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Original Article

Factors influencing spatial variability in the trophic transfer of essential nutrients from plankton to European sardine (*Sardina pilchardus*)

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Abstract

Phytoplankton play a crucial role in marine food webs as they supply essential fatty acids (FA) to higher trophic levels, from small pelagic fish to top predators, through the intermediary action of zooplankton. Thus, the composition and nutritional value of plankton communities expectably influence abundance and condition of predators potentially leading to spatial variation in trophic transfer. Through the analysis of the FA profile of zooplankton and European sardine (*Sardina pilchardus*), and of the community composition of phytoplankton and zooplankton, we investigated (i) large-scale spatial variability in the trophic transfer of FA from plankton to small pelagic fish and (ii) the factors influencing this transfer in the English Channel. We found that the FA composition of zooplankton and sardine differed between the western and eastern basins of the English Channel (WEC and EEC, respectively), reflecting differences in plankton community composition. The FA profile of sardine varied further with regard to energy allocation strategies and conditions. This suggests a strong bottom-up influence of plankton community composition on the spatial variability of FA transfer with an additional impact of fish physiological status. Understanding the reasons behind the separation pattern of sardines between the WEC and the EEC would be helpful to inform fisheries and ecosystem-based management advice.

Keywords: zooplankton; English Channel; fatty acids; taxonomic composition; fish physiology; ecosystem functioning

Introduction

Understanding the spatial distribution and variability in the trophic transfer of essential nutrients, such as certain fatty acids (FA), is crucial for a better grasp of ecosystem functioning (Brett and Müller-Navarra 1997, Galloway and Winder 2015). This knowledge can enhance our understanding of the spatial repartition of feeding grounds and of the fluctuations in fish stock recruitment (Garrido et al. 2007b). Furthermore, it could be used to develop more effective fisheries management strategies (Pethybridge et al. 2014) and to better inform marine protected area planning. Eicosapentanoic acid [20:5 ($n-3$), EPA], docosahexaenoic acid [22:6 ($n-3$), DHA], and arachidonic acid [20:4 ($n-6$), ARA] are essential nutrients for most marine animals as they are required for optimal physiological performance and health (Tocher 2003, Gladyshev et al. 2018). Furthermore, they must be obtained from the diet, as they cannot, or only to a limited extent, be synthesized by the consumer (Tocher 2010, Galloway and Winder 2015).

In the marine realm, essential fatty acids (EFA) are synthesized *de novo* by primary producers at the base of the food webs, which are mainly represented by phytoplankton (Galloway and Winder 2015). Herbivorous zooplankton incorporate and accumulate FA from their phytoplanktonic prey, thereby channelling these organic compounds to the next trophic level, including small pelagic fish, which in turn, serve as a vector of EFA to higher trophic levels (Dalsgaard et al. 2003, Mathieu-Resuge et al. 2024).

However, spatial variability in the distribution and trophic transfer of FA can be expected. The proportional composition of FA in phytoplankton varies with taxonomic composition and environmental condition (Galloway and Winder 2015) as does the quality and ingestability of phytoplankton for predators, e.g. with regard to cell morphology (Brett and Müller-Navarra 1997). The trophic transfer of FA is conservative—meaning the prey FA composition is largely retained in the predator—allowing the use of certain FA as trophic biomarkers (FATM) (Dalsgaard et al. 2003). Grazers and predators such as zooplankton and small pelagic fish may still contribute to the spatial variability in their FA profile via their taxonomical composition and physiological state combined with varying abiotic conditions leading to different feeding and energy storage/allocation strategies (Garrido et al. 2007b, Kattner and Hagen 2009, Bertrand et al. 2022). For instance, the FA composition of zooplankton sampled in the Puget Sound (US Northwest Coast) was mainly driven by taxonomic differences followed by season and region (Hiltunen et al. 2022).

Another example stands in the FA profile of storage lipids of *Acartia clausi* and *A. tonsa* that displayed species-specific responses to temperature (Werbrouck et al. 2016). For intermediate and higher trophic-level species such as the European sardine (*Sardina pichardus*), albacore tuna (*Thunnus alalunga*), and chub mackerel (*Scomber japonicus*), FAs were influenced by the individual's length in addition to phyto- and zooplankton community composition and biomass (Pethybridge et al. 2014, Bertrand et al. 2022, Ohshimo et al. 2022). Length could influence trophic transfer through ontogenetic shifts in diet, length-dependent metabolic rate, and energy allocation strategy with regard to growth and reproduction (Pethybridge et al. 2014, Bertrand et al. 2022, Ohshimo et al. 2022). Thus, a contribution of all trophic levels to spatial variability in the distribution and trophic transfer of FA may be expected.

To better understand spatial variation in the trophic transfer of FA, the objectives of our study were to (i) assess the spatial variability of zooplankton and sardine FA profiles in the English Channel (EC) considering phytoplankton and zooplankton community composition and environmental parameters as potential drivers and (ii) evaluate factors influencing the trophic transfer of EFA from zooplankton to the European sardine considering zooplankton FA proportion, environmental parameters (i.e. depth, temperature, and salinity), and fish physiology (i.e. length, condition, and spawning activity).

We hypothesize that the spatial pattern in FA distribution will differ between trophic levels due to varying locomotive abilities of zooplankton and small pelagic fish assuming that the EC provides a heterogeneous environment, especially between the western EC (WEC) and eastern EC (EEC) basins, as described by Dauvin (2012). Zoo- and phytoplankton with limited mobility and no active horizontal migration will experience similar environmental conditions. This lack of mobility, combined with small-scale variability in abiotic parameters and taxonomic composition, may result in a more heterogeneous spatial pattern in their FA profiles compared to small pelagic fish. Small pelagic fish occupy larger feeding areas and encounter more diverse environmental conditions and a variety of prey. They might hence work as spatial smoothers, reducing spatial variability in the availability of FA due to horizontal movement.

The European sardine is a pelagic species feeding on phyto- and zooplankton (Garrido et al. 2008, Nikolioudakis et al. 2012) and channelling energy to seabirds, marine mammals, and piscivorous fish (Campo et al. 2006, Certain et al. 2011). The sardine FA profile has been studied in the Mediterranean (Biton-Porsmoguer et al. 2020, Šimat et al. 2020), the Bay of Biscay (Mathieu-Resuge et al. 2024), the Iberian Sea (Garrido et al. 2008), and in the waters off Morocco (Mkadem and Kaanane 2020). Recently, Mathieu-Resuge et al. (2024) found significant differences in sardine FA profiles between the EC, the Bay of Biscay, and the Gulf of Lions that might be related to prey composition. While EC sardines were characterized by the calanoid trophic markers 20:1 ($n-9$) and 20:1 ($n-11$), FATM indicated a diatom-based food web in the Bay of Biscay and a dinoflagellate-based food web in the Golf of Lions. In the Bay of Biscay and parts of the Mediterranean, decreases in size-at-age, weight-at-age, and condition-at-age were observed, and food quantity and quality were suggested as possible drivers (Brosset et al. 2015, 2016, Menu et al. 2023). With regard to EC sardines, predictions based on an energetic model suggested an average decrease of 3.5% in size and 12.4% in weight since 2000 (Menu et al. 2023). Further information on sardines in this latter region remains scarce (Menu et al. 2023), but might be of interest to enhance understanding of the observed changes in sardine stocks inhabiting different environments. The present study provides valuable information with regard to ongoing and future changes in trophic dynamics as ocean warming might cause a potential decrease in EFA in phytoplankton (Hixson and Arts 2016).

Materials and methods

Sampling

Environmental, plankton, and fish samples (Fig. 1) were collected in the EC during the Channel Ground Fish Survey (CGFS; Giraldo et al. 2021 , https://doi.org/10.17600/18001250) in autumn 2021 (mid-September to mid-October) [see Supplementary Material (SM) Section S1]. The sampling period corresponded to the autumn spawning period of sardines taking place in October (Coombs et al. 2005, Stratoudakis et al. 2007). A subsample of minimum 5 sardine individuals was randomly selected at each station (total n sardines = 249, total n stations = 45) for subsequent lipid analysis of dorsal muscle. Salinity, temperature, and depth were measured using respective probes (Conductivity, Temperature, Depth sensors (CTD)) (n = 122). Phytoplankton and mesozooplankton (200 to >1000 μm) were sampled at 11 stations for taxonomic analysis. Mesozooplankton (500–1000 μm) was sampled at 39 stations and analysed for FA composition. Most samples, used in these different analyses, were collected at the same station. If this was not feasible, information from the closest sampling stations was used instead to investigate the relation among different trophic levels.

