dendrogram, and was then confirmed by the computation of the simple structure index ('ssi') criterion generally used in K-means partitioning (Spitz et al. 2014). Boxplots of centered-reduced concentrations were then performed according to these HCA groups, as done with the groups a priori defined according to taxa and habitats.

Elemental composition of cetaceans' diet

The concentrations of each element in the diet of eight cetacean species (i.e. predators) living in the Bay of Biscay (Table 2) were calculated, using published data on the relative contribution of each prey in the diet of these predators, and the present dataset for the elemental composition of prey items. We selected dietary studies based on stomach content analysis in the NE Atlantic, with a preference for references from the Bay of Biscay when available. According to published diet data, two groups (i.e. neritic versus oceanic) were also considered for the two small delphinid species *Delphinus delphis* and *Stenella coeruleoalba*, i.e. these two cetacean species were separated in *D. delphis* neritic versus oceanic and in *S. coeruleoalba* neritic versus oceanic (Table 2). The following calculation was done:

$$C_{e,p} = \sum_s W_{p,s} \times C_{e,s}$$

where $W_{p,s}$ is the relative contribution (in %) in terms of ingested biomass of the prey species s in the diet of the predator p, and $C_{e,s}$ is the concentration (in mg kg^{-1} ww) of the element e for the prey species s. $C_{e,p}$ is the final concentration of the element e in the diet of predator p obtained by the sum of the relative contribution of each prey species.

When a particular prey species was not analysed, we used the mean elemental concentration of the lowest taxonomic

Table 3. Coefficients of variation (CV, in %) calculated for each element and each major taxon with n > 1 (i.e. crustaceans, cephalopods, fish; jellyfish excluded), and for all species combined including the jellyfish (in italics). Within each taxon, the values used to calculate CV were average species concentrations for each element, in mg kg^{-1} wet weight. CV > 75% are in bold. n sp = number of species. Essential elements are first listed according to their type (macro-minerals versus trace elements), then by alphabetical order within each type of elements.

	N	P	As	Co	Cr	Cu	Fe	Mn	Ni	Se	Zn
Crustaceans (n sp = 7)	22	29	**79**	**92**	58	54	**110**	**89**	**165**	45	58
Cephalopods (n sp = 8)	7	12	**124**	**117**	**84**	63	55	57	**95**	41	41
Fish (n sp = 62)	16	37	**155**	70	**89**	**160**	**80**	**78**	**76**	**95**	39
All species (n sp = *78*)	*19*	*40*	***142***	***138***	***88***	***192***	***135***	***127***	***212***	***89***	*49*

level available (genus, family, order or taxon) in our present dataset of elemental concentrations for forage species from the Bay of Biscay. Similarly, when a dietary item was not given at the species level in published diet data, we used the mean elemental concentration of the corresponding lowest taxonomic level given in dietary data and available in the elemental concentration dataset. Finally, the percentage of feeding on the different groups of forage species defined by HCA by the different cetaceans and/or groups of cetaceans (for *D. delphis* and *S. coeruleoalba*) was estimated, from the relative contribution (in %) in terms of ingested biomass of the different forage species in the diet of these predators.

All data used in the present study are available under the depository system PANGAEA (Chouvelon et al. 2022).

Results

Variability of element concentrations (levels and distribution of data)

In terms of orders of magnitude, Co and Cr measured concentrations were all below 3 mg kg^{-1} dw (and specifically below 1 mg kg^{-1} for Co, except for *Sepia officinalis* at 1.04 mg kg^{-1} dw), while Mn, Ni and Se concentrations varied from less than 1 mg kg^{-1} up to ~40 mg kg^{-1} dw. Arsenic and Cu concentrations varied from ~1 mg kg^{-1} up to ~260 mg kg^{-1} dw. Iron and Zn concentrations varied from ~15 mg kg^{-1} up to ~170 mg kg^{-1} dw (Zn) or ~1000 mg kg^{-1} dw (Fe). Finally, P concentrations varied between ~6000 and ~38 000 mg kg^{-1} dw, while N concentrations varied from ~78 000 up to ~138 000 mg kg^{-1} dw.

All species considered, the most variable elements (with a CV > 75%) were in increasing order: Ni, Cu, As, Co, Fe, Mn, Se and Cr (Table 3). However, the high CV observed for Ni and Se were partly due to the particularly high values measured for the crustacean *Palaemon longirostris* (Ni) and the sandeel *Hyperoplus lanceolatus* (Se). When these two species were excluded, CV decreased from 212% to 86% for Ni, and from 89% to 43% for Se. The order of CV% also slightly changed when taxa were considered separately. The most variable elements became for crustaceans (in increasing order): Ni, Fe, Co, Mn and As; for cephalopods: As, Co, Ni and Cr; for fish (including both cartilaginous and bony fish): Cu, As, Se, Cr, Fe, Mn and Ni. The elements N, P and Zn were thus the least variable elements, with CV always < 75% whether species were considered together or at the taxon level (Table 3).

Density plots of concentrations evidenced different profiles in terms of diversity of concentrations measured for each element (Fig. 1). Cobalt, Cu and Fe had density plots with a clear maximum (peak) of concentrations towards low values, although a second but smaller peak towards fairly high values was also noticeable for Cu. Similarly, As, Mn, Ni and to a lesser extent Se had density plots with a maximum of concentrations towards low values, but these values were more spread out than in the case of Co, Cu and Fe. The macromineral P and the trace elements Cr and Zn had density plots with most concentrations towards relatively low values as well, but these values were highly spread-out. Finally, N had a density plot with highly spread-out values but with most concentrations towards relatively high values (Fig. 1).

Differences of element concentrations among taxa and habitats

Significant differences were found among taxa for several elements, according to post hoc multiple comparison tests after KW tests (Fig. 2, Supporting information), with four different patterns observed depending on the elements:

1) Cu and Zn: no significant differences between crustaceans and cephalopods on the one hand, nor between cartilaginous and bony fish on the other hand, but significantly higher concentrations measured in crustaceans and cephalopods compared to both types of fish (i.e. crustaceans = cephalopods > cartilaginous fish = bony fish);
2) Fe, Mn and Ni: significantly higher concentrations measured in crustaceans compared to cephalopods and both types of fish, that did not present significant differences (i.e. crustaceans > cephalopods = cartilaginous fish = bony fish);
3) Co: crustaceans > both types of fish, and cephalopods > bony fish (but crustaceans = cephalopods, cephalopods = cartilaginous fish and cartilaginous fish = bony fish);
4) P: bony fish > cephalopods (but crustaceans = cephalopods = cartilaginous fish and crustaceans = cartilaginous fish = bony fish).

No significant differences among taxa were revealed for N, As, Cr and Se (post hoc multiple comparison tests after KW tests, p-values > 0.05; Fig. 2, Supporting information).

Significant differences were also found among habitats for some elements, according to post hoc multiple comparison tests after KW tests (Fig. 3, Supporting information). Across the horizontal gradient (from the coast to upper slope/deep sea), two patterns of differences were observed:

1) for N: significantly higher concentrations measured in species from the coastal/shelf compared to both species from the shelf/upper slope and slope/deep-sea habitats, not significantly different (i.e. C/S > S/US = US/DS) (i.e.);
2) for Zn: significantly higher concentrations measured in species from the coastal/shelf habitat compared to species from the upper slope/deep-sea habitat only (i.e. C/S > US/DS, but CS = S/US and S/US = US/DS).

There was no significant difference among horizontal habitats for all other elements, namely P, As, Co, Cr, Cu, Fe, Mn, Ni and Se (post hoc multiple comparison tests after KW tests, all p-values > 0.05; Fig. 3 Supporting information).

