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► To cite this version:

Elsa Breton, Benoit Sautour, Oscar Demonio, Gregory Beaugrand, Laurent Seuront, et al.. Seasonal Variations in the Biodiversity, Ecological Strategy, and Specialization of Diatoms and Copepods in a Coastal System With Phaeocystis Blooms: The Key Role of Trait Trade-Offs. *Frontiers in Marine Science*, 2021, 8, pp.656300. 10.3389/fmars.2021.656300 . hal-04290562

HAL Id: hal-04290562

<https://hal.science/hal-04290562>

Submitted on 16 Nov 2023

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China
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Benjamin Alric,
Centre National de la Recherche
Scientifique (CNRS), France

*Correspondence:

Elsa Breton
elsa.breton@univ-littoral.fr

Specialty section:

This article was submitted to
Aquatic Microbiology,
a section of the journal
Frontiers in Marine Science

Received: 20 January 2021

Accepted: 30 July 2021

Published: 06 September 2021

Citation:

Breton E, Christaki U, Sautour B,
Demonio O, Skouroliakou D-I,
Beaugrand G, Seuront L, Kléparski L,
Poquet A, Nowaczyk A,
Crouvoisier M, Ferreira S,
Pecqueur D, Salmeron C,
Brylinski J-M, Lheureux A and
Goberville E (2021) Seasonal
Variations in the Biodiversity,
Ecological Strategy, and Specialization
of Diatoms and Copepods in a
Coastal System With *Phaeocystis*
Blooms: The Key Role of Trait
Trade-Offs. *Front. Mar. Sci.* 8:656300.
doi: 10.3389/fmars.2021.656300

Elsa Breton^{1*}, Urania Christaki¹, Benoit Sautour², Oscar Demonio³,
Dimitra-Ioli Skouroliakou¹, Gregory Beaugrand¹, Laurent Seuront^{1,4,5}, Loïck Kléparski^{1,6},
Adrien Poquet^{1,7}, Antoine Nowaczyk⁸, Muriel Crouvoisier¹, Sophie Ferreira⁹,
David Pecqueur¹⁰, Christophe Salmeron¹⁰, Jean-Michel Brylinski¹, Arnaud Lheureux⁸
and Eric Goberville³

¹ Univ. Littoral Côte d'Opale, CNRS, Univ. Lille, UMR 8187 LOG, Wimereux, France, ² Univ. Bordeaux, CNRS, UMR 5805 EPOC, Rue Geoffroy Saint Hilaire – Bâtiment, Pessac, France, ³ Unité Biologie des Organismes et Ecosystèmes Aquatiques (BOREA), Muséum National d'Histoire Naturelle, CNRS, IRD, Sorbonne Université, Université de Caen Normandie, Université des Antilles, Paris, France, ⁴ Department of Marine Resources and Energy, Tokyo University of Marine Science and Technology, Tokyo, Japan, ⁵ Department of Zoology and Entomology, Rhodes University, Grahamstown, South Africa, ⁶ Marine Biological Association, Citadel Hill, Plymouth, United Kingdom, ⁷ Univ. Côte d'Azur, CNRS, INSERM, IRCAN, Medical School of Nice, Nice, France, ⁸ Univ. Bordeaux, CNRS, UMR 5805 EPOC, Station Marine d'Arcachon, Arcachon, France, ⁹ Observatoire Océanologique de Banyuls s/mer, FR 3724 – Laboratoire Arago – SU/CNRS, Banyuls-sur-Mer, France, ¹⁰ Univ. Bordeaux, CNRS, OASU, UMS 2567 POREA, Allée Geoffroy Saint-Hilaire, Pessac, France

Although eutrophication induced by anthropogenic nutrient enrichment is a driver of shifts in community composition and eventually a threat to marine biodiversity, the causes and consequences on ecosystem functioning remain greatly unknown. In this study, by applying a trait-based approach and measuring niche breadth of diatoms and copepods, the drivers and underlying mechanisms of the seasonal species succession of these ecological communities in a coastal system dominated in spring by *Phaeocystis* blooms were explored. It is suggested that the seasonal succession of diatoms and copepods is the result of several trade-offs among functional traits that are controlled by the seasonal abiotic and biotic pressure encountered by the plankton communities. The results of this study highlight that a trade-off between competition and predator, i.e., weak competitors are better protected against predation, plays an important role in promoting plankton species richness and triggers the *Phaeocystis* bloom. As often observed in eutrophicated ecosystems, only the biotic homogenization of the copepod community and the shift in the diet of copepods toward *Phaeocystis* detrital materials have been detected during the *Phaeocystis* bloom. The diatom and copepod communities respond synchronously to fluctuating resources and biotic conditions by successively selecting species with specific traits. This study confirms the key role of competition and predation in controlling annual plankton succession.

Keywords: diatoms, copepods, *Phaeocystis*, biodiversity, functional traits, seasonality, trade-off

INTRODUCTION

Coastal eutrophication induced by anthropogenic nutrient enrichment is one of the major threats to biodiversity (Vitousek et al., 1997; Halpern et al., 2008; Howarth, 2008). However, assessing the impact of eutrophication on biodiversity is a difficult task, because the multiple drivers shaping biodiversity interact and operate at different interconnected temporal and spatial scales (e.g., White et al., 2010; Dray et al., 2012; Hill et al., 2016). Eutrophication may not only cause excessive blooms of opportunistic species, species loss (Smith and Schindler, 2009) but also, subtle changes in functional trait composition; and may even lead to a loss of functional diversity (FD) caused by a biotic homogenization by favoring generalist (species with broad environmental tolerances) over specialist (species well adapted to particular habitats) species: the latter showed narrower niche breadth and a lower tolerance to high nutrient levels (e.g., Clavel et al., 2011; Nelson et al., 2013; Villéger et al., 2014; Wengrat et al., 2018; Chihoub et al., 2020). Functional traits are biological characteristics that influence the performance and survival of organisms (Violle et al., 2007). Biotic changes may alter biodiversity by selecting species that possess functional traits that confer to them a selecting advantage. For instance, light limitation, which typically occurs under high primary production events, may select species with morphological features that allow them to enhance their buoyancy (Naselli-Flores et al., 2021 and references therein). Communities mainly composed of functionally redundant species may improve ecosystem resilience and stability (e.g., Biggs et al., 2020), but the loss of FD and/or specialist species may deteriorate ecosystem functioning (Olden et al., 2004; Pan et al., 2016; Alexander et al., 2017). Understanding how functional traits relate to associated ecological strategies (i.e., a combination of functional attributes reflecting how species cope with their environment) and ecological specialization across productivity gradients, which defines the degree of tolerance to changing environmental conditions, is, therefore, important to better measure ecosystem functioning and health.

Over the last decade, trait-based approaches have been increasingly used in plankton ecology to understand the drivers of biodiversity changes along environmental gradients and to propose ecological generalities and predictions across ecosystems. Because functional traits mediate the responses of the species to their abiotic and biotic environment (Violle et al., 2007), they help to: (i) better understand how organisms interact with their surrounding environment; and (ii) identify key processes that influence biodiversity such as trait trade-offs (e.g., Kneitel and Chase, 2004; Litchman et al., 2007). While functional identity informs on competitiveness and ecological strategies (e.g., predation avoidance, Shipley, 2010; Muscarella and Uriarte, 2016), FD, in combination with null modeling, informs on the degree of functional convergence of a community and detects mechanisms of community assembly (e.g., abiotic filtering and competitive interactions, Mason et al., 2013). As it may influence conclusions, trait choice is a critical issue (Zhu et al., 2017) when: studying resource traits (e.g., nutrient uptake and light absorption); under-dispersion of traits reflects environmental filtering and/or hierarchical competition (Mayfield and Levine,

2010); and over-dispersion of traits is related to a competition governed by niche differences (MacArthur and Levins, 1967; Cornwell and Ackerly, 2009). When focusing on defense traits against predation (e.g., setae and toxin production), under-dispersion is related to a high predation pressure by generalists, and over-dispersion to a high predation pressure by specialists (Cavender-Bares et al., 2009).