Lipid analysis

Lipid class composition quantification

Neutral lipids (mostly reserve lipids) were analysed via high-performance thin-layer chromatography and quantified by using a scanning densitometer. Eight neutral lipid classes (categorized as storage lipids: free FA, sterol esters, glyceride ethers, monoacylglycerol, diacylglycerol, wax ester, and triacylglycerol; considered as structural lipids: sterols) were identified based upon standards (Sigma-Aldrich, France) and colouring techniques. Results were expressed as milligrams of each identified neutral lipid class per gram of muscle/zooplankton wet weight. From these measurements, the triglyceride–sterol (TAG-ST) ratio was calculated to serve as a lipid condition index. This ratio reflects the amount of energy reserves stored as triglycerides, normalized by the structural lipid content represented by sterols. Sterols, as components of cell membranes, provide an indirect measure of structural biomass, which can be associated with the individual's size. The TAG–ST ratio thus enables comparison of energy reserves across individuals of different sizes.

FA analysis

Fatty acid methyl ester (FAME) composition of sardine muscle and zooplankton (500–1000 μm) was determined using a gas chromatograph system equipped with a JW DB wax, with an on-column injector at 60°C and an flame ionization detector at 300°C. FAME content was converted into FA content based on 23:0 internal standard. Total FA content was calculated as the sum of all identified FA. FA data were expressed

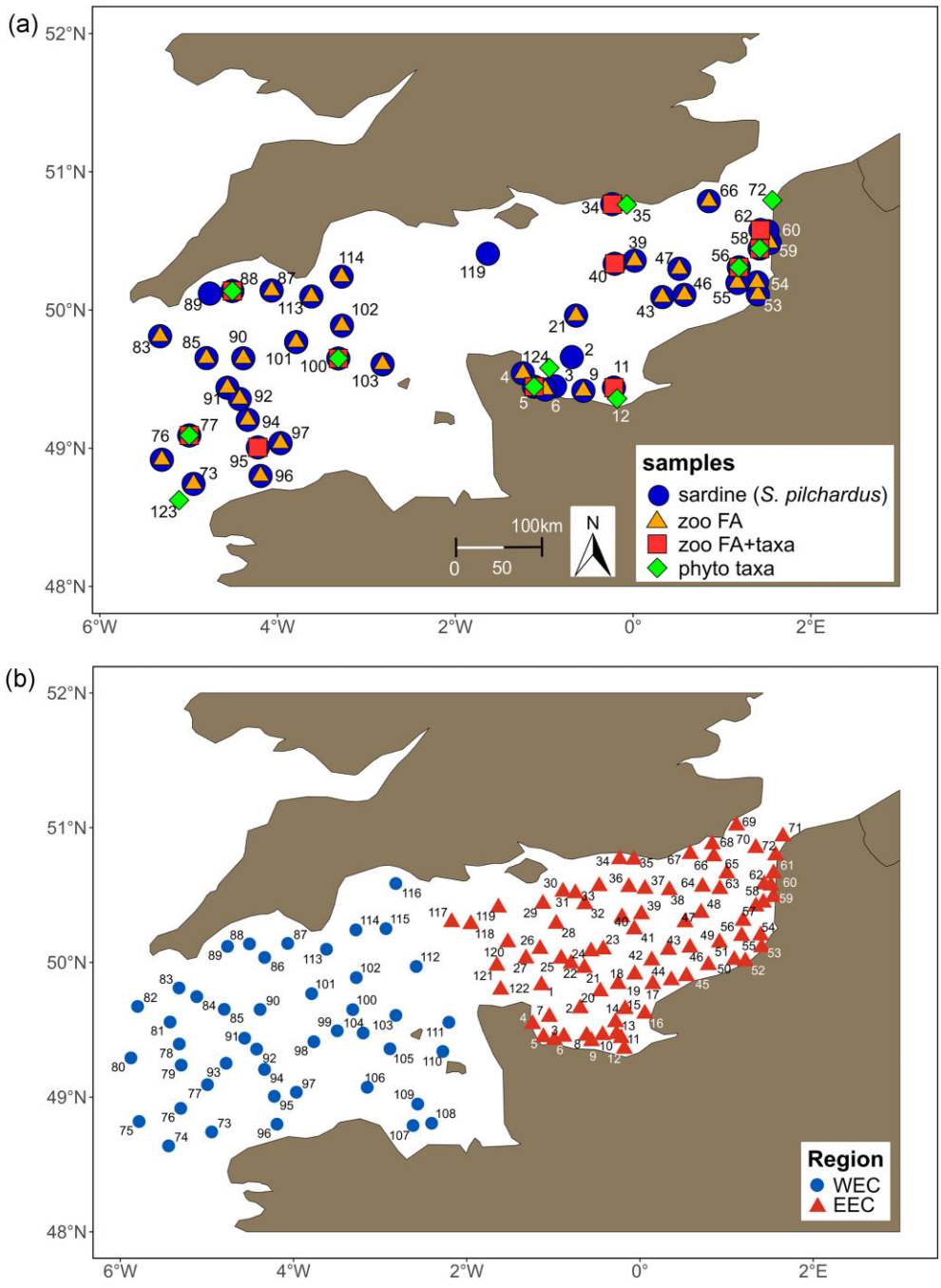

Figure 1. Location of sampling stations during the CGFS in autumn 2021. (a) Sardine (*Sardina pilchardus*) individuals (dots); zooplankton collected for lipid analysis only (triangles); zooplankton collected for lipid analysis and taxonomic analysis (quadrats); and phytoplankton (rhombs). (b) Sampling stations of environmental parameters (surface temperature, salinity, and depth) situated in the WEC (dots) and the EEC (triangles).

as a proportion of the total FA composition (%). For a full description of lipid analysis, see SM Section S2.

FA trophic markers

The following FA trophic markers (FATM) were used to investigate the trophic structure from plankton to sardines. The presence of diatoms was inferred from 16:2 ($n-4$), 16:3 ($n-4$), and 16:4 ($n-1$) marking diatoms only, from 16:1 ($n-7$) marking additionally Eustigmatophycea and Pavlovophycea, and from a high ratio of EPA/DHA. Dinoflagellates were marked by a low EPA/DHA ratio and high level of 18:5 ($n-3$) (Dalsgaard et al. 2003, Remize et al. 2022). The long-chain monounsaturated FA (MUFA) 20:1 ($n-9$) and 22:1 ($n-11$) were used as FATMs for *Calanus* spp. (Dalsgaard et al. 2003) (see SM Section S3).

Phytoplankton and zooplankton community composition

Phytoplankton taxonomical composition was analysed using the image acquisition system FlowCam and *EcoTransLearn* R-package (https://gitlab.ifremer.fr/LER-BL/EcoTransLearn, Wacquet and Lefebvre 2022). For further specifications see SM Section S4.