Across the vertical gradient (corresponding to the position of species in the water column), two patterns of differences were also observed:

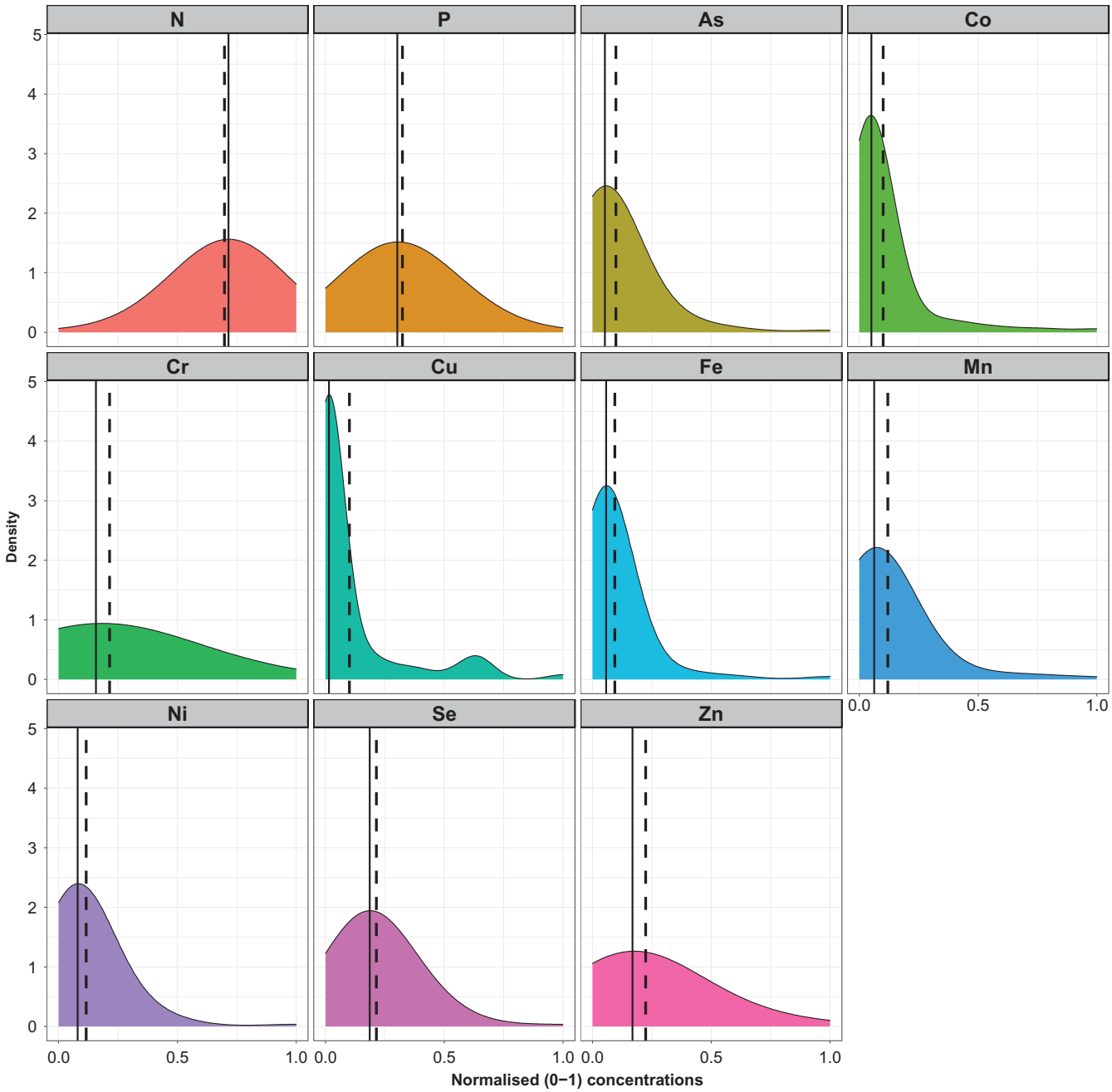

Figure 1. Density plots of mean elemental concentrations measured in the 78 forage species considered (data normalized between 0 and 1). Dotted lines represent the average of the 78 measured concentrations, and solid lines the median. From left to right and top to bottom, essential elements are first listed according to their type (macro-minerals versus trace elements), then by alphabetical order within each type of elements.

1) for As, Co, Cr and Mn: significantly higher concentrations measured in benthic species compared to both benthopelagic and pelagic species, not significantly different (i.e. B > BP = P);
2) for N and Ni: significantly higher concentrations measured in benthic species compared to pelagic species only (i.e. B > P, but B = BP and BP = P).

There was no significant difference among vertical habitats for P, Cu, Fe, Se and Zn (post hoc multiple comparison tests after KW tests, p-values > 0.05; Fig. 3, Supporting information).

Nutritional grouping of forage species

Among the eleven elements measured, eight contributed the most to the classification of species into different groups by the clustering analysis (i.e. > 50% of the variance explained by each of these elements in the definition of groups). These elements were Mn (83%) > Cu (78%) > Co (68%) > Fe

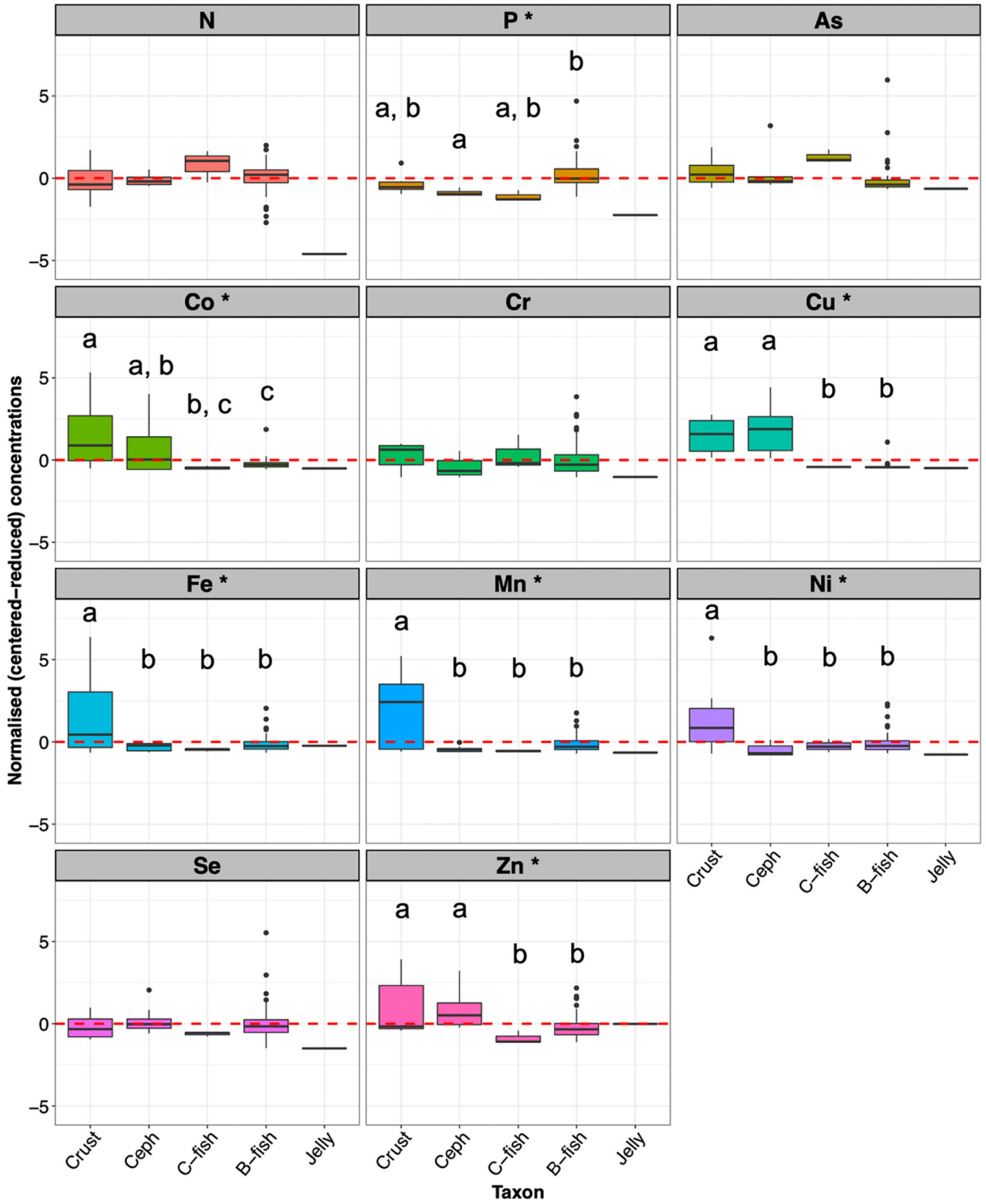

Figure 2. Boxplots of mean elemental concentrations measured in the 78 forage species considered (centered-reduced data), with species classified according to their taxon (Crust = crustaceans (number of species (n sp) = 7), Ceph = cephalopods (n sp = 8), C-fish = cartilaginous fish (n sp = 3), B-fish = bony fish (n sp = 59), Jelly = jellyfish (n sp = 1)). Dotted red lines correspond the mean (the mean equals to zero when data are centered-reduced). For each element whose at least two taxa significantly differed in their concentrations (indicated with '*'), an identical letter regroups taxa that are not significantly different in the corresponding facet, according to the results of post hoc multiple comparison tests with Holm adjustment method after a Kruskal–Wallis test, at $\alpha = 0.05$ (Supporting information). Note that jellyfish with n sp = 1 was not included in statistical tests. Essential elements are first listed according to their type (macro-minerals versus trace elements), then by alphabetical order within each type of elements.