The Eastern English Channel (EEC) is a well-mixed meso-eutrophic sea undergoing multiple environmental disturbances such as temperature rise (McLean et al., 2019) and nutrient enrichment, mainly from the Seine and Somme rivers (Thieu et al., 2009) as a result of anthropogenic activities in the watersheds, especially intensive agriculture practices (e.g., Garnier et al., 2019). This nutrient enrichment is known to trigger the recurrent spring *Phaeocystis* blooms of EEC (Lancelot et al., 1987; Lancelot, 1995; Breton et al., 2000, Breton et al., 2017; Grattepanche et al., 2011a,b; Bonato et al., 2016; Ménesguen et al., 2018). By affecting the diatom and copepod communities, two interacting key compartments of the ecosystem trophodynamics (Smetacek, 1999; Tréguer and Pondaven, 2000; Beaugrand et al., 2003; Kiørboe, 2011; Mitra et al., 2014; Steinberg and Landry, 2017), this prymnesiophyte can disrupt the structure of the food web (Schoemann et al., 2005; Nejstgaard et al., 2007), especially during the late winter/spring and summer/autumn periods (Gasparini et al., 2000; Antajan, 2004).

By applying a functional trait-based approach to diatom and copepod communities collected over the period 2007–2013, and by measuring niche breadth of resources used and environmental conditions tolerated both at the species- and community level, the aims were to: (i) understand how diatoms and copepods in coastal waters of the EEC respond to seasonally changing environmental conditions; (ii) determine what drives plankton species richness and ecological specialization; and (iii) test whether taxonomic (species richness) and FD [functional richness (FRic), functional evenness (FEve), and functional divergence (Rao Quadratic entropy, RaoQ)] of plankton communities were affected by *Phaeocystis* blooms. Protozooplankton biomass (i.e., the sum of heterotrophic dinoflagellate, ciliate, and tintinnid biomass) and co-occurring phytoplankton groups were also considered in this study because of: (i) the diverse trophic regimes and feeding strategies of copepods depend on their food environment (Kleppel, 1993); (ii) diatoms may also be the prey of other predators other than copepods (e.g., Grattepanche et al., 2011b); and (iii) knowledge of the whole community composition may help to better depict trade-offs.

MATERIALS AND METHODS

Datasets

Hydrological and phytoplankton samples were collected at high tide at coastal station “C” (50°40′75 N; 1°31′17 E, 20–25 m maximum depth), which belongs to the French monitoring network SOMLIT¹. Sampling was carried out on an average of every 3 weeks from February 2007 to December 2013. Subsurface (2 m depth) temperature (SST, °C) and salinity (S) were

¹www.somlit.fr

measured with a conductivity temperature depth (CTD) Seabird profiler equipped with photosynthetically active radiation (PAR, $E\ m^{-2}\ d^{-1}$) sensor (QSP 2300; Biospherical Instruments Inc.). Dissolved inorganic phosphorous (DIP, μM), inorganic silica (DSi, μM), and inorganic nitrogen [the sum of nitrates, nitrites, and ammonium; (DIN, μM)], total suspended matter (TSM, $mg\ L^{-1}$), chlorophyll *a* (Chla, $\mu g\ L^{-1}$), particulate organic carbon (POC, $\mu gC\ L^{-1}$), phytoplankton, and protozooplankton were measured by means of a Niskin Water Sampler (8 L). Nutrient concentrations were quantified according to Aminot and K erouel (2004) using autoanalyzer systems (Technicon, Alliance, and Seal Instruments), except for ammonium concentrations (NH_4), which were assessed by fluorimetry according to Holmes et al. (1999) and Taylor et al. (2007). TSM was determined by filtering a known volume of seawater through 47 mm precombusted and preweighed glass fiber filters (Whatman, GF/F, 47 mm), and drying it at 50°C for 24 h. POC was determined using a NA2100 Frisons CHN analyzer after filtration of 100–500 ml subsamples through precombusted glass fiber filters (Whatman, GF/F, 25 mm), then dried for at least 48 h at 50°C and exposed to HCl 1 N vapors for 5 h. Chla was estimated by fluorometry (Lorenzen, 1967) from subsample (100–250 ml) of seawater filtered through glass fiber filters (Whatman, GF/F, 25 mm) and free of pigment (extraction in acetone 90% in the dark at 4°C for 12 h). The minimal volume values corresponded to the *Phaeocystis* bloom period that leads quickly to filter clogging. The maximal volume value corresponds to the maximal value fixed by the SOMLIT network. The average daily PAR experienced by phytoplankton in the water column, for 6 days before sampling, was obtained from a diffuse fraction (k_d , m^{-1}) and global solar radiation (GSR, $Wh\ m^{-2}$) from the Copernicus Atmosphere Monitoring Service (CAMS) radiation service² using the formula of Riley (1957). GSR was converted into PAR by assuming PAR to be 50% of GSR and by considering $1\ W\ m^{-2} = 0.36\ E\ m^{-2}\ d^{-1}$ (Morel and Smith, 1974). Wind stress (Pa) and direction (i.e., eastward and northward components of horizontal winds), as proxies of regional turbulence (e.g., MacKenzie and Leggett, 1991), were obtained from the National Center for Atmospheric Research (NCAR, United States)³ and the National Centers for Environmental Prediction (NCEP, United States). Subsurface and near-bottom environmental values were averaged for niche analysis (refer below “Ecological specialization”).

Copepods were collected on 96 separate occasions (sampling frequency of 4 weeks) with vertical hauls from the bottom (ca. ~ 20–25 m depth) to the surface using a 200- μm mesh size working party (WP) 2 plankton net. The volume filtered was measured with a Tsurumi – Seiki (TSK) *flowmeter* (Tokyo Seimitsu Co. Ltd) and mounted on the mouth of the net (0.25 m^2 mouth area). The volume of filtered seawater varied between 1 and 11 m^3 , the lowest values being recorded during the *Phaeocystis* bloom (from mid-April to mid-May) as a result of rapid net clogging. All copepod samples were preserved with 4% formaldehyde buffered with borax. The composition and abundance of copepods were determined under

stereomicroscopy (Nikon SMZ1500) with 10–100x magnification in Dollfus chambers according to the determination key provided by Rose (1933). Copepod carbon biomass was calculated from (i) the median of the minimum and maximum weights for the CV and CVI copepodite stages; and (ii) the regression equations relating wet weight and dry weight (mg) to carbon (mg C, Wiebe, 1988). The minimum and maximum weights were estimated from the range values of copepodite length reviewed by Conway (2006) for the North Atlantic sector and species-specific length-weight relationships (Durbin and Durbin, 1978; Cohen and Lough, 1981; Williams and Robins, 1982; Dam and Peterson, 1991; Zakaria et al., 2018). The list of the copepod species identified in this study, the final carbon conversion factor values and their corresponding frequencies (%) and average biomasses ($\mu gC\ L^{-1}$), are shown in **Supplementary Table 1**. Diatom, *Phaeocystis*, and dinoflagellate samples were fixed with Lugol-glutaraldehyde solution (1% v/v, a fixative that does not disrupt *Phaeocystis* colonies; Breton et al., 2006) and were kept at 4°C in the dark until microscopy analysis. Other protozooplankton samples, i.e., ciliates and tintinnids, were fixed with formaldehyde (Grattepanche et al., 2011a). Samples were examined using an inverted microscope (Nikon Eclipse TE2000-S) with 100–400x magnification after sedimentation in 5–25 ml and 25–100 ml Hydrobios chambers for phytoplankton and protozooplankton, respectively. Identifications were identified at the species level when possible, according to taxonomic literature (Halse and Syvertsen, 1996; Hoppenrath et al., 2009, for phytoplankton; Schiller, 1931–1937; Maar et al., 2002; G omez and Souissi, 2007, for heterotrophic dinoflagellates; Kofoid and Campbell, 1929; Plankton Ciliate Project, 2002, for ciliates). For *Synechococcus* spp., picoeukaryotes, and cryptophytes, 5 ml samples were fixed with glutaraldehyde (1.33% v/v) and kept at –80°C until flow cytometry analysis (FACScan, BD Biosciences, Marie et al., 1999). Biovolumes were estimated using standard geometric forms according to Hillebrand et al. (1999). The number of *Phaeocystis* cells in the colonial stage of life was counted according to biovolume measurements of the colonies (Rousseau et al., 1990). Carbon biomass ($\mu gC\ L^{-1}$) of phytoplankton and heterotrophic dinoflagellates was calculated using the carbon conversion factors of Menden-Deuer and Lessard (2000). For *Phaeocystis* solitary cells, *Synechococcus* spp., and picoeukaryotes, the values of 89.5 $pg\ C\ cell^{-1}$ (van Rijssel et al., 1997), 154 $fg\ cell^{-1}$, and 1319 $fg\ cell^{-1}$ (Buitenhuis et al., 2012) were used, respectively. For flagellated and solitary colonial cells, only discriminated since 2007, the carbon conversion factors of 10.8 and 14.15 $pg\ C/cell$ were applied, respectively (refer **Table 1** in Schoemann et al., 2005). The biomass of ciliates and tintinnids was calculated using a conversion factor of 0.19 $pg\ \mu m^{-3}$ (Putt and Stoecker, 1989; refer **Supplementary Tables 1–4** and **Supplementary Data** for species list and biomass estimates).