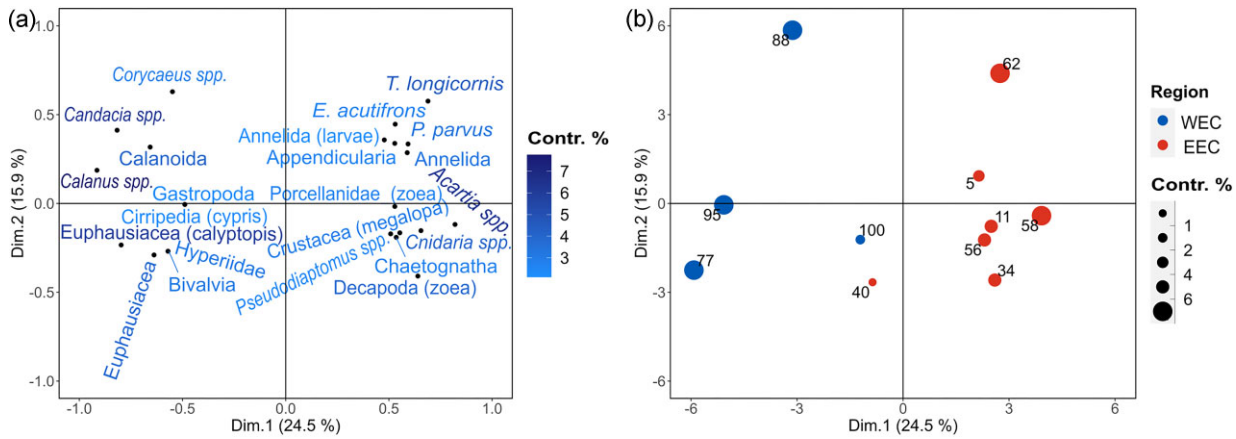

Figure 2. PCA taxonomic composition of zooplankton (500–1000 μm), first and second principal components. (a) Taxa (the darker the taxon, the higher its contribution to the first component); only taxa with a contribution >2% are displayed. (b) Sampling stations (the bigger the dot, the higher its contribution to the first component); blue and red dots were located in the WEC or the EEC, respectively; numbers represent sampling station ID.

Zooplankton samples scanned by a ZooScan (Gorsky et al. 2010) were subsequently treated by the machine-learning web application Eco-Taxa (http://ecotaxoserver.obs-vlfr.fr) for species determination and validated by zooplankton taxonomists. Species composition was determined for three size classes: 300–500, 500–1000, and >1000 μm.

Statistical analyses

Statistical analyses were conducted in R (software environment v4.1.2) with a significance level (P) set to $\leq .05$.

Spatial differences of environmental drivers and sardine biological parameters

Differences in environmental drivers (temperature, salinity, and depth) between the EEC and the WEC were tested (see SM Section S5).

Differences in sardine's length, weight, TAG–ST ratio, and Le Cren's condition index (weight-to-length ratio; SM Section S6) between the basins were evaluated using generalized linear mixed models (GLMM) (see SM Section S7).

Assessments of spatial patterns in FA profile and taxonomic composition

Principal components analysis (PCA) was used to assess spatial patterns in (i) FA profiles of sardines and zooplankton (500–1000 μm) and (ii) taxonomic composition of zooplankton (500–1000 and 300 to >1000 μm) and phytoplankton (see SM Section S7). The quantity of wax esters was used as a supplementary variable in the PCA applied to zooplankton FA.

Factors influencing trophic transfer

GLMM and generalized additive models (GAM) were used to evaluate the influence of environmental and sardines biological characteristics on the trophic transfer of three EFA (EPA, DHA, and ARA) from zooplankton to sardines. Proportion of one EFA in sardines was modelled as a function of the fixed covariates: proportion of the respective EFA in zooplankton, Le Cren's condition index (both continuous variables), spawning activity, and region (both categorial variables). Spawning activity was determined from gonad maturation status with premature and mature individuals classed as spawning, while post-spawning and immature individuals were classed as non-spawning (see SM Section S6). The covariate 'region' was used as a proxy for the environmental state in the model as environmental parameters (temperature, salinity, and depth) were strongly correlated and differed significantly between the WEC and the EEC (see SM Section S5). For further details on model construction, selection, and verification, see SM Section S8.

Results

Biological parameters of sardines

Sardines collected in the WEC were significantly smaller in length and lighter in weight than sardines in the EEC but did not differ in terms of condition (TAG–ST ratio and Le Cren's index). Further, inter-regional differences were observed with regard to the sex ratio and spawning activity. More females were caught in the East (females: 69, males: 48), whereas males were more numerous than females in the West (males: 71, females: 58). Females and males differed significantly in terms of length and weight but not with regard to the TAG–ST ratio and Le Cren's condition index. A PCA applied to the FA profile of males and females did not indicate intersexual differences in the overall FA profile (see SM Section S8, Fig. S32E). More spawning individuals were found in the EEC (~95% of all individuals) than in the WEC (~68%).

Taxonomic composition of zoo- and phytoplankton

Zooplankton

Zooplankton of the size ranges 300–500, 500–1000, and >1000 μm represented, respectively, 90%, 9%, and 1% of the overall 300 to >1000 μm abundance. The first three principal components of a PCA implemented with taxonomic data of the size class 500–1000 μm explained 24.5%, 15.9%, and 11.8% of the variance, respectively. Differences were observed in the community composition between the WEC and the EEC (Fig. 2). These differences were also obtained when using a non-size-differentiated dataset including the entire size range sampled (see SM Section S9). Taxa contributing mostly to this differentiation were *Candacia* spp., *Calanus* spp., Euphausiacea larvae and Euphausiacea for the WEC; and *Acartia* spp.

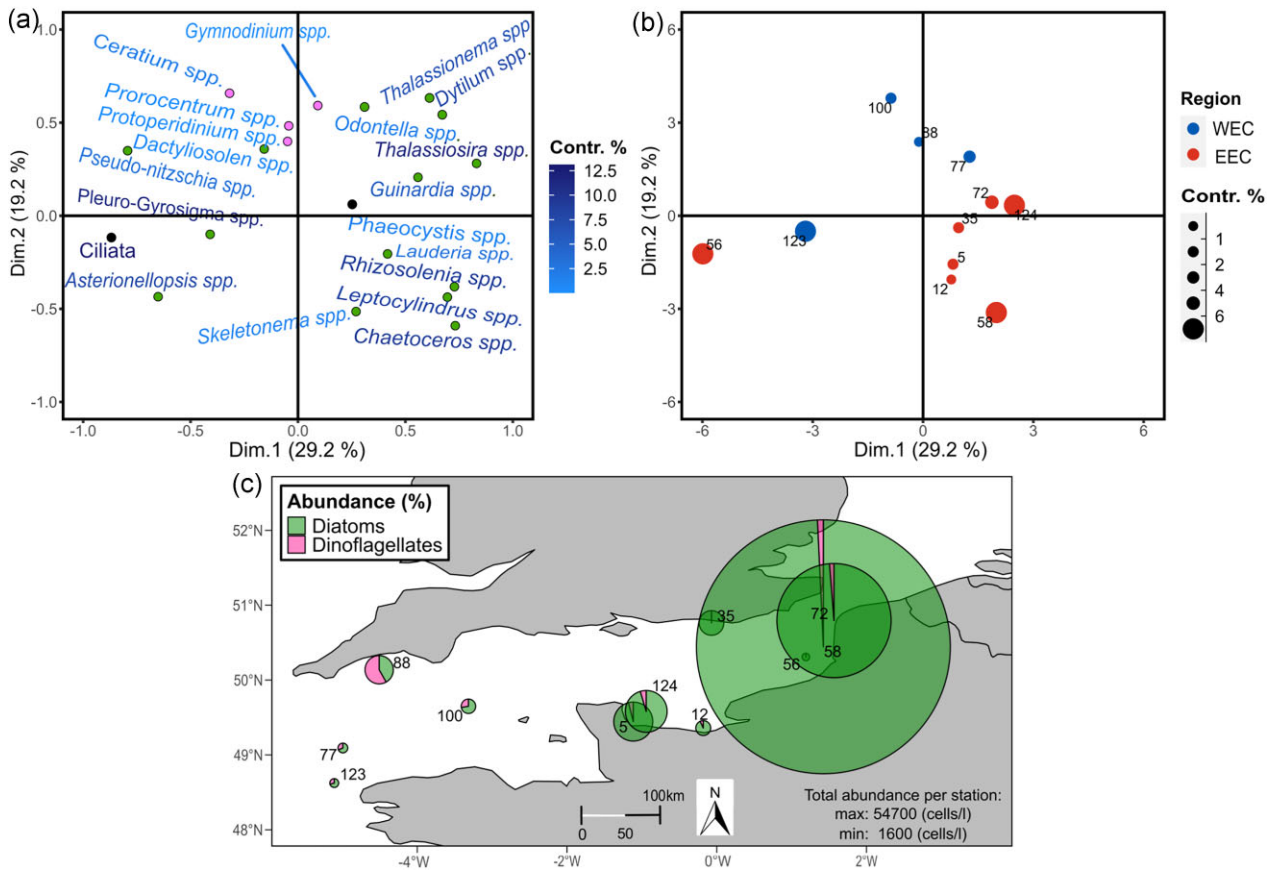

Figure 3. PCA taxonomic composition of phytoplankton, first and second principal components. (a) Taxa (the darker the taxon, the higher its contribution to the first component); only taxa with a higher contribution than 1% are depicted; pink, green, and black dots represent dinoflagellate, diatom, and other species, respectively. (b) Sampling stations (the bigger the dot, the higher its contribution to the first component); blue and red dots were located in the WEC or the EEC, respectively; numbers represent sampling station ID. (c) Relative abundance of diatoms (green) and dinoflagellates (pink) to total abundance per station (size of pie charts represents abundance in cells/l).

and *Temora longicornis* for the EEC (Fig. 2). When using all size classes, *Paracalanus parvus*, annelid larvae, and *Euterpina acutifrons* characterized the EEC whereas *Calanus* spp., crustacea larvae, *Candacia* spp., *Corycaeus* spp., and Oithonidae characterized the WEC (see SM Section S9).