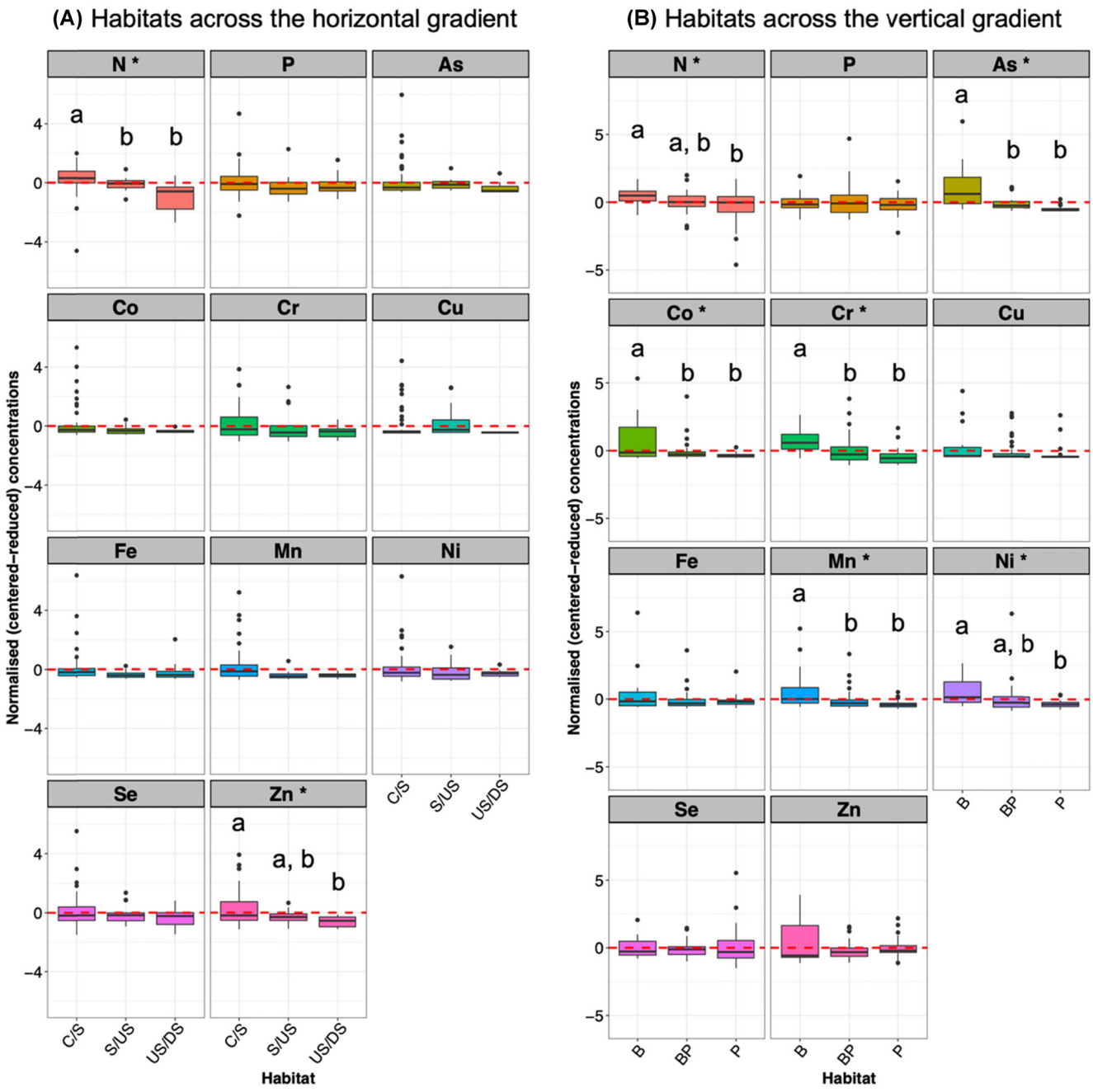

Figure 3. Boxplots of mean elemental concentrations measured in the 78 forage species considered (centered-reduced data), with species classified according to their habitat across the (A) horizontal or (B) vertical gradient (horizontal gradient: C/S = coastal/shelf (number of species (n sp) = 50), S/US = shelf/upper slope (n sp = 16), US/DS = upper slope/deep sea (n sp = 12); vertical gradient: B = benthic (n sp = 14), BP = benthopelagic (n sp = 39), P = pelagic (n sp = 25)). Dotted red lines correspond the mean (the mean equals to zero when data are centered-reduced). For each element whose at least two habitats significantly differed in their concentrations (indicated with '*'), an identical letter regroups habitats that are not significantly different in the corresponding facet, according to the results of post hoc multiple comparison tests with Holm adjustment method after a Kruskal–Wallis test, at $\alpha = 0.05$ (Supporting information). Essential elements are first listed according to their type (macro-minerals versus trace elements), then by alphabetical order within each type of elements.

(61%) > Ni (58%) > n = P (54%) > Zn (53%). The elements contributing the least to the definition of groups were thus As, Cr (43% each) and Se (29%).

The clustering analysis subdivided the 78 species into 1) two groups containing crustaceans exclusively (group 3) or crustaceans and cephalopods (group 2), and 2) five groups

containing mainly fish species (group 1 and group 4–7). However, group 1 was also composed of some crustacean and cephalopod species, especially those of the Loliginidae family for cepalopods, while group 7 also contained the jellyfish species (Fig. 4, 5, Table 4).

Group 2 and 3 containing mainly benthic to benthopelagic crustaceans and/or cephalopods were characterized by the highest concentrations in Cu (group 2), and in Co, Fe, Mn, Ni, Zn (group 3). In contrast, group 4–6 gathered only fish species (Fig. 4, Table 4). Group 4 was mainly composed of benthic to benthopelagic fish species from the shelf, including cartilaginous fish species from this habitat (namely *Scyliorhinus canicula* and *Leucoraja naevus*). It had the highest concentrations in As, Cr and N but the lowest concentrations in Fe and Zn (Fig. 5, Table 4, Supporting information). Group 5 was clearly defined by small (schooling) pelagic to benthopelagic fish species such as mackerel or horse mackerel and included almost all species of the Ammodytidae (sandeels), Clupeidae (sardines, sprats) and Sparidae (bream-like fish) families (Fig. 4). It was characterized by the highest Se concentrations, and the highest Zn concentrations among the fish groups (Fig. 5, Table 4, Supporting information). Similarly to group 4, group 6 was composed of benthopelagic to benthic fish from the shelf, but it included most of the flatfish species instead of cartilaginous fish species and had the highest values in the macro-mineral P. Group 7 composed of pelagic to benthopelagic fish from the upper slope/deep sea habitat (i.e. oceanic area) and also comprising the sole jellyfish species was characterized by the lowest values in N, P, As, Cu, Ni and Se. It had intermediate values for other elements, and no element had the highest concentrations for this group (Fig. 5, Table 4, Supporting information). Finally, group 1 contained the highest number and the highest diversity of species among the 78 considered, although these species mainly encompassed pelagic to benthopelagic species (whether they belonged to crustaceans, cephalopods or fish). More specifically, it included all species of the Gadidae and Myctophidae families among fish (Fig. 4, 5, Table 4). It was characterized by the lowest concentrations in Co, Cr and Mn, presented intermediate concentrations for the other eight elements, and thus no element showed the highest concentration values – as did group 7 (Fig. 5, Table 4, Supporting information).