Phytoplankton and Copepod Species Traits

Information on resource traits is scarce in the literature for most phytoplankton species (Litchman and Klausmeier, 2008; Breton et al., 2017). Consequently, an *a posteriori* approach

²<http://www.soda-pro.com/web-services/radiation/cams-radiation-service>

³<https://psl.noaa.gov/data/gridded/data.ncep.html>

TABLE 1 | List of the diatom and copepod traits used in this study and their functional meaning.

Traits	Type ^a	Range/Category	Ecological process/Functional meaning	References
Phytoplankton/diatoms				
Biovolume	Numerical (R and D)		The “master trait” for resource acquisition, reproduction, and predator avoidance	Litchman and Klausmeier, 2008
S/V cell ratio	Numerical (R)	0.02–4.62 μm ⁻¹	Competitive ability under nutrient limitation, silica requirement	Grover, 1989; Karp-Boss et al., 1996; Leynaert et al., 2004; Takabayashi et al., 2006; Musielak et al., 2009; Lovecchio et al., 2019
Coloniality	Ordinal (R and D)	0: No, 1: <5 cells, 2:[5–20], 3:[20, 100], 4:>100	Competitive ability under nutrient limitation	Grover, 1989; Karp-Boss et al., 1996; Takabayashi et al., 2006; Musielak et al., 2009; Bjærke et al., 2015; Lovecchio et al., 2019
Apparent degree of silicification	Ordinal (R and D)	0: <500; 1:>501 μm 1: Slightly, 2: Medium, 3: Heavily	vulnerability to predation Silica requirement, vulnerability to predation	Djeghri et al., 2019 Martin-Jézéquel et al., 2000; Martin-Jézéquel and Lopez, 2003; Pančić et al., 2019
Tychoipelagic/Benthic occurrence	Binary	0: Pelagic; 1: Tychoipelagic/Benthic	Use of resources and habitat	
Maximum Linear Dimension (MLD)	Numerical (R and D)	3–447 μm	Cell buoyancy, vulnerability to photo-inhibition	Grover, 1989; Key et al., 2010; Schwaderer et al., 2011; Naselli-Flores et al., 2021
			Capacity at capturing the fluctuating light and persisting in subsurface waters	Naselli-Flores et al., 2021
Defense	Ordinal (D)	0–4 (0: No defence, 4 many defence traits) ^b	Predator avoidance	Pančić and Kiørboe, 2018
Copepods				
Maximum size	Numerical (R and D)	1: ≤1 mm, 2: [1; 2], and 3: >2 mm	Feeding, growth, reproduction, survival	Litchman et al., 2013
Trophic regime	Fuzzy coded (R)	Carnivory, Herbivory, Detritivory, Omnivory ^c	Feeding, growth, reproduction, survival	Litchman et al., 2013
Feeding mode	Ordinal (R and D)	0: Passive, 0.5: Mixed, 1: Active	Feeding, survival	Kiørboe, 2011; Litchman et al., 2013

^aR and D: Resource and Defense trait, respectively.

^bSee **Supplementary Table 3** and **Supplementary Data**.

^cSee Chihoub et al. (2020) for more details.

to defining resource use and requirement traits was used. For each species, biovolume (V , μm^3), maximum linear dimension (MLD, μm), and the surface to biovolume cell ratio (S/V ratio) were calculated from the median values of a series of microscopic measures over the entire 1996–2019 diatom datasets acquired at Station “C” (Breton unpublished data). The apparent degree of silicification (1: slight; 2: medium; 3: heavy) and Tychoipelagic/benthic habit (0: pelagic; 1: tychoipelagic/benthic) was based on information from phytoplankton taxonomic literature (e.g., Halse and Syvertsen, 1996; Hoppenrath et al., 2009). The potential degree of coloniality (0: None; 1: <5 cells; 2: 5–20 cells; 3: >20 cells) was assessed through the cultivation of each diatom species under F/20 medium and with a light:dark cycle of 12:12 h at an irradiance of 400 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (Daylight HQIT-WD 250 W F, OSRAM GmbH, Munich, Germany).

Biovolume is a key trait because it relates to the various ecophysiological attributes for resource acquisition, reproduction, and predator avoidance (Litchman and Klausmeier, 2008; **Table 1**). Species with high S/V cell ratio and long cellular chain length that favor cell suspension in the water column and increase nutrient flux have a great competitive

ability under nutrient limitation (Grover, 1989; Karp-Boss et al., 1996; Takabayashi et al., 2006; Musielak et al., 2009; Lovecchio et al., 2019). Higher S/V cell ratio and weaker silicified species have also been related to lower silica requirement under laboratory conditions [(Leynaert et al., 2004) and to DSi limitation (Martin-Jézéquel et al., 2000; Martin-Jézéquel and Lopez, 2003)]. Cell elongation enhances both cell buoyancy (Grover, 1989; Naselli-Flores et al., 2021) and protection against photoinhibition, especially for larger cells (Key et al., 2010; Schwaderer et al., 2011). The binary trait “Tychoipelagic/benthic habit” may be informative of resource use and requirement, as benthic diatoms are often highly photosynthetic efficient species and potentially facultative heterotrophs (Cahoon, 1999). This trait may be also an indicator of ecosystem health, as demonstrated by the positive relationship between the FD of benthic diatoms and the productivity of coastal waters in the Baltic Sea (Virta et al., 2019). Besides reflecting resource use and/or requirement, prey biovolume (Litchman and Klausmeier, 2008), the degree of coloniality (Bjærke et al., 2015), and the apparent degree of silicification (Pančić et al., 2019) mirror ecological processes/functions linked to predation. By including: (i) the capacity to produce mucous or toxins; (ii) the presence of

setae and/or spicules (that also favor buoyancy; Van den Hoek et al., 1995); (iii) the degree of silicification; and (iv) coloniality, the composite of defense traits reflect alteration of copepod grazing (Pančić and Kjørboe, 2018). The composite trait was obtained by summing the scores of each of these traits (refer **Supplementary Table 5** and **Supplementary Data**).

The carbon-to-chlorophyll ratio for phytoplankton (C/Chla ratio, in $\mu\text{gC } \mu\text{gChla}^{-1}$) and timing of bloom initiation of diatoms (in months) were then calculated. Although not being traits *per se* (Litchman and Klausmeier, 2008), they are the outcome of processes linking the actual traits of species and the alleviation, or accentuation, of external limiting factors, such as grazing pressure or nutrients/light availability (Thackeray et al., 2008; Jakobsen and Markager, 2016). The C/Chla ratio was calculated using microscopic counts and the cell carbon was computed from the equations of Menden-Deuer and Lessard (2000). Timing of bloom initiation of diatoms at Station “C” (refer **Supplementary Data**) was based on the cumulative biomass-based threshold method (Brody et al., 2013), using mean monthly diatom abundances over the period 1996–2019 and a limit value of 20%.

For copepods: (i) maximum size (mm); (ii) trophic preference (herbivory, carnivory, detritivory, and omnivory); and (iii) feeding mode (0: passive, 1: active, and 0.5: mixed feeding) were selected, as they directly/indirectly influence species fitness through growth, reproduction, and/or survival (Litchman et al., 2013; Kjørboe and Hirst, 2014). Most of them are responsive to changes in environmental conditions (McGinty et al., 2018). Data were obtained from the copepod trait database constructed by Benedetti et al. (2016) and completed by Brun et al. (2017), and references therein. For each copepod species, all available information on species size was compiled, and the maximum size value as representative of adult species was kept, note that sexual dimorphism was not considered. The degree of herbivory (carnivory, detritivory, or omnivory) was coded following Mondy and Usseglio-Polatera (2014). In this study, a coefficient of (i) 1/3 for omnivore; (ii) 2/3 for omnivore-herbivory (dominance of herbivory in copepod diet) or 2/3 for omnivore-carnivory (dominance of carnivory in copepod diet), with 1/4 for the two other diet categories; and (iii) 1 for species with carnivore/herbivore/detritivore diets, and 0 for the two other diet categories (refer Chihoub et al., 2020 for more details) was applied.