Phytoplankton

Differences in phytoplankton taxonomic composition between the EEC and the WEC were shown by the first two axes of a PCA, representing 48.4% of the overall variance (Fig. 3a and b). Diatom species dominated in the EEC, whereas diatoms and dinoflagellates characterized the WEC (Fig. 3). Taxa that contributed the most to overall abundance and that were characteristic for the EEC were *Chaetoceros* spp., *Guinardia* spp., *Leptocylindrus* spp., and *Rhizosolenia* spp. The WEC was characterized by the diatom genera *Thalassionema* spp., *Thalassiosira* spp., and *Dytilum* spp. and by several dinoflagellate genera such as *Gymnodinium* and *Protoperidinium*. Dinoflagellates displayed, however, lower abundance and contribution to the first axis of the PCA compared to diatoms.

Spatial pattern of the FA profile of zooplankton and sardine

For zooplankton, 43 FA were identified. Overall, saturated FA were dominated by palmitic acid (16:0, ~16%). The dominant MUFA were palmitoleic acid 16:1 (*n*−7) (~4%) and oleic acid 18:1 (*n*−9) (~4%). Polyunsaturated FA (PUFA) were dominated by DHA (~23%) and EPA (~18%) (Table 1).

For sardine, we identified 45 FA. As for zooplankton, 16:0 was the dominant saturated FA (~21%), whereas 18:1 (*n*−9) (~9%) followed by 16:1 (*n*−7) (~4%) and 18:1 (*n*−7) (~3%) were the most abundant MUFA. PUFA were dominated by DHA (~22%) followed by EPA (~11%) (Table 1).

The complete set of FA of sardines and zooplankton is provided in the SM (Section S10).

Spatial segregation patterns

The first two components of the PCA explained 59.4% of the variance in sardine FA and 49.0% of the variance in zooplankton FA profiles (Fig. 4). A clear spatial segregation pattern was visible for both zooplankton and fish. Zooplankton from the WEC was characterized by a higher proportion of the Calanus markers 22:1 (*n*−11) (~1.8% of total FA) and 20:1 (*n*−9) (~0.8% of total FA) when compared to zooplankton from the EEC (~0.1% and 0.3% of total FA, respectively). The positioning of wax ester quantity on the negative side of the first axis of the PCA applied to zooplankton indicated a higher quantity of wax esters in zooplankton in the WEC compared to the EEC (Fig. 4a and b). Similarly, diatom versus dinoflagellates markers in zooplankton [16:2 (*n*−4), 16:3 (*n*−4), 16:4 (*n*−1), 16:1 (*n*−7), and 18:5 (*n*−3), ratio EPA/DHA] indicated

Table 1. FATMs and 20 most important FAs for zooplankton (500–1000 μm) and sardine (*Sardina pilchardus*) caught in the WEC and the EEC during autumn 2021.[a]

	 WEC $n = 20$ Mean ± SD	EEC $n = 19$ Mean ± SD	 WEC $n = 129$ Mean ± SD	EEC $n = 117$ Mean ± SD
	Saturated FA (%)			
14:0	6.7 ± 2.3	4.6 ± 1.9	3.7 ± 1.0	3.9 ± 1.1
16:0	16.0 ± 1.0	15.6 ± 1.2	20.9 ± 2.1	21.5 ± 1.2
18:0	3.6 ± 1.1	5.2 ± 1.0	5.0 ± 0.6	6.0 ± 0.8
Total SFA	28.6 ± 1.2	28.5 ± 1.9	31.6 ± 0.9	33.5 ± 0.9
	Monounsaturated FA (%)			
16:1 (*n*−7)	**3.6 ± 1.0**	**5.4 ± 1.5**	**3.7 ± 1.0**	**5.1 ± 1.4**
18:1 (*n*−9)	4.3 ± 1.3	3.3 ± 1.3	7.9 ± 3.2	11.5 ± 2.9
18:1 (*n*−7)			2.4 ± 0.5	3.3 ± 0.6
20:1 (*n*−11)	0.1 ± 0.0	0.5 ± 0.4	0.3 ± 0.2	0.1 ± 0.1
20:1 (*n*−9)	**0.8 ± 0.5**	**0.3 ± 0.2**	**2.1 ± 1.2**	**1.7 ± 0.5**
22:1 (*n*−11)	**1.8 ± 1.6**	**0.1 ± 0.1**	**1.9 ± 1.6**	**0.1 ± 0.2**
22:1 (*n*−9)	0.2 ± 0.1	0.1 ± 0.1	0.5 ± 0.2	0.5 ± 0.3
Total MUFA	13.9 ± 2.9	14.2 ± 2.8	21.4 ± 3.3	24.1 ± 2.5
	Polyunsaturated FA (%)			
16:2 (*n*−4)	**0.4 ± 0.2**	**0.7 ± 0.5**	**0.2 ± 0.2**	**0.4 ± 0.3**
16:3 (*n*−4)	**0.2 ± 0.1**	**0.7 ± 0.7**	**0.1 ± 0.2**	**0.4 ± 0.3**
16:4 (*n*−1)	**0.7 ± 0.3**	**1.4 ± 0.7**	**0.2 ± 0.3**	**0.5 ± 0.4**
18:2 (*n*−6)	1.9 ± 0.6	0.9 ± 0.2	1.2 ± 0.4	0.6 ± 0.2
18:3 (*n*−3)	1.1 ± 0.8	1.2 ± 0.6	1.1 ± 0.3	0.7 ± 0.3
18:4 (*n*−3)	4.7 ± 2.2	2.7 ± 1.3	2.1 ± 0.6	1.6 ± 0.5
18:5 (*n*−3)	**0.3 ± 0.2**	**0.1 ± 0.1**		
20:4 (*n*−6)	0.8 ± 0.3	1.5 ± 0.4	1.1 ± 0.4	1.3 ± 0.3
20:5 (*n*−3)	16.1 ± 2.4	20.9 ± 2.2	10.5 ± 2.3	12.7 ± 1.9
22:4 (*n*−6)	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.2	0.3 ± 0.2
22:6 (*n*−3)	25.8 ± 3.7	20.8 ± 3.4	25.7 ± 6.8	18.9 ± 5.3
EPA/DHA	**0.6 ± 0.3**	**1.1 ± 0.3**	**0.4 ± 0.1**	**0.7 ± 0.1**
Total PUFA	56.1 ± 3.3	54.9 ± 2.5	46.3 ± 3.7	41.8 ± 2.5

[a]Values are reported as mean ± standard deviation by region. *n* indicates number of stations. FATM are written in bold.

the presence of a silica-rich diatoms-based food web in the EEC and a more dinoflagellate-based food web in the WEC (Table 1).

Sardines displayed similar patterns. Both Calanus markers were associated to the western stations. The proportion of 22:1 (*n*−11) was more than twice as high in western sardines (WEC: ∼1.92% of total FA) than in eastern sardines (EEC: ∼0.11% of total FA). A dominance of diatom-rich diet in the EEC sardines was indicated by the respective markers. The dinoflagellate marker 18:5 (*n*−3) was not detected in the FA profile of sardines.

Factors influencing trophic transfer of EFA

Factors influencing the trophic transfer of EPA, DHA, and ARA from zooplankton to sardine were investigated using GLMM and GAM (Table 2 and Figs 5–7).