Elemental composition of cetaceans' diets and their predation on nutritional groups

The calculation of the average elemental composition of the diet of eight cetacean species and/or groups of cetaceans based on diet information (for *D. delphis* and. *S. coeruleoalba*) evidenced contrasted exposure of these predators to the different elements through the trophic pathway. While the quality of diets did not differ strongly in N concentrations, they differed much more in P, Cu, Se and Zn concentrations, for instance (Fig. 6). Diets of common minke whales *Balaenoptera acutorostrata*, neritic common dolphins *D. delphis* and harbour porpoises *Phocoena phocoena* were thus the most concentrated in P, the least concentrated in Cu and presented intermediate to high concentrations in Se and Zn. Alternatively, diets of common fin whales *B. physalus*, bottlenose dolphins *Tursiops truncatus*, oceanic common dolphins *D. delphis* and both neritic and oceanic striped dolphins *S. coeruleoalba* showed intermediate concentrations in P, Cu, Se and Zn. Finally, diets of the deep diving delphinids *Grampus griseus* and *Globicephala melas* were the least concentrated in P but showed the highest concentrations in several elements including Cu (by far), Se and Zn (Fig. 6).

The contribution of the different nutritional prey groups (as defined by HCA) to the elemental supply of predators as well as the estimated % of feeding on these groups by predators (Table 5) further showed that group 1 is a highly consumed group by many predators (i.e. group with the highest species diversity but with the lowest to intermediate concentrations in all elements). Alternatively, 1) group 2 (containing cephalopods) appears clearly mainly consumed by *G. griseus* and *G. melas*, and to a lesser extent by both neritic and oceanic *S. coeruleoalba*; 2) group 5 (containing small pelagic schooling fish) is mainly consumed by *B. acutorostrata* and the small delphinids from the shelf (neritic *D. delphis*, and to a lesser extent *P. phocoena* and *T. truncatus*); 3) group 3, 4, 6 and 7 are almost not consumed, or very little, by the cetacean (predator) community considered.

Discussion

Our results evidenced a large diversity of elemental composition (micro-nutrients) within the community of forage species (n = 78) available to high-trophic level consumers in the Bay of Biscay, NE Atlantic, revealing a board range of resource quality available to predators. Considering the elements individually, this variability of elemental composition appeared mainly driven by taxonomy and the habitat of forage species. The forage species were then classified into groups of different nutritional qualities for predators, highlighting that all prey are possibly not equivalent resources based on their composition in eleven essential elements. This nutritional grouping suggested that any changes in prey communities and/or in predators' diet could affect the fluxes of essential elements through food webs.

Variability in forage species' elemental composition: origin and drivers

Very few studies have investigated the concentrations of such a diversity of essential elements in such a variety of marine species – encompassing whole crustaceans, cephalopod mollusks and both cartilaginous and bony fish – as in the present study (Asante et al. 2008, Cipro et al. 2018). Studies reporting essential element concentrations in marine organisms indeed generally focus 1) on a quite limited number of species (< 10) or on a particular taxon or group of species (Fowler 1986, Ridout et al. 1989, Naeem et al. 2011, Sofoulaki et al. 2018, Chouvelon et al. 2019, Figueiredo et al. 2020); 2) on specific tissues (i.e. human-edible tissues such as the muscle,

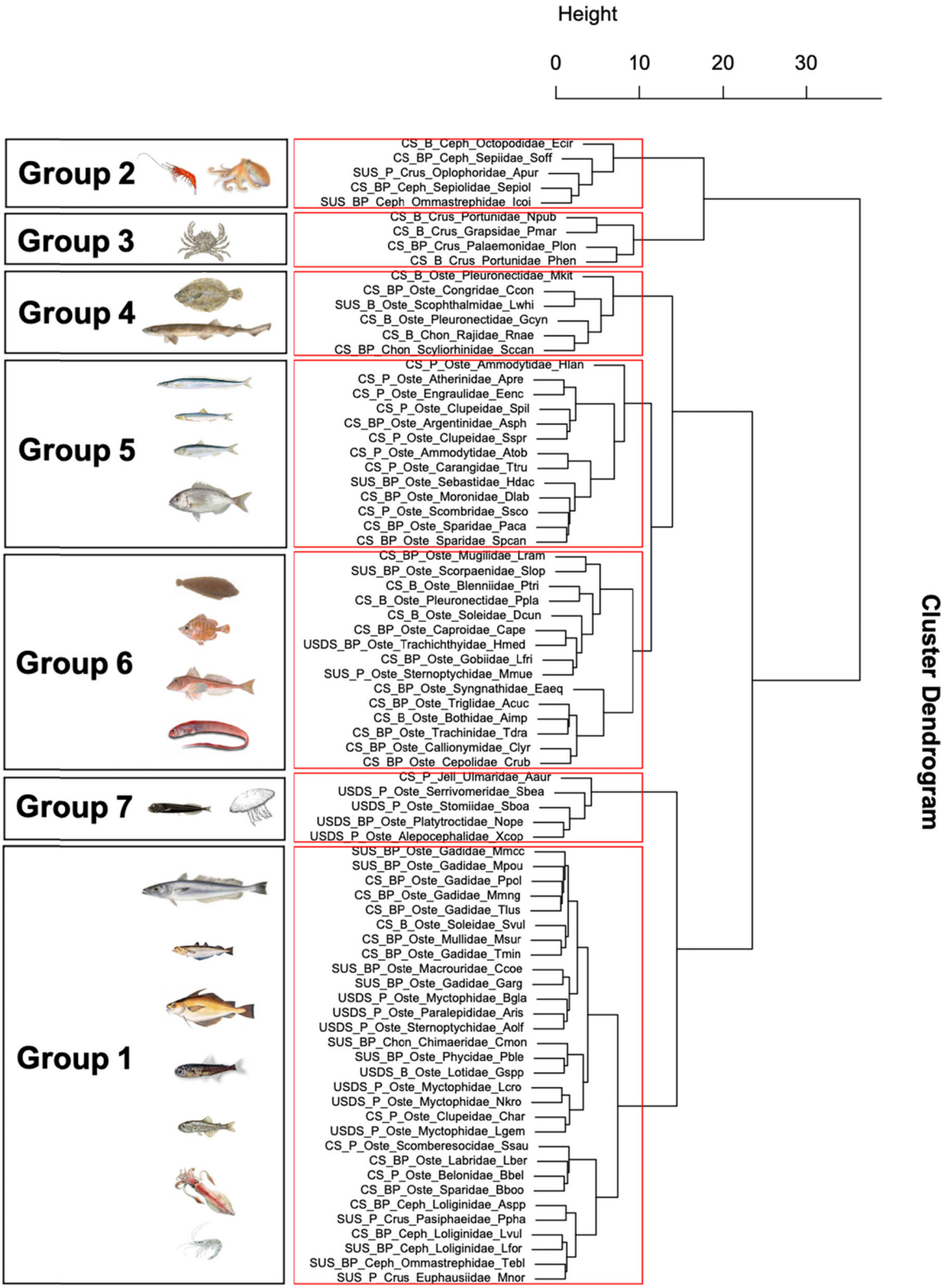

Figure 4. Grouping of species following the hierarchical clustering analysis (HCA) performed using Ward's minimum variance method. The codes for species and habitats area indicated in Table 1. Detailed description of the groups is given in Table 4 and numerical results of the HCA (i.e. mean ± standard deviations of each element concentration for each group) are given in the Supporting information.