FD Metrics

In this study, four metrics (Step 1, refer **Supplementary Figure 1** for a description of the five main steps of the statistical method) to characterize the functional structure and diversity of diatom and copepod communities were used as follows: (i) community-weighted mean (CWM); (ii) FRic, (iii) FEve; and (iv) Rao Quadratic entropy (RaoQ) as a proxy of functional divergence. CWM, the mean trait value among each community weighted by the relative biomass of each species (Garnier et al., 2004), is a proxy of functional identity. FRic corresponds to the volume of functional niche space filled by a species within a community (Villéger et al., 2008). FEve corresponds to the regularity with which species biomass in a community is distributed along the minimum spanning tree that links

all species in the multidimensional trait space (Mason et al., 2005). RaoQ is the sum of pairwise distances between species, weighted by the relative biomass within the multidimensional trait space. This index was selected over the functional divergence metric for its stronger ability to detect assembly rules (Botta-Dukát, 2005; Botta-Dukát and Czúcz, 2016). The FD indices of the diatom community were calculated from the biovolume, the apparent degree of silicification, coloniality, the S/V cell ratio, MLD, and defense traits (as shown in **Supplementary Table 5**). For each observation (i.e., sampling unit), functional metrics were computed on log-transformed species biomass, to reduce a potential influence of outliers, using the R package (R version 3.5.3, 2019) “FD” (Laliberté and Legendre, 2010). A preliminary principal coordinate analysis (PCoA; “vegan” package; and Oksanen et al., 2011) was performed to calculate the multidimensional trait space for each sampling day and FD was calculated from a dissimilarity matrix calculated using both the PCoA axis, as new functional traits, and the Gower distance (Gower, 1971). The Gower distance allows us to combine traits of different types, including ordinal (Podani, 1999; **Table 1**). A square root transformation (“sqrt”), or a Lingoes correction for negative values (Lingoes, 1971), was applied when the distance matrix “species \times species” was not Euclidean. The quality of the functional space (i.e., the similarity between the functional space and initial functional trait values) based on the corrected distance matrix varied from 0.64 to 0.94. The inference of environmental filtering and biotic interactions (Step 2, **Supplementary Figure 1**) was estimated from the deviation [standardized effect size (SES); Gotelli and McCabe, 2002] between functional metrics calculated on a given (i.e., observed) diatom community and functional values obtained from a random community: for each sampling date, trait data were randomized 999 times (“permatfull” in the “vegan” package), while maintaining species richness and abundance constant. SES was calculated as follows:

$$SES = \frac{x_{obs} - \bar{x}_{ran}}{\sigma_{ran}} \quad (1)$$

where x_{obs} is the observed values of the functional metric at a given date; \bar{x}_{ran} is the mean, and σ_{ran} is the SD of the FD of randomly assembled communities. Assuming a normal distribution of the random communities, the traits derived from the sampling dates falling into the 95th (or higher) percentile of the random distribution were considered “over-dispersed” (i.e., niche differentiation being the major process driving community assembly) and trait falling into the 5th (or lower) percentile were considered “under-dispersed” (i.e., environmental filtering as the major process).

Ecological Specialization

Ecological specialization (Step 3, **Supplementary Figure 1**) was estimated by means of the multidimensional outlying mean index (OMI, hereafter called “environmental tolerance,” Dolédec et al., 2000) and unidimensional niche breadth analysis using the “ade4” (Chessel et al., 2004; Dray et al., 2007) and “hypervolume” packages (Blonder et al., 2014). The OMI was selected because it does not rely on any expected species response curves to environmental gradients and outperforms classical

methods such as canonical correspondence or redundancy analysis (Dolédéc et al., 2000). The OMI analysis seeks combinations of environmental variables that maximize average species marginality, i.e., the squared Euclidean distance between the mean environmental conditions used by a species and the mean environmental conditions available to this species. Hypervolume estimates the niche breadth of one or several dimensions from the calculation of uni or multivariate kernel density. This method captures irregular shapes and does not require a specific density function, unlike OMI analysis that requires normal distribution: estimation of the hypervolume is, therefore, more accurate when high-dimensional or holey datasets are considered. An accurate estimate of kernel density requires high amounts of trait/environmental data, which rises as dimensionality increases, however (e.g., about >67 and >770 for three and five dimensions, respectively, Silverman, 1986). For a comprehensive assessment of environmental gradients, the calculation was, therefore, based on the ecological specialization of long-term diatom and copepods datasets, collected between 1996 and 2019 at the station “C,” and from 2001 to 2017, respectively, in the downstream part of the Gironde estuary (Breton et al., 2000; Schapira et al., 2008; Breton et al., 2017; Richirt et al., 2019).

Environmental tolerance was based on species biomass, considering: (i) SST, S, Pa, nutrients, and PAR for diatoms; and (ii) SST, S, Pa, TSM, and POC for copepods. Unidimensional niche breadth related to resources (DIN, DIP, DSi, and light for diatoms; TSM and POC for copepods) was determined from kernel density using the environmental conditions encountered by species when present with a Silverman bandwidth estimator and a 0% quantile threshold (Blonder et al., 2014). An increase in these two indices of ecological specialization mirrors an decrease in the degree of specialization of the diatom or copepod community. Trophic homogenization within the copepod community was assessed from trophic preferences and feeding mode, as recommended by Mondy and Usseglio-Polatera (2014). For each copepod species and trophic trait, we first calculated the taxon specialization index (TSI) using the Gini-Simpson index (Gini, 1912; Simpson, 1949). Each TSI, where the trophic preference (the feeding mode) describes the degree of omnivory (the capacity to alternate between passive and active feeding), was then scaled by its respective minimum and maximum values to account for the different number of categories among traits (Mondy and Usseglio-Polatera, 2014). The community specialization index (CSI) was finally computed as the CWMs of each TSI: a value of 0 (1) corresponds to truly generalists (truly specialists).

All analyses were performed with R (R Development Core Team), version 3.5.3.

Exploratory Analyses

First, box plots (Step 4, **Supplementary Figure 1**) were computed combined with a locally weighted scatterplot smoothing (LOESS; Jacoby, 2000) curve in association with a 95% confidence interval (function “geom_smooth,” package “ggplot2,” Wickham, 2016) to depict the seasonal variations. Monthly differences were assessed by a Kruskal–Wallis test, followed by a *post hoc* Nemenyi

test (Legendre and Legendre, 1998; package “PMCMRplus,” Pohlert, 2014). To explore and summarize seasonal changes in the abiotic environment, a principal component analysis (PCA) was performed with the “ade4” package. To explore seasonal variations in both the mean values of key biological traits and in the degree of ecological specialization of the diatom and copepod communities, a PCoA (Step 4, **Supplementary Figure 1**) was computed on a community dissimilarity matrix (Gower distance) using monthly data of niche breadth and CWMs of different functional attributes. The coupling (Step 5, **Supplementary Figure 1**) between the environment and key biological attributes (species biomass, functional structure, ecological specialization, and FD of diatoms and copepods) was then estimated by computing two separated co-inertia analysis (COIA; Dolédéc and Chessel, 1994; Dray et al., 2003) on monthly means using the “ade4” package. Prior to all multivariate analysis, and for each variable, skewness of the data was removed to reach normality and all variables were to have a mean of zero and a SD of one (“caret” package; Kuhn et al., 2016). The principle of COIA consists of finding co-inertia axis by maximizing the covariance between the row coordinates of two matrices (in this study, the environmental variables and either diatoms or copepods). It defines axis that simultaneously explain the highest possible variance in each of the two matrices and describes their closest common structure. First, a PCA was performed on each matrix, and then applied the COIA (Dray et al., 2003). Explanatory environmental variables were: Pa and direction, S, SST, DIN, DIP, DSi, and protozooplankton biomass. While PAR and copepods biomass were included as additional explanatory environmental variables for diatoms, diatom biomass was added, the defense trait against predation (expressed as CWM) for copepods, and the abundance of their main predators (i.e., Chaetognaths, fish larvae and jellyfish; Hirst and Kiørboe, 2002). The COIA was sequentially built for: (i) environment vs. diatoms; and (ii) environment vs. copepods, with a manual backward selection of the significant variables to obtain the highest coupling coefficients, the strength of the coupling being based on the multidimensional correlation coefficient (RV; Robert and Escoufier, 1976). The variables included in the final COIA were selected (i) only if they displayed a significant seasonal trend in box-plots (refer the final list above), and depending on both (ii) the RV value and (iii) the contribution of variables to the construction of the co-inertia axis. The latter was estimated by means of Pearson correlation calculated between the variables and the scores of samplings on the COIA axis. Although the loadings describe how each variable contributes to each co-inertia axis, such information can be retrieved by the correlation coefficient between the variables and the co-inertia axis. A Monte Carlo permutation procedure (1,000 permutations) was applied to compute the RV and statistical significance. For PCA, PCoA, and COIA analyses, an ascending hierarchical classification (AHC) was used with Ward’s aggregation criterion on the two first component coordinates (“hclust” function of the “ade4” package) to reveal monthly clusters.