Proportions of the EFA were significantly higher in non-spawning than in spawning fish as indicated by negative estimates and *P*-values. Negative estimates for EPA and ARA indicated significantly higher proportions of EPA and ARA in the sardines sampled in the EEC compared to those collected in the WEC (*P*-value: <.001, <.001, respectively). Proportions of EPA and ARA were positively correlated with their proportion in 500–1000 μm zooplankton (*P*-value: <.001, <.001, respectively). Sardine and zooplankton DHA proportions were not significantly correlated (*P*-value: 0.85). Le Cren's condition index significantly influenced the proportion of EPA but was not correlated to sardine's DHA and ARA proportions (*P*-values: .047, .25, .82, respectively). Details on the approach to model selection and verification are given in SM Section S8.

Discussion

Spatial variability in the FA composition of zooplankton and sardines was observed with FA profiles differing between the WEC and the EEC. This pattern reflects variations in the taxonomic composition of phyto- and zooplankton, as well as environmental conditions, indicating a strong bottom-up control of the transfer of FA.

The transfer of EPA, DHA, and ARA from zooplankton to sardine was influenced by dietary proportions of EPA, DHA, and ARA in zooplankton, as well as sardines' spawning activity, body length, and condition. This suggests that morphological and physiological characteristics of sardines might be further drivers of the observed spatial pattern in sardine FA profiles as sardines' body length and spawning activity differed between the EEC and the WEC.

Potential drivers of spatial variability of FA profiles—plankton community composition and biological parameters of sardine

Phyto- and zooplankton community composition differed between the EEC and the WEC possibly due to differences in hydrological conditions (Beaugrand et al. 2000). Dinoflagellate species displayed a higher relative contribution to the community in the WEC compared to the EEC,

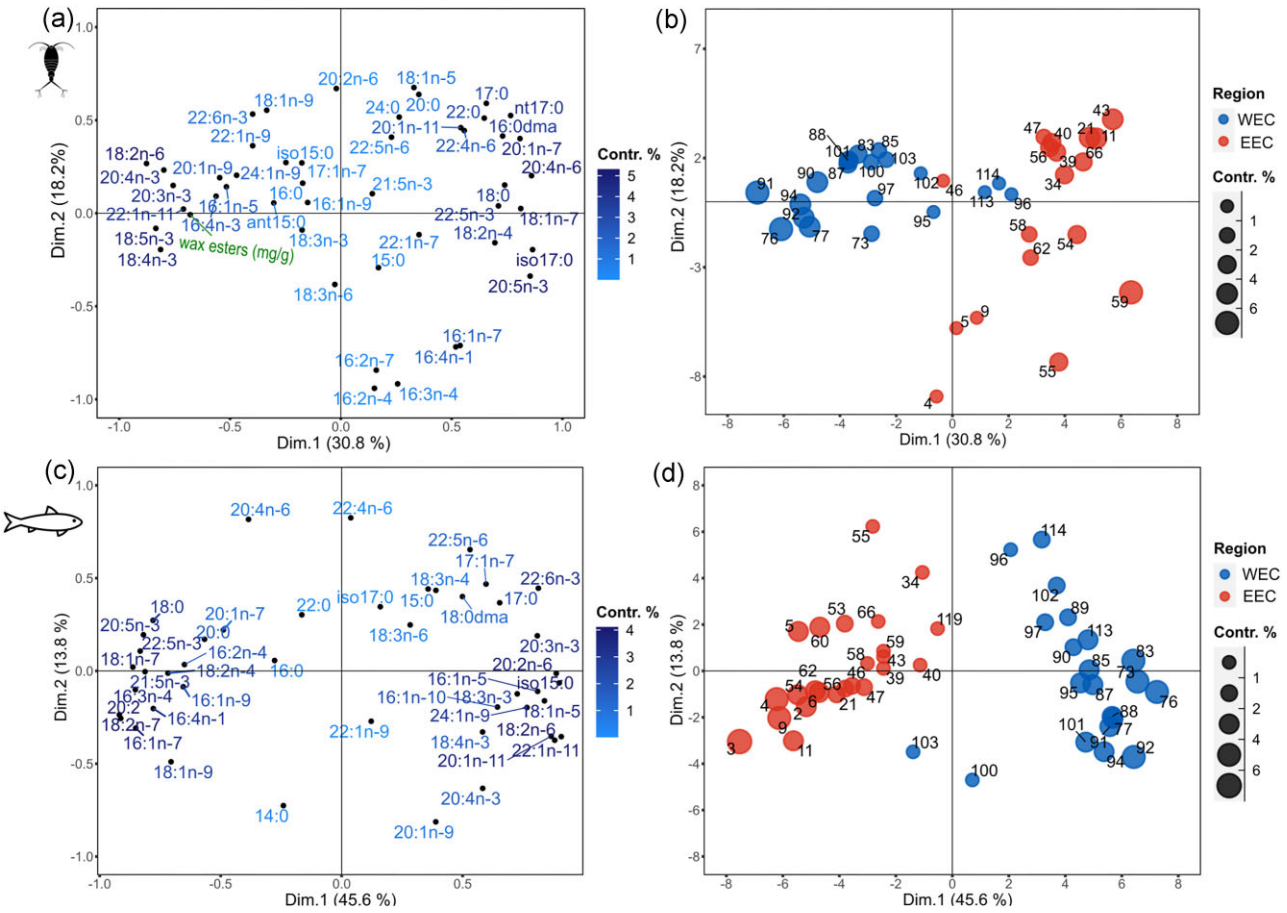

Figure 4. First and second components from a PCA on the FA profiles of zooplankton (500–1000 μm) (a and b) and sardine (*ardina*) (c and d) collected in the WEC (blue) and EEC (red) during autumn 2021. Panels (a) and (c) display FA (the darker the taxon, the higher its contribution to the first component). Panels (b) and (d) display sampling stations (the bigger the dot, the higher its contribution to the first component; numbers represent sampling station ID).

Table 2. Factors influencing trophic transfer of EFAs between zooplankton and sardine (*Sardina pilchardus*) caught in the EC in autumn 2021.[a]

			EPA	DHA		ARA
Intercept (SE)			−1.52 (0.22)***	−0.29 (0.43)		−4.26 (0.17)***
edf (s)/estimates (SE)	Zooplankton FA* region	WEC	1.0 (s)*	0.01 (0.02)	Zooplankton FA	0.17 (0.04)***
		EEC	4.3 (s)***	−0.01 (0.01)		
	Le Cren's index* region	WEC	3.0 (s)	−0.77 (0.46)	Le Cren's index	−0.04 (0.15)
		EEC	1.0 (s)*	−0.86 (0.36)*		
	Spawning		−0.27 (0.03)***	−0.18 (0.06)**	Spawning	−0.29 0.04) ***
	Region		−0.37 (0.22)	0.56 (0.58)	Region	−0.15 (0.04)***
AIC			−1223	−662		−2075.5
Type			GAM	GLMM		GLMM
n			233	233		234

[a]Estimates with standard error (SE) indicate significant and non-significant positive or negative correlations between a covariate and the proportion of the respective EFA in sardine. Zooplankton FA indicates the proportion of the respective EFA in zooplankton, Le Cren's index represents fish condition, spawning indicates spawning activity, region represents the western and eastern basins of the EC. AIC: Akaike's Information Criteria; type: model used; *n*: number of sampling stations; (s): parameters integrated in the model as a spatial smoother; *edf*: estimated degrees of freedom for the smoothed terms. ***$P < .001$, **$P < .01$, and *$P < .05$.

a finding that was also reported by other studies conducted in autumn (Widdicombe et al. 2010, White et al. 2015).

The WEC zooplankton community was rather oceanic as indicated by the presence of taxa like *Calanus* spp., *Candacia* spp., and Euphausiacea. In contrast, the EEC was characterized by the presence of taxa associated to coastal regions such as *T. longicornis*, *P. parvus*, *E. acutifrons*, and *Acartia* spp. (Fransz et al. 1991, Sautour and Castel 1993, Krause et al. 1995).