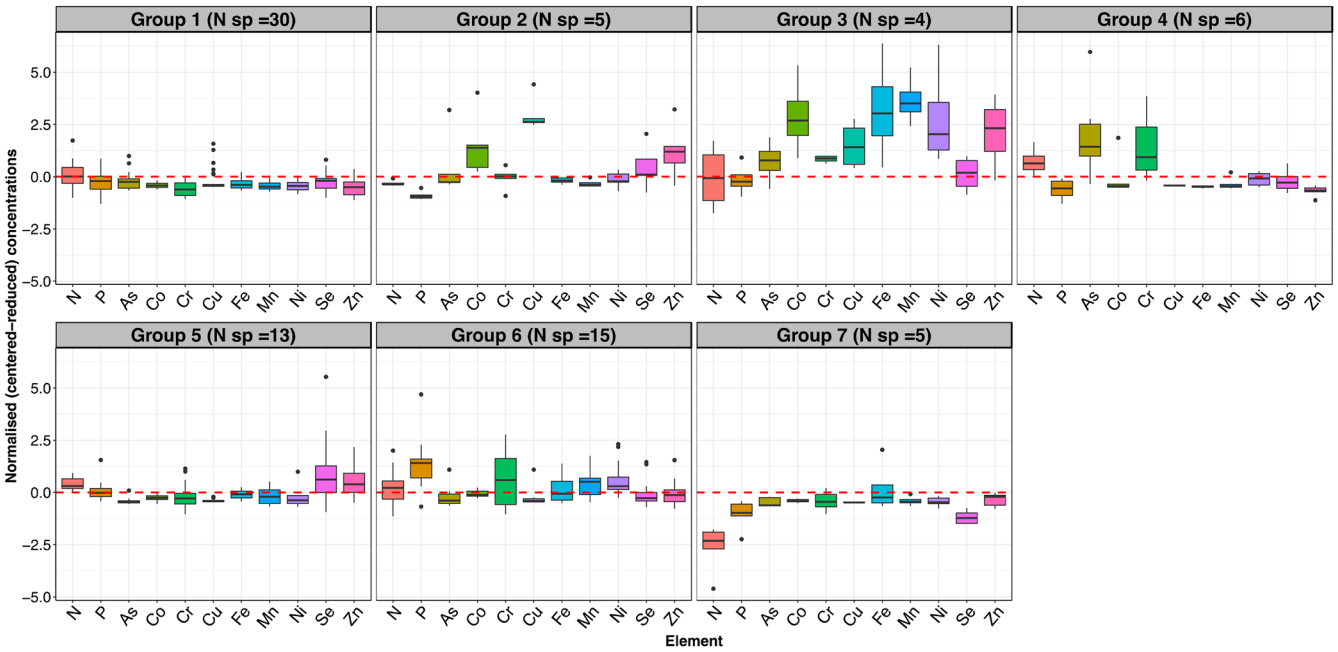

Figure 5. Boxplots of mean elemental concentrations measured in the 78 forage species considered (centered-reduced data), with species classified according to the groups defined by the hierarchical clustering analysis (HCA) performed using Ward's minimum variance method. Dotted red lines correspond the mean (the mean equals to zero when data are centered-reduced). N sp = number of species in each HCA group. Essential elements are first listed according to their type (macro-minerals versus trace elements), then by alphabetical order within each type of elements.

or bioaccumulation and/detoxification organs such as the liver in the case of fish; Windom et al. 1973, Carvalho et al. 2005, Siscar et al. 2014, Le Croizier et al. 2016, Bodin et al. 2017, Lozano-Bilbao et al. 2019); 3) on a limited number of essential elements, for their documented interaction with potentially toxic non-essential elements such as Hg (e.g. Se; Pedro et al. 2019).

The concentrations we measured for the various elements were globally in the same orders of magnitude than the concentrations previously reported for whole marine

Table 4. Description of the species groups derived from the hierarchical clustering analysis (HCA) presented in Fig. 4, both in terms of main species composition and elemental composition. The detailed species composition of groups is available on Fig. 4. The numerical results of the HCA groups (i.e. mean concentrations of each group for each element) are given in the Supporting information. N sp = number of species in the group. When several essential elements indicated, they are first listed according to their type (macro-minerals versus trace elements), then by alphabetical order within each type of elements.

		Elemental composition	
HCA group (N sp)	Main species composition	Elements for which the group has the highest values	Elements for which the group has the lowest values
Group 1 (N sp = 30)	Pelagic to benthopelagic bony fish from the shelf and upper slope/deep sea (oceanic), including all species of the Gadidae and Myctophidae families, and some pelagic to benthopelagic crustaceans and cephalopods	–	Co, Cr, Mn
Group 2 (N sp = 5)	Benthic to benthopelagic cephalopods, and one (oceanic) crustacean species	Cu	–
Group 3 (N sp = 4)	Benthic to benthopelagic crustaceans from the shelf	Co, Fe, Mn, Ni, Zn	–
Group 4 (N sp = 6)	Cartilaginous fish species from the shelf, and other benthic to benthopelagic bony fish species (including flatfish) from the shelf	N, As, Cr	Fe, Zn
Group 5 (N sp = 13)	Small pelagic to benthopelagic bony fish from the shelf, including most species of the Ammodytidae, Clupeidae and Sparidae families	Se	–
Group 6 (N sp = 15)	Benthopelagic to benthic bony fish species (including flatfish) from the shelf	P	–
Group 7 (N sp = 5)	Pelagic to benthopelagic bony fish species from the upper slope/deep sea (oceanic), and the jellyfish species	–	N, P, As, Cu, Ni, Se

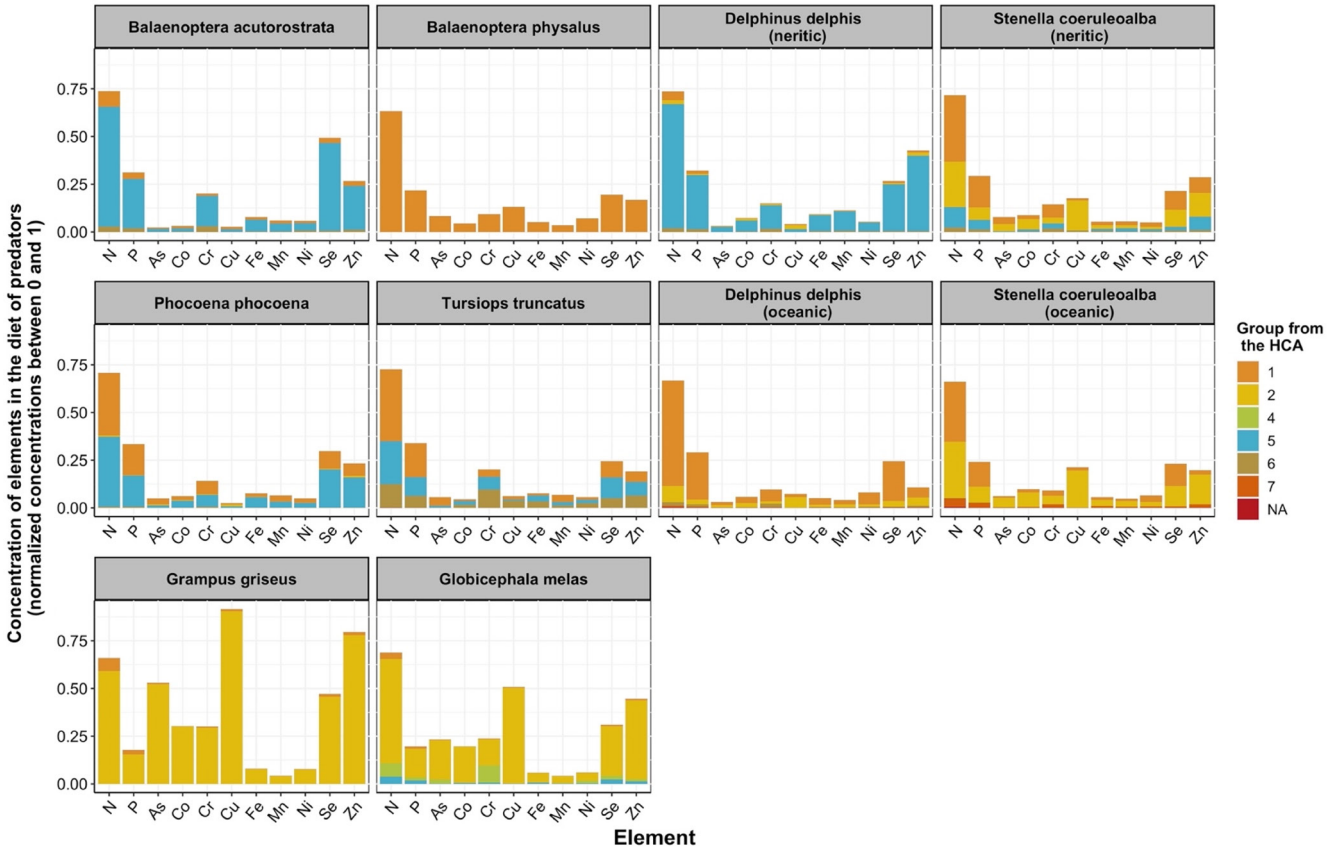

Figure 6. Average elemental composition of the diet of predators (cetacean community) from the Bay of Biscay, with one facet per predator, based on normalized prey item concentrations (in mg kg^{-1} wet weight) between 0 and 1 for each element and on the average percentage of biomass of each prey item in the diet of predators. For each element, the contribution of the different forage species groups (as defined by the hierarchical clustering analysis, HCA) to the elemental supply is also indicated by the color code. Essential elements are first listed according to their type (macro-minerals versus trace elements), then by alphabetical order within each type of elements.