A variation partitioning (VP) analysis (Step 5, **Supplementary Figure 1**; “vegan” package; Borcard et al., 1992; Legendre and Legendre, 2012) was finally performed to estimate

the contribution of *Phaeocystis* blooms, water masses, hydrometeorological (Pa and/or direction as proxies), and local environmental conditions (S, nutrients, PAR, and predator and/or prey biomass) on changes in the functional structure (i.e., the CWMs), ecological specialization (i.e., environmental tolerance and niche breadths), and FD (SES-RaoQ) of the diatom and copepod communities. To explain variations in species richness of the diatom and copepod communities, the contribution of assembly rules was added using SES-RaoQ as a proxy. SES-RaoQ is known to be the most appropriate FD index (Botta-Dukát and Czúcz, 2016) to detect both environmental filtering (trait convergence) and competition based on niche difference (trait divergence). As for the COIA, variables that attest to the hydrometeorological and local environmental conditions (abiotic and prey biomass) were selected backward to obtain the lowest residual proportion. To explore the effect of *Phaeocystis* blooms on species richness, functional structure, ecological specialization, and FD of the diatom community, a Kruskal–Wallis test was performed using different classes of *Phaeocystis* biomass [1: <100; 2: (100, 500); 3: (500, 1000); 4: >1,000 $\mu\text{gC L}^{-1}$] coming from the 1996 to 2019 dataset (refer “Ecological specialization”).

RESULTS

Abiotic Environment and Plankton Composition and Biomass

The first principal component (PC1, 48.5% of the total variance) showed a seasonal gradient from relatively high turbulent (Pa as a proxy), less saline, nutrient-rich (DIN, DIP, and DSi), and poor PAR winter conditions to calm and relatively lighted, but nutrient-limited ($\text{DSi} < 2 \mu\text{M}$, $\text{DIN} < 1 \mu\text{M}$, and $\text{DIP} < 0.2 \mu\text{M}$), and saline summer conditions (Figure 1 and Supplementary Figure 2). The second principal component (PC2, 18% of the total variance) was mainly driven by wind direction (both north and eastward winds) and SST, suggesting that SST increased as north and eastward winds increased. The temperature–salinity diagrams mainly discriminated water masses according to temperature (Supplementary Figure 3). The vertical structure of water masses also showed seasonal variations; the spring–summer water masses (from March to August) being saltier and colder at the bottom depth; autumn–winter conditions (from September to February) were reversed.

Phytoplankton biomass was mainly composed of diatoms, except when *Phaeocystis* colonies prevailed (from March to mid-May, Figure 2A). Zooplankton biomass was mainly composed of copepods, except during the seasonal outburst of the meroplankton that was mainly composed of Echinodermata (in May, mainly *Pluteus* larvae, Figure 2B). While a slight decrease was observed during the peak of *Phaeocystis*, the biomass of diatoms followed the same seasonal dynamics as protozooplankton (sum of heterotrophic dinoflagellates and ciliates) and copepods (Figures 3A–D). Protozooplankton and copepod biomass progressively increased from winter months to May–June (Figures 3C,D), before decreasing. The C/Chla ratio

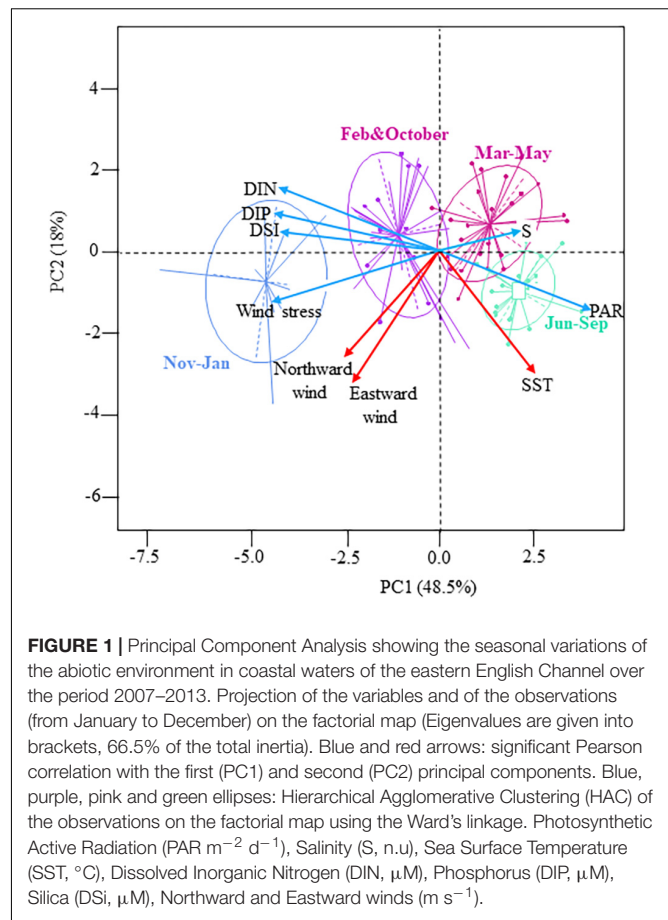
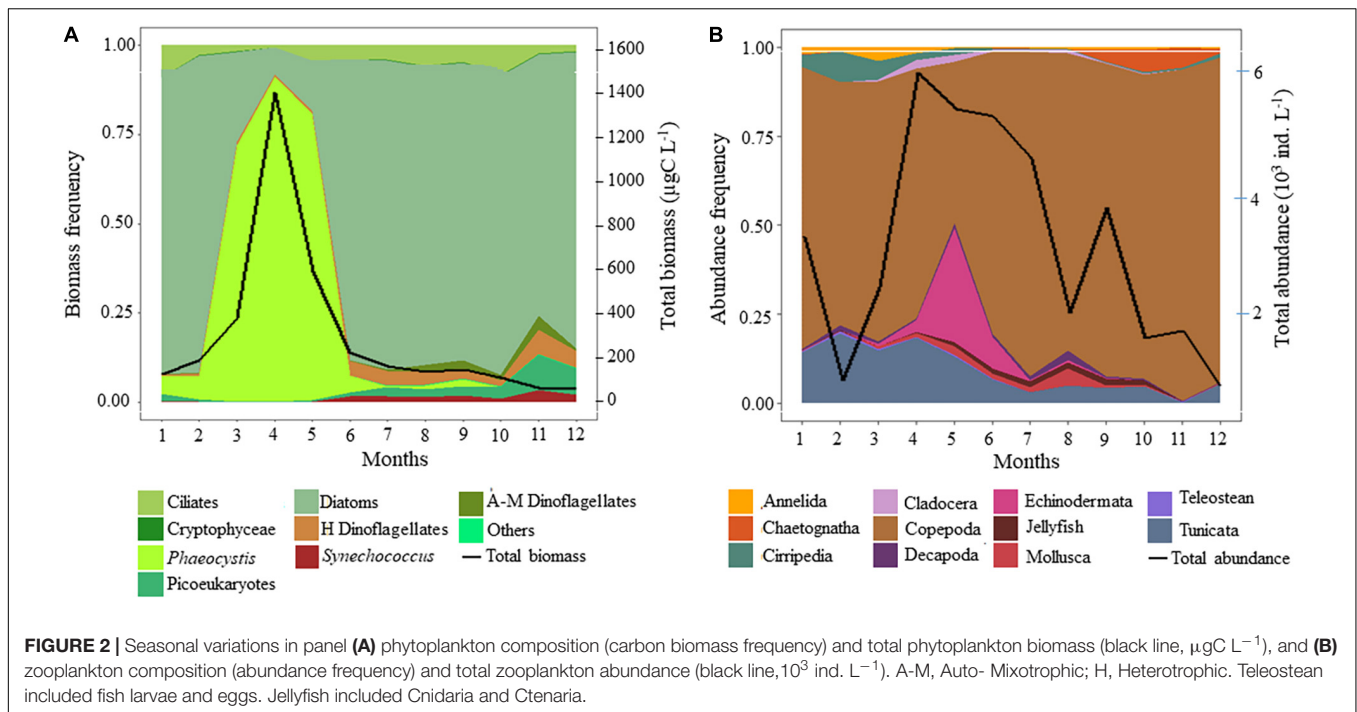