The WEC is deeper and influenced by Atlantic waters whereas the EEC is shallower with a higher turbulence (Stanford and Pitcher 2004, Dauvin 2012) thus favouring diatom species instead of dinoflagellates (Margalef 1978). Furthermore, the EEC is characterized by high riverine discharges (Stanford and Pitcher 2004, Dauvin 2012), which probably

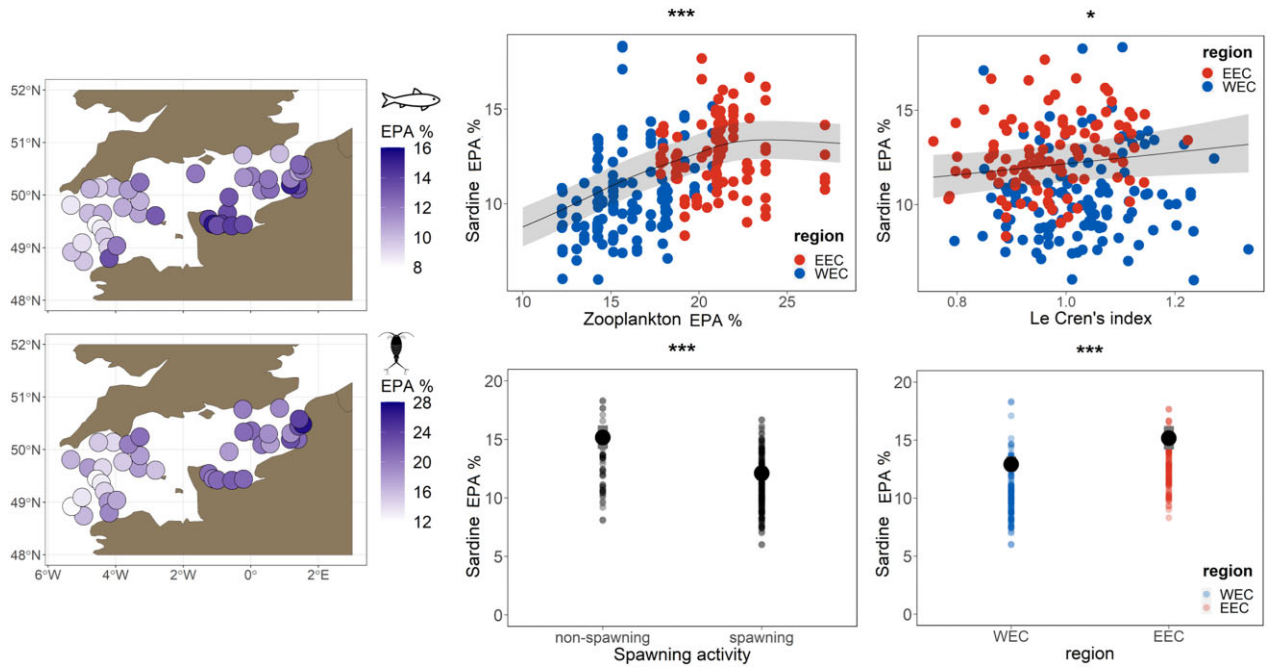

Figure 5. Factors influencing trophic transfer of EPA revealed by GAM. The relation of EPA percentage in zooplankton (500–1000 μm) and sardine (*Sardina pilchardus*) and all significant factors influencing trophic transfer revealed by the GAM are displayed. Significance level is displayed in the heading of the respective plots: ***$P < .001$, **$P < .01$ and, *$P < .05$. Zooplankton and sardines were caught in the EEC (red) and the WEC (blue) during autumn 2021.

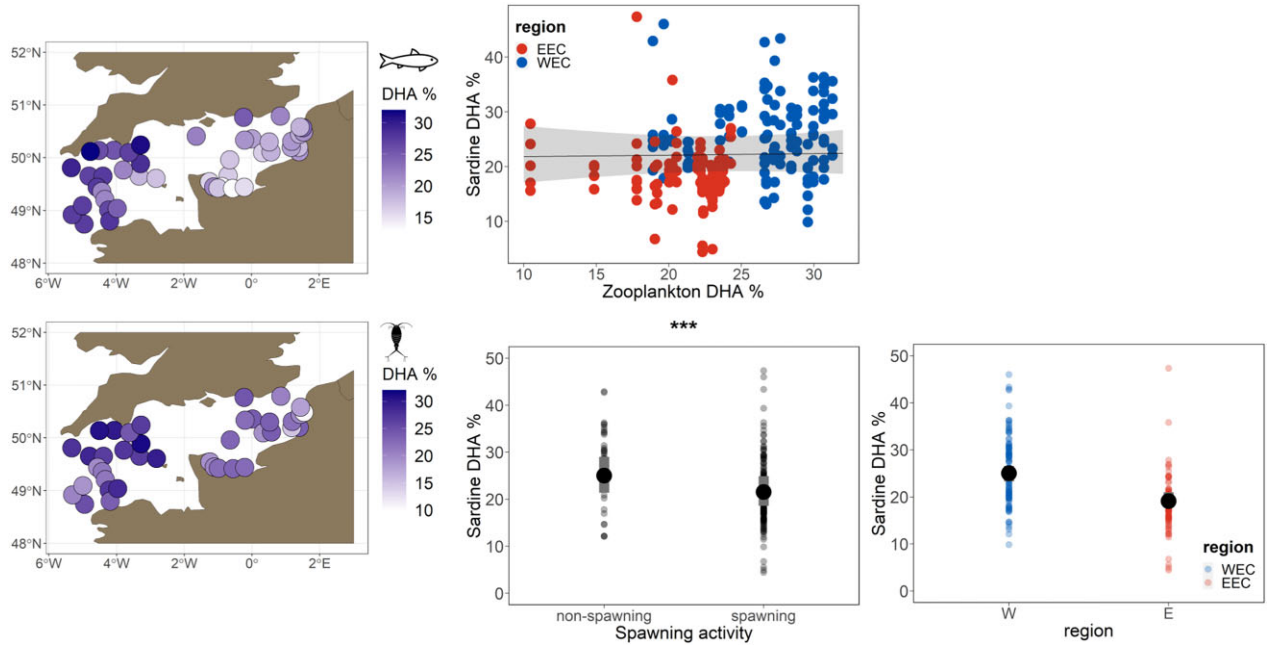

Figure 6. Factors influencing trophic transfer of DHA revealed by GLMM. The relation of DHA percentage in zooplankton (500–1000 μm) and sardine (*Sardina pilchardus*) and all significant factors influencing trophic transfer revealed by the GAM are displayed. For DHA also the relation to zooplankton DHA and region is shown although not significant. Significance level is displayed in the heading of the respective plots: ***$P < .001$, **$P < .01$, and *$P < .05$. Zooplankton and sardines were caught in the EEC (red) and the WEC (blue) during autumn 2021.

contributed to the lower salinity levels in the EEC than in the WEC during the study period. Although significant, mean differences of temperature and salinity between the basins were little (16.6°C vs. 17°C; ~35 vs. 34 practical salinity unit (PSU)) (see SM Section S5).

Biometrical and physiological parameters of sardines differed between basins. Sardines in the EEC were larger in size and heavier in weight compared to their counterparts in the WEC. This was related to higher contribution of females in the EEC that were longer and heavier than males. The smaller