organisms (Fowler 1986, Ridout et al. 1989, Asante et al. 2008, Eisler 2010a, b, Naeem et al. 2011, Cipro et al. 2018, Chouvelon et al. 2019, Pedro et al. 2019, Figueiredo et al. 2020). However, these orders of magnitude largely differed among elements, which first reflect the relative natural abundance of the different elements on Earth (Erickson 1973). These differences also probably reflect the relative usefulness of the different elements in biological functions (e.g. element N with the highest order of magnitude as major component of proteins throughout the biota, while essential trace elements with lower orders of magnitude are only implied in specific enzymatic activities). Besides, these functions depend on the type of organisms and likely lead to taxa and species differences in terms of concentrations.

The taxa and species differences we found in elemental composition are thus firstly due to well-documented physiological differences. For instance, Cu is one constituent of the respiratory pigment (hemocyanin) of crustaceans and mollusks, including cephalopods. These organisms therefore naturally accumulate Cu in relatively high proportions in their tissues (White and Rainbow 1985). Overall, crustaceans and cephalopods were shown to present higher concentrations in a number of trace elements compared to fish (Asante et al. 2008, Eisler 2010a, b, Cipro et al. 2018), these elements being specifically accumulated in the hepatopancreas (also called digestive gland) in the case of crustaceans (White and Rainbow 1986) and cephalopods (Penicaud et al. 2017). Similarly, with regard to As or N differences among fish, cartilaginous fish were already demonstrated to present higher total As concentrations than bony fish and to have a N-enriched urea content (Windom et al. 1973, Withers et al. 1994, Eisler 2010b). Among fish, sandeels *Ammodytes* spp. were also previously reported to present relatively high Se concentrations compared to other species (Pedro et al. 2019). More broadly in aquatic animals, species-specific regulation and/or detoxification mechanisms of elements (especially metals and metalloids) have been reported to maintain the homeostasis of trace essential elements and/or instead to regulate non-essential ones, leading to species significant differences in their bioaccumulation, even between taxonomically close species (Luoma and Rainbow 2005, Pan and Wang 2009). These regulation mechanisms generally involve specific metal-binding proteins such as metallothioneins or metallothionein-like proteins (Wang and Rainbow 2010), although some essential elements (e.g. Se, Zn) can also be involved

Table 5. Estimation of the percentage (%) of feeding on the different groups of forage species (as defined by the hierarchical clustering analysis, HCA) by the different cetacean community from the Bay of Biscay, NE Atlantic. Percentages ≥ 80% in a predator diet are in bold.

HCA group	*Balaenoptera acutorostrata*	*Balaenoptera physalus*	*Delphinus delphis* (neritic)	*Phocoena phocoena*	*Stenella coeruleoalba* (neritic)	*Tursiops truncatus*	*Delphinus delphis* (oceanic)	*Stenella coeruleoalba* (oceanic)	*Grampus griseus*	*Globicephala melas*
Group 1	11.3	**100***	6.5	47.7	49.8	57.3	**82.0**	45.9	9.2	4.6
Group 2	0	0	3.2	1.1	34.9	0	12.3	43.1	**90.8**	**81.1**
Group 3	0	0	0	0	0	0	0	0	0	0
Group 4	0	0	0	0	0	0	0	0	0	9.0
Group 5	**83.4**	0	**87.5**	50.1	12.8	30.0	0	0	0	5.3
Group 6	5.3	0	2.8	1.1	2.5	12.5	3.3	0.1	0	0
Group 7	0	0	0	0	0	0	1.9	10.3	0	0
NA (undetermined fish or cephalopod)	0	0	0	0	0	0.2	0.5	0.6	0	0

* Consideration of a diet exclusively based on the Euphausiid species *Meganyctiphanes norvegica* in the Bay of Biscay, following diet data available in other areas of the NE Atantic (Víkingsson 1997), with *M. norvegica* included in the group 1 by the HCA.

in the detoxification of non-essential metals such as Hg and cadmium (Cd) (Ikemoto et al. 2004, Imed et al. 2009, Siscar et al. 2014, Gerson et al. 2020). Overall, these differences among taxa and species highlight that the 'window of essentiality' – corresponding to the range of optimal concentrations for essential elements – is clearly not the same for all types of organisms.

The differences we observed among taxa or species may also be due to differences in their exposure to the elements of concern, which in turn depends on several factors such as the habitat or foraging area (potentially more or less contaminated in some elements), the food items ingested (e.g. crustaceans versus fishes), the trophic level of species, etc. However, these factors are probably minor in comparison to the species-specific physiological regulation mechanisms. We indeed observed relatively few differences among species when they were classified according to their habitat across the horizontal gradient, for instance (i.e. from coastal to oceanic areas). Interestingly, only the elements N and Zn (i.e. elements with spread-out values on density plots, and with relatively low CV%) differed significantly among species from these habitats, with higher concentrations measured in coastal species compared to the oceanic ones. Across the vertical gradient, the differences were significant for slightly more elements, with benthic species having higher concentrations than pelagic and/or benthopelagic species in N, As, Co, Cr, Mn and Ni. This pattern may be firstly due to the fact that almost all the crustacean and cephalopod species considered were classified as benthic, while having generally higher concentrations in most of these elements. Previous studies also reported differences in the concentrations of trace elements between organisms depending on benthic versus pelagic food sources, for instance (Bustamante et al. 2003, Le Croizier et al. 2016, Cipro et al. 2018), but the trends of concentrations between both types of organisms vary according to the elements considered and the study areas. Here, beyond the possible effect of habitat groups' species composition, the 'benthic > pelagic' and 'coastal > oceanic' trends we found for some elements may be partly related to the environmental features of our study system. In the Bay of Biscay, the continental shelf covers over 220 000 km^2 and two main river plumes (i.e. the Loire and the Gironde rivers) influence its hydrological and chemical structures, especially in the more coastal parts (Planque et al. 2004, Puillat et al. 2004, Waeles et al. 2004). Besides, sediments are well known to act as a sink for many trace elements having a high affinity with organic matter or fine particles, especially in coastal areas (Sharifuzzaman et al. 2016). Consequently, organisms living and feeding near sediments and/or in more coastal areas (i.e. at the vicinity of river mouths) may be more impacted by additional inputs of elements than their remote counterparts. Although food has been proven to be the dominant route of trace element uptake in marine organisms such as fish (Mathews and Fisher 2009), the intake through abiotic matrices such as sediment or aqueous phases may be not negligeable for certain species (Xu and Wang 2002, Hédouin et al. 2010). Either way, the trace element content of their food will also be affected by the

environment (sediment or aqueous phases), especially if these species are feeding on benthic detritivores or filter-feeders.

In terms of a potential effect of the species' trophic level on the variability observed in elemental composition, unfortunately our dataset did not allow us to test this effect (through the analysis of nitrogen stable isotope compositions as a proxy of trophic positions, for instance; Campbell et al. 2005, Ikemoto et al. 2008). However, only the biomagnification (i.e. increasing concentrations with increasing trophic level) of the non-essential trace element Hg is well-documented in aquatic food webs (Lavoie et al. 2013, Sun et al. 2020). Among essential elements such as those studied here, Zn is sometimes thought to biomagnify in (fish) food chains (Wang 2002, Mathews and Fisher 2008, Sun et al. 2020), but conclusions regarding other elements often differ (Reinfelder et al. 1998, Luoma and Rainbow 2005, Cheung and Wang 2008). The elements As and Ni are rather documented to biodilute in food webs, for instance, leading to lower concentrations measured in higher-trophic level species (Sun et al. 2020).