FIGURE 1 | Principal Component Analysis showing the seasonal variations of the abiotic environment in coastal waters of the eastern English Channel over the period 2007–2013. Projection of the variables and of the observations (from January to December) on the factorial map (Eigenvalues are given into brackets, 66.5% of the total inertia). Blue and red arrows: significant Pearson correlation with the first (PC1) and second (PC2) principal components. Blue, purple, pink and green ellipses: Hierarchical Agglomerative Clustering (HAC) of the observations on the factorial map using the Ward’s linkage. Photosynthetic Active Radiation (PAR $\text{m}^{-2} \text{d}^{-1}$), Salinity (S, n.u.), Sea Surface Temperature (SST, $^{\circ}\text{C}$), Dissolved Inorganic Nitrogen (DIN, μM), Phosphorus (DIP, μM), Silica (DSi, μM), Northward and Eastward winds (m s^{-1}).

showed strong seasonal variations, with maxima in April–May and minima in winter (Figure 3E).

Functional Structure and Ecological Specialization of the Diatom and Copepod Communities

Seasonal variations in the functional structure and ecological specialization of the diatom community characterized with LOESS over the period 2007–2013 (Supplementary Figures 4A,C,E,G,I,K,M,O and Supplementary Figures 5A,C,E,G,I,K) were similar to those obtained over the period 1996–2019 (Supplementary Figures 4B,D,F,H,J,L,N,P and 5B,D,F,H,J,L). However, Nemenyi tests revealed that monthly changes were more pronounced when using the 24-year time series. The PC1 of the PCoA (PCoA1; 51% of the total variance) (Figure 4A) suggested a seasonal shift in the functional structure and ecological specialization of diatom communities from the autumn fall winter to the spring period. This shift was characterized by a seesawing from communities exhibiting high silicification, low S/V ratio, presence of tychopeagic/benthic species, PAR specialization, and generalists relative to nutrient use, to more environmentally tolerant diatom communities (from May to July). During early spring and the *Phaeocystis* bloom period, communities exhibited an intermediate position



(Figure 4A). The PC2 (PCoA2; 15% of the total variance) revealed that large-size diatom species with defense against predation prevailed from January to March and in October (Figure 4A). Although weakly associated with the first two principal components, we detected, for both time series, that CWM-MLD values peaked during the maximum of the *Phaeocystis* bloom (i.e., April; Supplementary Figures 4E,F).

For copepods, the PCoA (the PCoA1 and PCoA2 explaining 56% and 22% of the total inertia, respectively, Figure 4B) showed that the communities were mainly composed, from February to May, of large omnivorous active feeders (i.e., high CWM-feeding mode values), omnivores with a relatively high propensity to detritivory and environmentally tolerant species, and generalists for TSM and POC. A contrasting pattern between the CWM-omnivorous and the CSI-trophic regime was detected. From June to September, communities were mainly composed of small and passive feeders with a low propensity to detritivory and specialists for both TSM and POC. In October, carnivorous copepods, with specialized feeding modes and specialized environmental requirements, dominated the community.

Accordingly, the CSIs of copepods for trophic regime and feeding mode had high values. Concerning the functional structure of the copepod community (Supplementary Figures 6A–M), significant monthly changes were only seen for maximum size (Supplementary Figure 6A) and feeding mode (Supplementary Figure 6B).

Species Richness and FD of Diatom and Copepod Communities

The annual cycle of diatom species richness exhibited a bimodal pattern (Figure 5A and Supplementary Figure 7A), with a

peak in February–March and September–October. No significant monthly change was detected (Nemenyi test, $p > 0.05$). The annual cycle of copepod species richness was unimodal, peaking in August–September (Figure 5B). No monthly variation was detected between the volume of filtered seawater and copepod species richness ($N = 96$, $r^2 = 10^{-5}$, $p > 0.05$).

Patterns of FD of the diatom community (Figures 5C–H, refer Supplementary Table 5 and “diatom.defense.traits” in Supplementary Data for more details on the calculation), differed among functional indices, independently of the sampling period (Supplementary Figures 7B–G). Fric (SES-Fric, Figures 5C,D and Supplementary Figures 7B,C) and divergence (SES-RaoQ, Figures 5E,F and Supplementary Figures 7D,E) for resource use and predation avoidance were lower than expected by chance. FEve values (SES-FEve, Figures 5G,H and Supplementary Figures 7E,G) were also not different from those expected by chance. The SES-Fric and SES-RaoQ were significantly negatively correlated to species richness for both resource use and predation avoidance (SES-Fric: $r = -1$, $p < 0.001$ and $r = -0.98$, $p < 0.001$, respectively; SES-RaoQ: $r = -0.78$, $p < 0.001$, $r = -0.77$, $p < 0.001$, respectively). SES-FEve was not correlated with species richness ($r = 0.21$, $p > 0.05$ and $r = 0.01$, $p > 0.05$, respectively).

For copepods, the SES-Fric (Figure 5I) and SES-RaoQ (Figure 5J) were also significantly negatively correlated with species richness, but to a lesser extent ($r = -0.43$, $p < 0.001$, $r = -0.34$, $p < 0.001$, respectively). Omnivory and herbivory, because of their respective high significant correlation with detritivory ($r = 0.9$, $p < 0.001$) and carnivory ($r = -0.91$, $p < 0.001$), were discarded from the calculation. The SES-Fric (Figure 5I) values for copepods were not different from those expected by chance. SES-RaoQ (Figure 5J) and SES-FEve