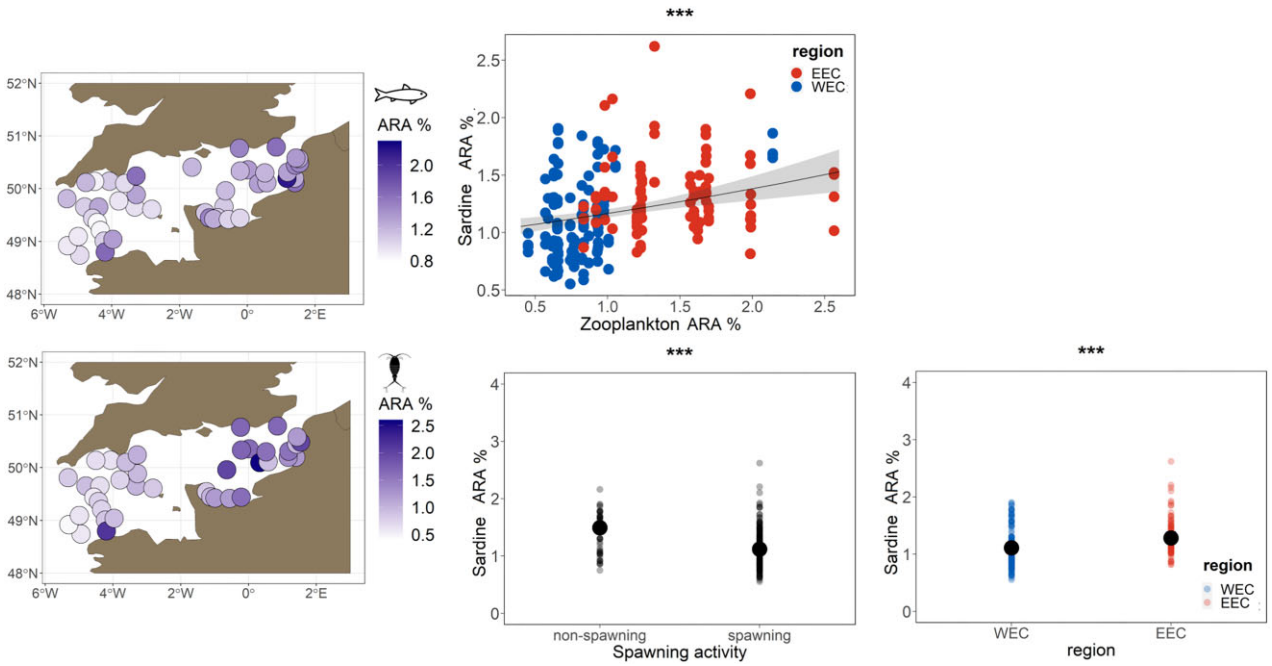

Figure 7. Factors influencing trophic transfer of ARA revealed by GLMM. The relation of ARA percentage in zooplankton (500–1000 μm) and sardine (*Sardina pilchardus*) and all significant factors influencing trophic transfer revealed by the GLMM are displayed. Significance level is displayed in the heading of the respective plots: $^{***}P < .001$, $^{**}P < .01$, and $^{*}P < .05$. Zooplankton and sardines were caught in the EEC (red) and the WEC (blue) during autumn 2021.

mean length of sardines in the WEC could also have been related to ontogenetic stage as well, considering that non-spawning individuals were smaller than spawners and that the proportion of spawning individuals was lower in the WEC than in the EEC (see SM Section S7, Fig. S4). The differences in length and weight observed between the two basins were not explained by dissimilar feeding conditions, since both condition indices used in this study (i.e. TAG–ST ratio and Le Cren's index) did not vary between basins and sex.

Spatial variability in FA profiles of zooplankton and sardine

The dichotomy in the FA profile of sardines and zooplankton between the EEC and the WEC reflected the spatial differences in phyto- as well as zooplankton community composition. FATM indicated the presence of *Calanus* spp., wax ester-producing species, and the presence of dinoflagellates in the WEC whereas diatom-specific FATM [i.e. 16:2 ($n-4$), 16:3 ($n-4$), 16:4 ($n-1$), and 16:1 ($n-7$), EPA/DHA ratio] appeared to be characteristic of the EEC. The use of wax esters as energy storage is known in herbivorous calanoid copepods, such as *Calanus* spp. and Euphausiacea (Kattner and Krause 1989, Dalsgaard et al. 2003, Lee et al. 2006). Small calanoid copepods as those characterizing the EEC are less likely to produce lipid storages in form of wax esters as their omnivorous life style facilitates access to nutritional resources throughout the year decreasing the need for long-term lipid storage (Kattner and Hagen 2009, Benedetti et al. 2015). Thus, the association of wax esters to the WEC appears to be in accordance with the zooplankton taxonomic characteristics of the two basins.

In previous studies, the FA composition of phyto- and zooplankton communities was found to be mainly driven by their taxonomy as well as, in case of zooplankton, their dietary composition (Gladyshev et al. 2010, Galloway and Winder 2015, Hiltunen et al. 2022). Thus, we suggest that the spatial pattern in phyto- and zooplankton community composition observed in the present study might be a strong driver of the spatial variability in the zooplankton FA composition (Gladyshev et al. 2010, Galloway and Winder 2015, Hiltunen et al. 2022).

The FA profile of sardines displayed the same spatial pattern as zooplankton, with the FA profile of individuals differing between the WEC and the EEC. As discussed earlier, the FATM detected in sardine muscle suggested a strong bottom-up control exerted by the dietary options available to sardines. This was further supported by the taxonomic composition of other zooplankton size classes (300 to >1000 μm) that serve as sardine prey (Garrido et al. 2007a, 2015) and which FA profile was not analysed here, but followed the same spatial east–west pattern (see SM Section S9). Sardines display opportunistic feeding behaviour that varies ontogenetically, spatially, and temporally and that ranges from small copepods, micro- and phytoplankton to bigger prey such as mesozooplankton and fish eggs (Garrido et al. 2007a, Nikolioudakis et al. 2012, Costalago et al. 2015).

An influence of diet on sardine FA composition was also suggested by other studies (Bertrand et al. 2022, Mathieu-Resuge et al. 2024). Field studies directly comparing prey FA composition with sardine FA composition, however, are limited (Shirai et al. 2002, Garrido et al. 2008). The present study provides additional evidence of a strong bottom-up control in the transfer of FA from zooplankton to small pelagic fish, such as European sardines. As a consequence, changes in plankton communities might not only affect size and weight of small pelagic fish via declines of prey abundance and morphological characteristics such as size but also due to altered availability of essential nutrients (Menu et al. 2023).

Environmental conditions and biometrical (i.e. size and weight) and physiological (i.e. condition and spawning activity) characteristics of sardines could have also contributed to the spatial separation of sardine FA profiles. Length might influence FA composition via energy allocation strategy with regard to reproduction and growth (Pethybridge et al. 2015, Ohshimo et al. 2022). As discussed earlier, non-spawning individuals were more abundant in the WEC and they were smaller compared to their spawning counterparts. Thus, one could hypothesize that more individuals allocated energy towards growth in the WEC than in the EEC. Maturity at length data for sardines in the EC would help to verify this hypothesis. Length might further influence FA composition via ontogenetic variation in prey selectivity. We did not observe a decrease of EPA/DHA ratio with length, as was observed instead by Bertrand et al. (2022) with regard to age and that was proposed to be related to a diet shift towards more macrozooplankton in older individuals. Nevertheless, a different feeding strategy of smaller individuals more abundant in the WEC could explain the dissimilar FA compositions.

Temperature and salinity were shown to influence organisms' FA profiles (Arts and Kohler 2009, Hunt et al. 2011, Holm et al. 2022). In the present study, the mean surface temperature (16.6°C vs. 17°C) and mean surface salinity (~35 vs. 34 PSU) differed only slightly between the basins. Thus, an environmental effect on the transfer of EFA in the study area was, likely indirect, mediated through differing hydrological conditions and nutrient regimes influencing phyto- and zooplankton dynamics, composition, and quality.

Factors influencing the trophic transfer of EFA

The GLMM and GAM used to investigate factors influencing the trophic transfer of EPA, DHA, and ARA further supported the strong bottom-up control exerted by the dietary sources in the transfer of EFA, as well as an influence of sardine physiological status.

EPA and ARA were significantly correlated with zooplankton FA proportions, in contrast to DHA. This could be related to a stronger regulation of this physiologically important EFA by the organism making a link to trophic sources more complex. Furthermore, while the relation of sardine and zooplankton ARA was linear not indicating a difference in the relationship between the WEC and EEC, the relation of EPA was non-linear, with a positive linear relationship in the WEC, while the relation in the EEC seemed to stabilize reaching a plateau. This might be related to the differences in zooplankton EPA proportions between the basins that were globally higher in the EEC compared to the WEC (except within a short range between 18% and 21%). Thus, the change of the relationship between sardine and zooplankton EPA (from a positive slope to a plateau) might be either due to a region effect, or to a saturation effect, or both. Within the common range of zooplankton EPA proportions (18%–21%), similar sardine EPA proportions were observed in both basins. This might indicate that the non-linear relation revealed by the model represents the general trophic relationship between sardine and zooplankton EPA instead of region-specific processes. The proportion of EPA in zooplankton in the WEC might not have been sufficient to attain the optimal EPA proportion required by sardines resulting in a positive linear relationship. Sardines in the EEC, by contrast, might have attained the necessary EPA proportion resulting in an asymptotic relationship of prey and consumer EPA. Similar saturation effects have been observed for other FA such as cetoleic acid [22:1 ($n-11$)] (Henderson et al. 1982, Lie and Lambertsen 1991, Stubhaug et al. 2007).