Towards a nutritional typology of marine forage species in the NE Atlantic

Based on the elemental composition in two essential macrominerals and nine trace elements, the clustering analysis separated the 78 forage species into seven groups of different elemental profiles. As it could be expected, this clustering preliminary showed a certain redundancy with the groups a priori defined according to taxa or ecological features (habitats) of species. For instance, crustaceans and/or cephalopods constituted groups separated from fish species, further highlighting the strong effect of the physiology in the differences observed and mentioned above. However, this clustering provided new insights and a more functional dimension in the definition of the quality of forage species available for predators, at least on a finer scale, based on the elemental composition and no longer on taxa or habitat and especially regarding fish prey species. The five groups containing mainly fish species (group 1 and group 4–7) were indeed characterised by very different profiles in terms of main elemental composition. This probably reflects the high diversity of element assimilation, bioaccumulation, storage and/or regulation (through excretion for instance) existing among organisms and among fish species in particular (Luoma and Rainbow 2005, Pouil et al. 2018), here the most represented taxon in terms of the number of species analysed.

According to differences in the forage species or prey groups they select, cetacean species then showed contrasting diet qualities in terms of elemental composition, although the use of concentrations of the closest taxonomical level instead of the specific value of the species (when a particular prey species could not be analysed) may have induced a bias given the high inter-species variability we found for some elements. However, for all the predators considered, more than 50% and up to 100% of the prey values used had a taxonomic level at least equal to the family or lower (i.e. genus, or the species directly), which should minimise this bias. Among the forage species analysed, when several species from a same family were analysed, they were indeed generally classified in the same nutritional group (e.g. Ammodytidae, Gadidae, Myctophidae, etc.). Overall, fish group 1 and 5 as well as group 2 (containing cephalopods) were thus estimated to be the most consumed groups by cetaceans. For group 1, this is likely because it includes fish from the Gadidae family (e.g. *Micromesistius poutassou*, *Merlangius merlangus*, *Trisopterus* spp.), the European hake *Merluccius merluccius* and cephalopods from the Loliginidae family, which are important prey species for cetaceans such as *P. phocoena* and *T. truncatus* on the continental shelf (Spitz et al. 2006b). Group 1 also encompass fish from the Myctophidae family (e.g. *Notoscopelus kroeyeri*) that are key resources for small delphinids feeding on the continental slope and in oceanic waters (Ringelstein et al. 2006, Pusineri et al. 2007). However, group 1 was unlikely to contribute to a particular elemental composition of cetacean diets, given its low or intermediate levels in all the elements analysed. Conversely, the diets of minke whales *B. acutorostrata* and small delphinids from the shelf, especially neritic common dolphins *D. delphis* (Windsland et al. 2007, Meynier et al. 2008) and to a lesser extent harbour porpoises *P. phocoena* (Spitz et al. 2006b) targeting small pelagic schooling fish from the continental shelf (e.g. Clupeidae, mackerel, horse mackerel, European anchovy or sandeels) – here mainly included in group 5 – had the highest concentrations of Se. In a similar way, group 2 containing cephalopods contributed the most to the diet of the teuthophageous (i.e. feeding on cephalopods) cetacean species *G. griseus* and *G. melas* (Spitz et al. 2011, MacLeod et al. 2014), and to a much lesser extent to the diet of striped dolphins *S. coeruleoalba* in both neritic and oceanic areas (Ringelstein et al. 2006, Spitz et al. 2006a). Consequently, the diets of these cetaceans (especially *G. griseus* and *G. melas*) were enriched in Cu and in other elements for which cephalopods had relatively high concentrations compared to fish (i.e. Co and Zn), but were depleted in P (due to the significant difference for P: fish > cephalopods).

Most of the forage fish species constituting the poorly consumed group 3 (crustaceans) and group 4, 6 and 7 (fish groups) by cetaceans actually had relatively high moisture percentages, and are also documented to present particularly low energy densities (Spitz et al. 2010b) – especially those of group 7. The fish species belonging to group 7 also presented the lowest concentrations (on a ww basis) in several essential elements (including Cu and Se), as a probable effect of biodilution considering their high water content (at least in part). On the contrary, the highly consumed group 5 by small delphinids from the shelf included energy-rich fish species (Clupeidae, mackerel, horse mackerel, European anchovy; Spitz et al. 2010b), in addition to be Se-enriched. Energy density is considered as a major determinant of food quality for cetaceans (Bowen et al. 1995, Spitz et al. 2012) and hence, energy-rich forage species can be selected by predators with high energy requirements (Spitz et al. 2010a, 2012, 2018). Therefore, similarly to energy density, some marine predator species such as cetaceans may neglect some types

of forage species and forage preferentially on prey types that optimize the fulfilling of their requirement in terms of micro-nutrients, although these nutritional needs are complex to specifically assess in wild cetaceans and were not the subject of the present study. More generally, prey selection processes are a likely combination of different filters in terms of prey characteristics (abundance, catchability, energy content and/or nutritional content including essential elements, etc.). Regardless of the mechanisms behind these selection processes, this study thus shows that cetaceans' diets generate contrasting micro-nutrient intakes within the community of cetacean species in the NE Atlantic, depending on the forage species and/or types of forage species they feed on.

Implications for predators and marine food web functioning

Whatever the diversity of forage species in the environment, our results – especially density plots considering elements individually – evidenced that predators will be mostly exposed to rather low concentrations of some elements (e.g. Co, Cu, Fe…) or high concentrations of other elements (i.e. N) through the trophic pathway, while they will face a larger range of concentrations for other elements (e.g. P, Cr, Zn…). However, the diversity in (aquatic) diet composition has been recently shown to increase the likelihood of being sufficiently provisioned in several essential micro-nutrients (and fatty acids) in humans (Bernhardt and O'Connor 2021), although also increasing the intake of some contaminants such as non-essential (and potentially toxic) trace elements. This probably also applies for marine predators like cetaceans. In that sense, our classification based on eleven elements emphasized that all prey are not interchangeable nor equivalent, as already shown for another major determinant of food quality for predators, namely the energy density (Spitz et al. 2010b). More specifically, this approach allows identifying which prey species may be interchangeable (within a same group, for instance) and which are definitively not. Even within the same nutritional group (as defined here), differences of concentrations for a given element may be indeed important too among the regrouped species (based on eleven elements). For instance, for the four well-documented essential elements in mammals that are Cu, Fe, Se and Zn, there was sometimes a major difference (expressed as a ratio) between the species with the highest concentration (on wet weight basis) and the species with the lowest concentration within a group. As such, within group 1, the ratio between the least concentrated species in Cu (i.e. the oceanic fish *Lampacnytus crocodilus*, 0.22 mg kg^{-1} ww) and the highest concentrated species (i.e. the oceanic shrimp *Pasiphaea sivado*, 16.2 mg kg^{-1} ww) equals 74. For Fe within group 7, this ratio between the lowest Fe concentration (those of the oceanic fish *Normichthys operosa*, 3.0 mg kg^{-1} ww) and the highest (those of the oceanic fish *Serrivomer beani*, 106.9 mg kg^{-1} ww) equals 36. For Se, the highest ratio is calculated within group 5 and equals 17, between the clupeid *Sprattus sprattus* (0.38 mg kg^{-1} ww) and the Ammodytidae *Hyperoplus lanceolatus* (6.37 mg kg^{-1} ww). For Zn, differences are less important, but this ratio still reaches ~3 within several groups. Some prey species or prey types can be therefore considered as 'super contributors' in certain essential elements such as Cu (e.g. benthic cephalopods) and Se (e.g. sandeels). The predators' exposure and/or the fulfilling of their needs for these elements will thus depend on the availability of these prey, and/or on their ability to capture them. Furthermore, significant differences were observed among habitats for some elements, namely N and Zn whose concentrations were lower in oceanic and/or deep-sea forage species. Any significant changes in prey availability, changes in predators' diet or foraging area due to environmental or human-induced effects (e.g. overfishing of a group of species, disturbance in optimal foraging habitats, etc.) could thus affect predatory species, although intermediate levels of most micro-nutrients may be sufficient to fulfil the nutritional needs of most predators.