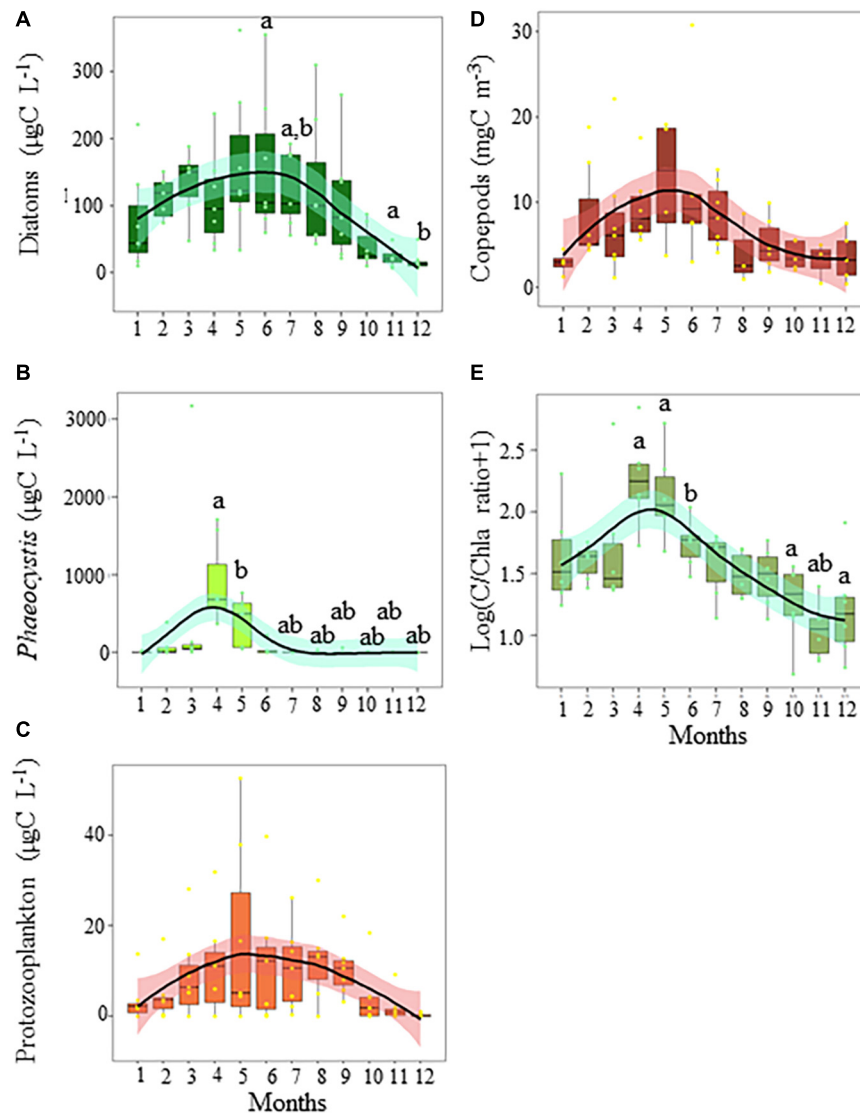


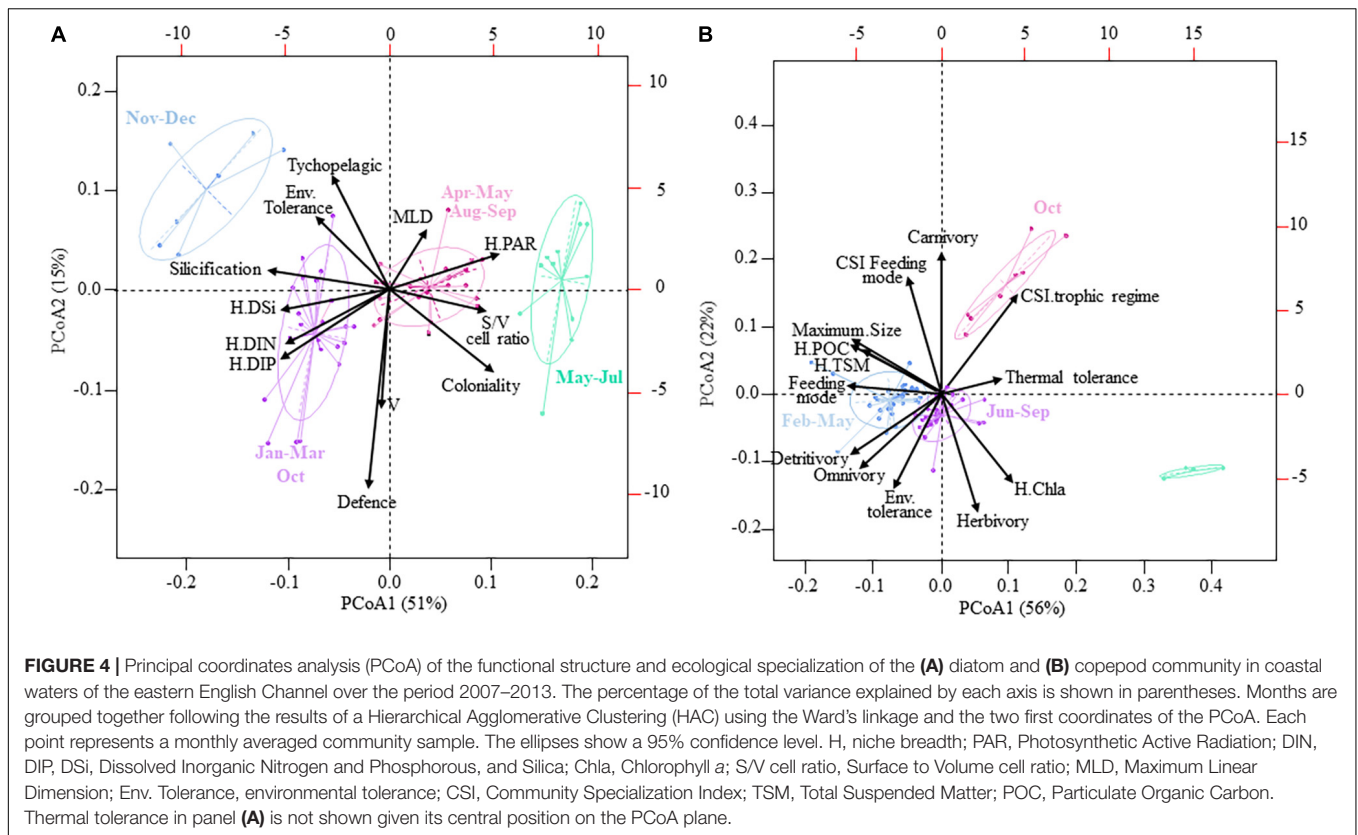
FIGURE 3 | Seasonal variations in the biomass (mgC L^{-1}) of panel **(A)** diatoms, **(B)** *Phaeocystis*, **(C)** protozooplankton (ciliates and dinoflagellates), **(D)** copepods (mgC m^{-3}), and **(E)** the C/Chla ratio in coastal waters of the eastern English Channel over the period 2007–2013. Black horizontal line inside box: median; box: first to third quartiles; whiskers: 1.5 times the interquartile range (IQR); dots: monthly data including outliers (> 1.5 times IQR). The labels a and b show significant differences between months ($p = 0.05$, Nemenyi test). The solid line and ribbon represent LOESS smoothing and the 95% confidence interval, respectively.

(Figure 5K) values were mostly lower and higher, respectively, than expected by chance. FD indices did not show seasonal patterns (e.g., note the large 95% confidence intervals of the LOESS fits in Figures 5I–K and Supplementary Figure 6A–M).

Relationships Between the Functional Structure, Ecological Specialization, and FD, and the Abiotic and Biotic Environment

Co-inertia analysis showed a significant coupling ($n = 63$, $RV = 0.49$, $p = 10^{-3}$) between the structure of diatom communities and abiotic/biotic conditions (Figures 6A,B,

Supplementary Figures 8A,B, and Supplementary Table 6A). A seasonal pattern was delineated by the COIA (Supplementary Figures 8A,B). Although all environmental parameters were significant in structuring the seasonality of diatom communities, some were more important than others (Supplementary Table 6A). The first COIA axis (explaining 86% of the total inertia, Figure 6A) showed that diatom communities, composed predominantly of slightly silicified species, with a relative high S/V cell ratio, and the ability to form colonies, were associated to calm weather conditions and more saline seawater with relatively higher PAR, but low nutrients. Diatom communities, with mainly specialist species for nutrients but generalists for PAR, were also sensitive to environmental variations (relatively