Spawning activity was negatively correlated to the proportion of all three EFA tested. The study period was within the autumn reproduction period of sardine in the EC (Stratoudakis et al. 2007). EPA, DHA, and ARA are known to be important for oocyte and sperm quality (Pérez et al. 2007, Butts et al. 2015) as well as for fish embryo and larvae development (Izquierdo 1996, Tocher 2010). Thereby the incorporation of EFA into sardine oocytes led to decreasing concentrations of these FA in the muscle (Garrido et al. 2007b, 2008). With regard to relative values of FA, similar patterns were observed in Japanese sardine (*Sardinops melanostictus*) (Yasuda et al. 2021). In this species, proportions of DHA and ARA were lower during the spawning season than during the non-spawning period, and the proportion of EPA decreased with declining total muscle lipid content, indicating a decrease of this FA during spawning with regard to absolute values (Yasuda et al. 2021). The inclusion of both female and male sardine data in the models (see SM Section S7, Table S3) and in the PCA analysis on the overall FA profile did not show any influence of sex on the results. This is in accordance with Garrido et al. (2008b), who did not find differences between sexes in the FA composition (absolute values).

Spawning activity and the TAG–ST ratio were related (see SM Section S8, Fig. S5), with non-spawning individuals having a lower TAG–ST ratio meaning lower fat reserves than spawning individuals. Thus, the correlation between spawning activity and the three EFA tested could also represent a relation of EPA, DHA, and ARA to the TAG–ST ratio. DHA and ARA decreased with increasing the TAG–ST ratio (see SM Section S8, Fig. S31). A negative correlation of DHA and ARA proportion with the total lipid content was also observed in Japanese sardine (Yasuda et al. 2021), and the proportion of total $n-3$ PUFA decreased with total lipid content in *Perca fluviatilis* (Mairesse et al. 2006). This result was suggested to be related to the proportion of structural to neutral lipids (Mairesse et al. 2006, Gladyshev et al. 2018, Yasuda et al. 2021). Fish in poor condition can be expected to have relative higher proportions of structural lipids than fish in good condition with a higher share of neutral storage lipids. Thus, the relative values of EFA, which are most prominent in the structural phospholipids, might decrease in fish of good condition because the share of storage lipids increases, although the absolute values of EFA might not. EPA did not display a negative relationship with the TAG–ST ratio and was positively correlated to Le Cren's condition index. This finding was similar to Japanese sardine in which the proportion of EPA did not decrease during the spawning period in contrast to DHA and ARA (Yasuda et al. 2021). Due to the diverse physiological roles of EPA, ARA, and DHA (Tocher 2003), other physiological processes such as immune or stress response might explain the difference in the relation to the lipid and morphological condition observed and their spatial variation. Those could be investigated in future studies (Gladyshev et al. 2018).

In the present study, the FA profile of total muscle lipids was used, meaning that lipids were not separated in polar and neutral lipids. The main focus of this study was to compare the spatial variability in the FA signature of predator and prey. Thus, using total FA was adequate as neutral lipids mostly reflecting the diet dominate total lipids in fat fish species such as sardine that stock lipid reserves in muscle tissue (Bandarra

et al. 1997, Couturier et al. 2020). Furthermore, the FA profile of total lipids is the one available to higher trophic levels and using total lipids allowed to compare the FA profile of sardines in the EC to other regions. Future studies could profit from analysing the FA profile of sardine muscle polar and neutral lipids separately, as this would allow a more detailed insight in FA transfer with regard to the use and metabolism of FA by sardines (Bertrand et al. 2022, Mathieu-Resuge et al. 2024).

Spatial separation of sardines in the EC

The spatial dichotomous pattern of sardine FA profiles, combined with the association of FATM to either the WEC or the EEC, indicates that sardines only resided and fed in either one basin of the EC during the study period and the preceding weeks corresponding to the incorporation time of the FA profile. Consequently, against our initial hypothesis, sardines did not smoothen the spatial variability of the plankton FA profile as their movement radius did not cover the spatial heterogeneity of zooplankton FA profiles in the EC but corresponded to its spatial pattern. A smoothing effect would have been possible in case of sardine migration between the basins. Thus, possible smoothing of spatial variability in FA profiles between zooplankton and small pelagic fish does not only depend on different mobility and horizontal movement radius of plankton and fish individuals but also on the spatial heterogeneity of the zooplankton community composition (driven by spatial variability of environmental conditions) in relation to fish movement radius.

Celtic Sea and EC sardines are considered separately from the Bay of Biscay and are defined as a single stock based on a higher growth rate and the presence of all life stages (eggs, larvae, recruits, and adults) in ICES subarea 7 suggesting a self-sustaining stock unit (ICES 2017). There is little information about sardines from the EC. The finding that sardines from the North Sea and the WEC did not differ genetically (Kasapidis et al. 2012) does not indicate the presence of different populations in the WEC and the EEC. However, differences within the same species between the WEC and the EEC have been reported for sole (*Solea solea*) and cod (*Gadus morhua*) regarding abundance trends (Araújo et al. 2006, ICES 2023). These spatial differences might be related to a restricted movement radius and spawning ground fidelity (Pawson 1995, Neat et al. 2014, Vandamme et al. 2021). Sole and cod are benthic or demersal; thus, the characteristic pattern of sardines in the two basins in autumn provides a unique case for a pelagic species. Although sampling took place during the autumn spawning period, which might suggest an influence of spawning behaviour on the spatial separation pattern, sardines are not known to display distinct spawning locations, spawning site fidelity, or seasonal migrations that would indicate natal homing (Petitgas et al. 2010). To verify and better understand the spatial pattern of sardine in the EC, data spanning several years and seasons are necessary. Nevertheless, the spatial pattern of FA in sardines corresponds to the spatial segregation pattern found for other species and ecosystem compartments (Beaugrand et al. 2000, Dauvin 2012, Luczak and Spilmont 2012). It further fits into the larger context of biogeographical studies (Spalding et al. 2007, Longhurst 2010), which affiliated the WEC and the EEC to different ecoregions, biomes, and provinces. This might suggest that evaluations of sardine biometrical parameters considering the predicted decrease of size and weight (Menu et al. 2023) should be conducted separately for the WEC and the EEC due to potential local patterns arising from differences in prey composition and therewith potentially prey quality.

Conclusion

A strong spatial dichotomous pattern of zooplankton and sardine FA profiles was found between the WEC and the EEC in autumn 2021. Similar spatial patterns in the taxonomic composition of phytoplankton, zooplankton, and FATM, as well as correlations of EFA in sardine muscle and zooplankton, indicated a strong bottom-up control in the trophic transfer of FA, which was mostly driven by taxonomic composition of the dietary source. Furthermore, the physiological status of sardines with regard to spawning, energy allocation strategy, and condition was found to influence trophic transfer—a finding that should be taken into account when using FATM. Sardines did not smooth spatial variability in FA, indicating a residence of individuals either in the WEC or the EEC immediately prior and during the study period. This information is relevant to inform ecosystem models and management strategies. The potential of small pelagic fish as spatial smoothers in other regions would be an interesting topic for future research as small pelagic fish such as herring are known to display large-scale migrations, spanning entire shelf seas and connecting oceans and coastal areas (Corten 2001, Varpe et al. 2005). Furthermore, the assessment of the spatial variability in quantitative FA profiles of zooplankton and sardine would complete information on the transfer and availability of EFA to higher trophic levels.

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Author contributions

C.G., F.P., and C.J.N. designed the research. C.Q. conducted and led the laboratory work. C.J.N. wrote the main manuscript with contributions from P.S., C.Q., and G.W. and valuable inputs from C.G., P.M., S.L., and A.L. All authors gave final approval for publication.

Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

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Data availability

The datasets generated and analysed during the current study are available on the SEANOE database (doi.org/10.17882/104844)).

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