As long-lived and high trophic level species, cetaceans are known to accumulate significant amounts of non-essential and potentially toxic trace elements with age and trough food, such as Cd or Hg. At an evolutionary scale, they have developed mechanisms to limit their toxic effects. For instance, the capacity to demethylate the highly toxic form of Hg (i.e. methylmercury) by sequestering Hg with Se under a non-toxic form (i.e. formation of tiemannite granules) has been reported for a long time in marine mammals (Koeman et al. 1973, Martoja and Berry 1980, Caurant et al. 1994). More broadly, the protective effect of Se against Hg but also Cd toxicity has been documented in different types of vertebrate organisms including fish, birds and mammals (Ikemoto et al. 2004, Imed et al. 2009, Siscar et al. 2014), although it is still under debate (Pelletier 1986, Gerson et al. 2020). We may thus hypothesize that any deficiency linked to diet changes may impair the protective mechanisms against toxic elements and more generally any enzymatic activity functioning (and associated biological functions) involving these essential elements in cetaceans. In the North Sea, for instance, sandeel stocks *Ammodytes marinus* collapsed drastically in the 1990s partly due to overfishing and climate change (Lindegren et al. 2018), while it constituted a major prey species for a number of predators including seabirds, seals and harbour porpoises (Santos et al. 2004, Church et al. 2019, Wilson and Hammond 2019). Sandeels' decline was then described to have potentially 1) decreased the breeding success and/or survival of kittiwakes (Oro and Furness 2002, Carroll et al. 2017), 2) increased the likelihood of starvation in harbour porpoises (MacLeod et al. 2007), 3) induced harbour seal's decline due to competition for food resources with grey seal (Wilson and Hammond 2019). In the present study, the two forage species from the Ammodytidae family (corresponding to sandeels) clearly showed the highest concentrations of Se compared to all other fish species. Hence, we may wonder into which extent this Se-enriched prey decline may have also contributed to the reported effects observed on seabird and marine mammal species whose sandeel was a major prey, these predators being notably subject to high bioaccumulation of Hg. However, mechanisms of Hg–Se interactions

are complex, not fully elucidated so far (Gerson et al. 2020), and in the absence of precise data on harbour porpoises' selenium requirements and/or measurement of the Hg:Se ratio in their tissues as an indicator of potential health risk of Hg toxicity on cetaceans (Kershaw and Hall 2019), it remains hazardous to make this assumption. As comparison, a recent study in the eastern Canadian Arctic focusing specifically on Se, Hg and essential fatty acids suggested a rather limited effect of changing prey fish communities on food quality for aquatic predators, although higher Se concentrations were also observed in sandeel fishes *Ammodytes* spp. compared to other prey fish species (Pedro et al. 2019). This could be the consequence of 1) a lower number of prey species considered compared to the present study (n = 7 versus 78), and 2) a much lower difference found for Se concentrations between sandeel fishes (1.15 ± 0.16 mg kg^{-1} ww) and other fish species (0.30–0.69 mg kg^{-1} ww) than those we observed (4.15 ± 3.14 on average for the two Ammodytidae species analysed, versus 0.70 ± 0.26 on average for the 60 other fish species). Thus, our present results based on a wider number of forage species and on a wider number of essential elements still raise the issue of prey quality including micro-nutrients (especially essential trace element contents) in the proper functioning of marine food webs.

The differences we observed in N and Zn between forage species from coastal versus oceanic and deep-sea habitats are also interesting from a predator point of view, which may live and forage in different ecosystems. Nitrogen indeed constitutes a proxy of proteins and is considered as a determinant of food quality as well (Bowen et al. 1995). Alternatively, in biological organisms, Zn has been shown to be involved in protective mechanisms against Cd toxicity, similarly to Se. Moreover, Zn deficiency can intensify Cd accumulation and toxicity (Brzóska and Moniuszko-Jakoniuk 2001). This is because Cd^{2+} and Zn^{2+} ions resemble and can compete for uptake into various cells and binding to intracellular sites. Hence, Cd may displace Zn in a number of biological processes (Brzóska and Moniuszko-Jakoniuk 2001) and in Zn-poor marine environments in particular, Cd has been shown to replace Zn as co-factor in enzymes such as the carbonic anhydrase in phytoplankton cells (Price and Morel 1990, Lee and Morel 1995). However, this has not been documented in vertebrates and for most vertebrate organisms, Cd is well-documented to be rather highly toxic, impacting for instance growth and lipid storage in fish (Pierron et al. 2007, Lucia et al. 2010). Interestingly in the Bay of Biscay, oceanic prey species of cetaceans (especially cephalopods) were reported to present particularly high concentrations of Cd, compared to more neritic prey species (Lahaye et al. 2005). We may thus wonder if this is a consequence of Zn deficiency (favouring Cd accumulation in the absence of Zn) or to effective higher Cd levels in the oceanic environment. Overall, this suggests that the availability of some essential elements such as N and Zn can vary among marine ecosystems (here coastal versus oceanic). Consequently, the key elements for defining food quality may vary from one ecosystem to another, depending on the distribution of concentrations of each element within the forage species community in the considered ecosystem. Indeed, an element may be limiting in one ecosystem and quite abundant in another. From a predator point of view, the risk associated with a potential deficiency will then not be the same according to the ecosystems, because the limiting elements are not the same according to the ecosystems.

Conclusions and prospects

Our results emphasized significant differences in the elemental composition of 78 forage species from the NE Atlantic, primarily due to physiological differences among taxa or species in terms of elemental regulation mechanisms. Crustaceans and/or cephalopods thus broadly showed higher concentrations in Co, Cu, Fe, Mn, Ni and Zn than fish, for instance, while bony fish had significantly higher P concentrations than cephalopods. Differences among species from different habitats were also revealed (with coastal > oceanic species for N and Zn, and benthic > pelagic for N, As, Co, Cr, Mn and Ni), which could be partly explained by differential elemental exposure in the different environments. The 78 forage species were then classified into contrasted nutritional groups based on their elemental composition, with some of these groups being highly consumed by certain cetacean species considered here as predators (namely the Se-enriched group composed of small schooling fish including clupeid or Ammodytidae fish, for instance, or the Cu-enriched group mainly composed of benthic cephalopods), while other groups are clearly poorly consumed. More broadly, our approach emphasized that prey essential elemental composition can be considered as another determinant of prey quality, especially for elements (namely Se and Zn) being also involved in protective mechanisms against non-essential toxic trace elements. Our results further suggested that the limiting aspect of some elements in certain ecosystems or prey may contribute to their definition as determinants of quality, also for human consumption purposes (as several forage species analysed here are also consumed by humans).

In future work, considering the speciation of some elements could be of great interest, especially for the metalloids As and Se. Here, only the total concentrations of elements were measured. Yet, the speciation can be determinant for the essentiality and/or toxicity of some of the elements considered (namely As; Baeyens et al. 2009), and the protective effect of Se against Hg in particular strongly depends on its chemical forms (Rayman et al. 2008, Ralston and Raymond 2010). Further studies may also consider potential seasonal variability in the concentration of the elements, which could depend on biological processes such as the reproduction period for some essential elements or in some species (e.g. through excretion phenomena, or concentration or dilution in the body related to weight loss or gain, etc.). Finally, investigating the potential influence of non-essential and potentially toxic trace element

concentrations (namely Hg, Cd but also lead – Pb or silver – Ag) on the dynamic of essential elements (i.e. on the variations of concentrations in essential elements), by analysing interactions between Se and Hg or Zn and Cd concentrations for instance, could constitute a step further in the definition of quality determinants in marine food webs and ecosystems.

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Author contributions

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Data availability statement

Data are available from the PANGAEA Repository: <https://doi.org/10.1594/PANGAEA.940861> (Chouvelon et al. 2022).

Supporting information

The supporting information associated with this article is available from the online version.

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