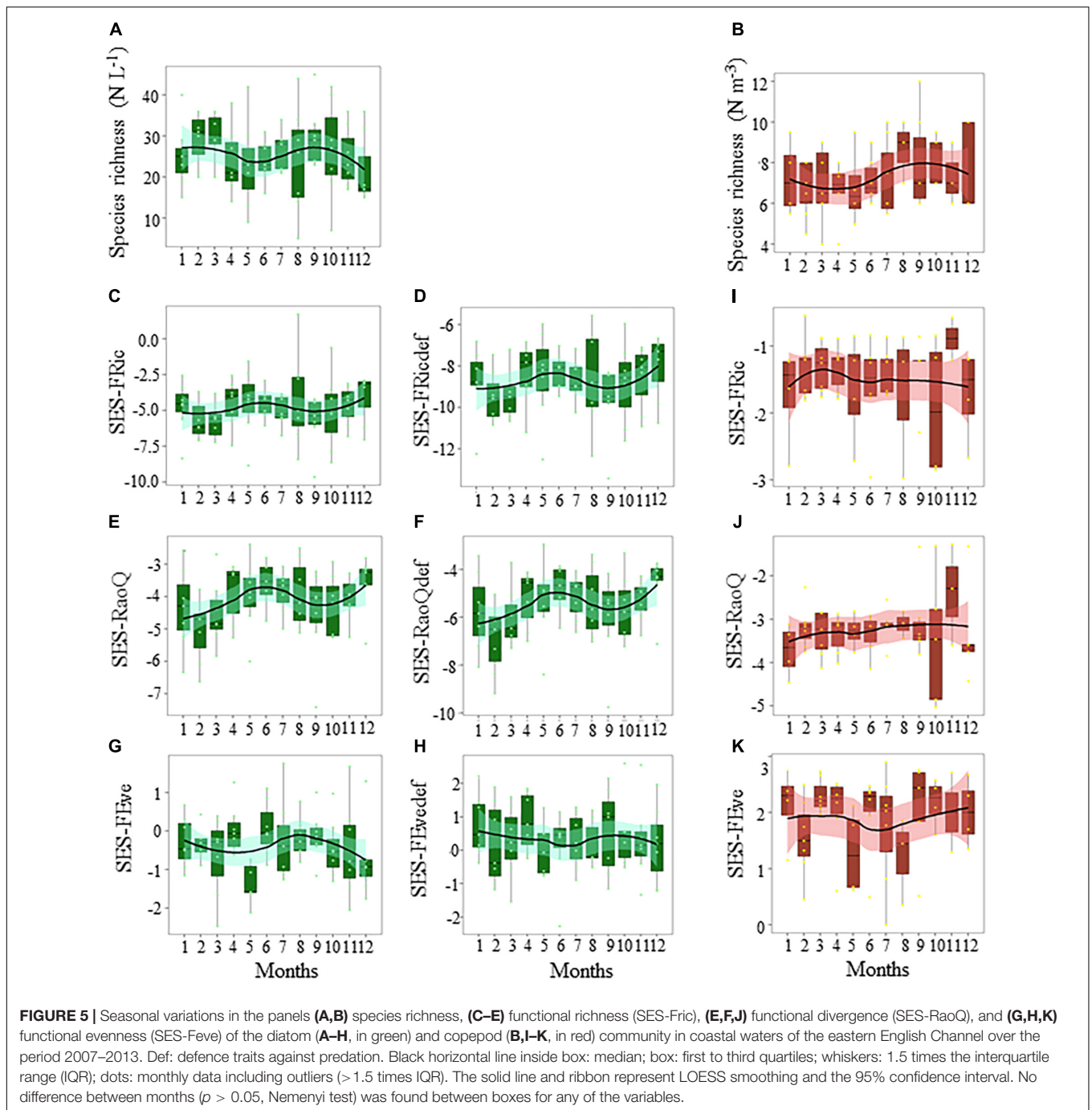


low “Tol” values); slightly silicified species bloomed later in the year. According to the second COIA axis (8% of the total inertia; **Figure 6A**), most diatoms with high defense levels against predation and DIN generalists were associated with colder seawater, rich in *Phaeocystis* biomass and characterized by a high C/Chla ratio, and large-bodied generalist omnivore copepod species. Under such conditions, diatom biomass was maximal. The third COIA axis (3% of the total inertia; **Figure 6B**) showed that species-rich diatom communities, characterized by the dominance of small MLD species, were associated with copepod communities dominated by specialist species. The SES-FRiC and SES-RaoQ of the diatom community were the lowest for both resource use and predation avoidance (**Figure 6B**).

The coupling strength between functional structure (i.e., the CWMs), ecological specialization (i.e., environmental tolerance and niche breadth), and FD (SES-RaoQ and SES-FRiC) of copepods, and environmental conditions (refer section “Materials and Methods”) was low but significant ($n = 63$, $RV = 0.36$, $p = 0.001$, **Figure 6C**). The seasonality of the coupling was unclear (**Supplementary Figure 8C**). The first co-inertia axis (explaining 84% of the total inertia) revealed that large, active-feeding, and omnivore copepod species (i.e., low CSI-trophic regime values) were associated with relative calm weather conditions, more saline *Phaeocystis*-rich waters, characterized by higher proportions of diatoms with defense levels against predation (**Figure 6C** and **Supplementary Table 6B**), and relative high abundance of jellyfish and fish larvae, but low abundance of chaetognaths. Copepods were tolerant to

environmental fluctuations, with a propensity to detritivory. The second co-inertia axis (12% of the total inertia) exhibited that species-rich copepod communities were mainly composed of passive-feeding and trophic specialist species (i.e., high CSI-trophic regime values) with a low propensity to detritivory. Copepod species were also sensitive to environmental variations, especially under warm conditions and a high protozooplankton and jellyfish biomass (**Figure 6C**); this coincides with the lowest SES-FRiC and SES-RaoQ values occurring in the copepod communities.

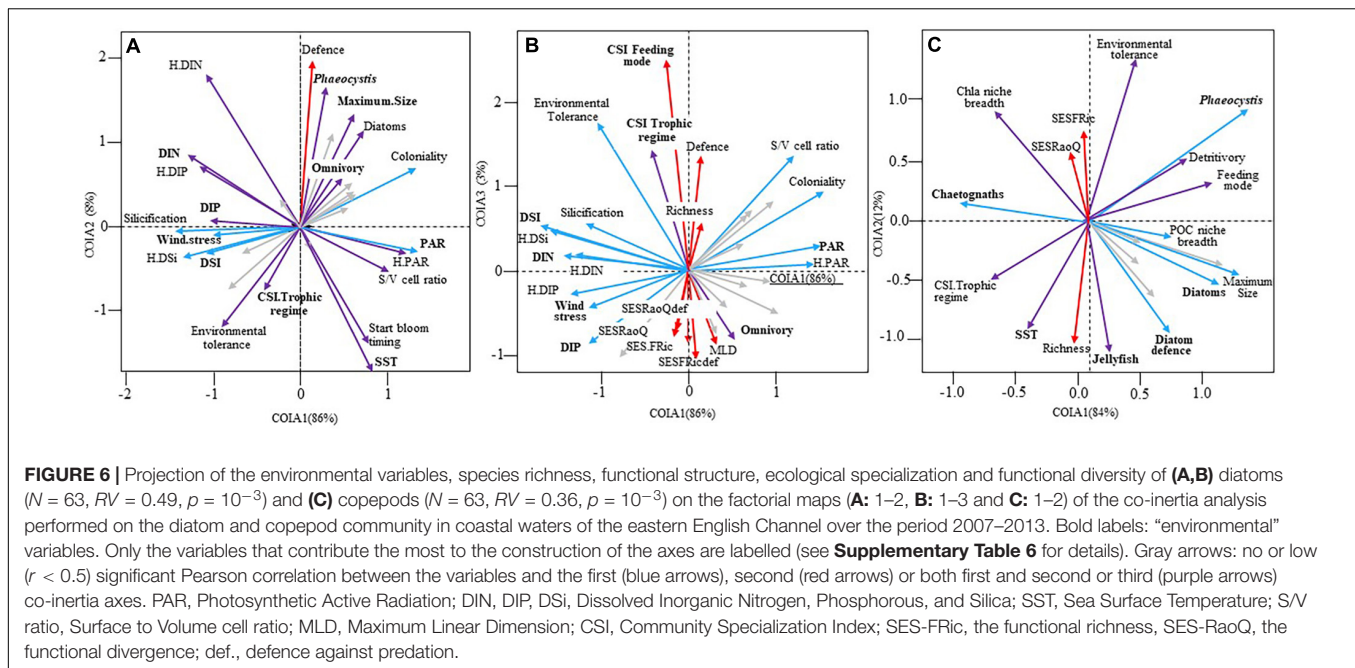
Variation partitioning analysis (VP, **Figure 7A**) exhibited that seasonal variations of the functional structure and ecological specialization of the diatom and copepod communities were not related to seasonal changes in environmental conditions, as shown by the high residual values. It was detected that the local environment contributed the most to the explained variance (i.e., 49%) in the functional structure and ecological specialization of the diatom community (adjusted $r^2 = 0.18$, $p = 0.001$, i.e., 18% of the total variations of the diatom community), followed by hydrometeorological features (3%, $p = 0.001$) and the interaction between the local environment and hydrometeorological features is 16% (**Figure 7A**). The variations in the structure of the diatom community were also explained, but to a lesser extent, by the *Phaeocystis* bloom (1%, $p = 0.001$), predator biomass, and size (1%, $p = 0.001$), and their interactions (2%). The *Phaeocystis* bloom was the most contributing process to the functional structure and ecological specialization of the copepod community (15%, $p = 0.001$, **Figure 7B**). Hydrometeorological



features (5%, $p < 0.05$) and their interaction with the *Phaeocystis* bloom (4%), and the interaction between the local environment and predators (3%), played a minor role. In contrast to the functional structure and ecological specialization of diatom and copepod communities, the proportion of unexplained variance was low (3%) for diatom species richness. Diatom species richness was mainly explained by the convergence of a combination of traits: SES-RaoQ decreased as species richness decreased (92% of the total variations in diatom species richness, $p = 0.001$, Figure 7C). As for the functional structure and ecological

specialization, most of the variations of copepod species richness remained unexplained (69%), and the most contributing drivers are both the convergence of a combination of traits (Figure 7D) and its indirect influence through interaction with the local environment (27%).

Phaeocystis biomass had no significant effect on the diatom species richness, biomass, FD (i.e., SES-FR, SES-FEve, and SES-RaoQ), ecological specialization (i.e., niche breadths), or the functional structure (i.e., CWMs) of the diatom community (Supplementary Figure 9).



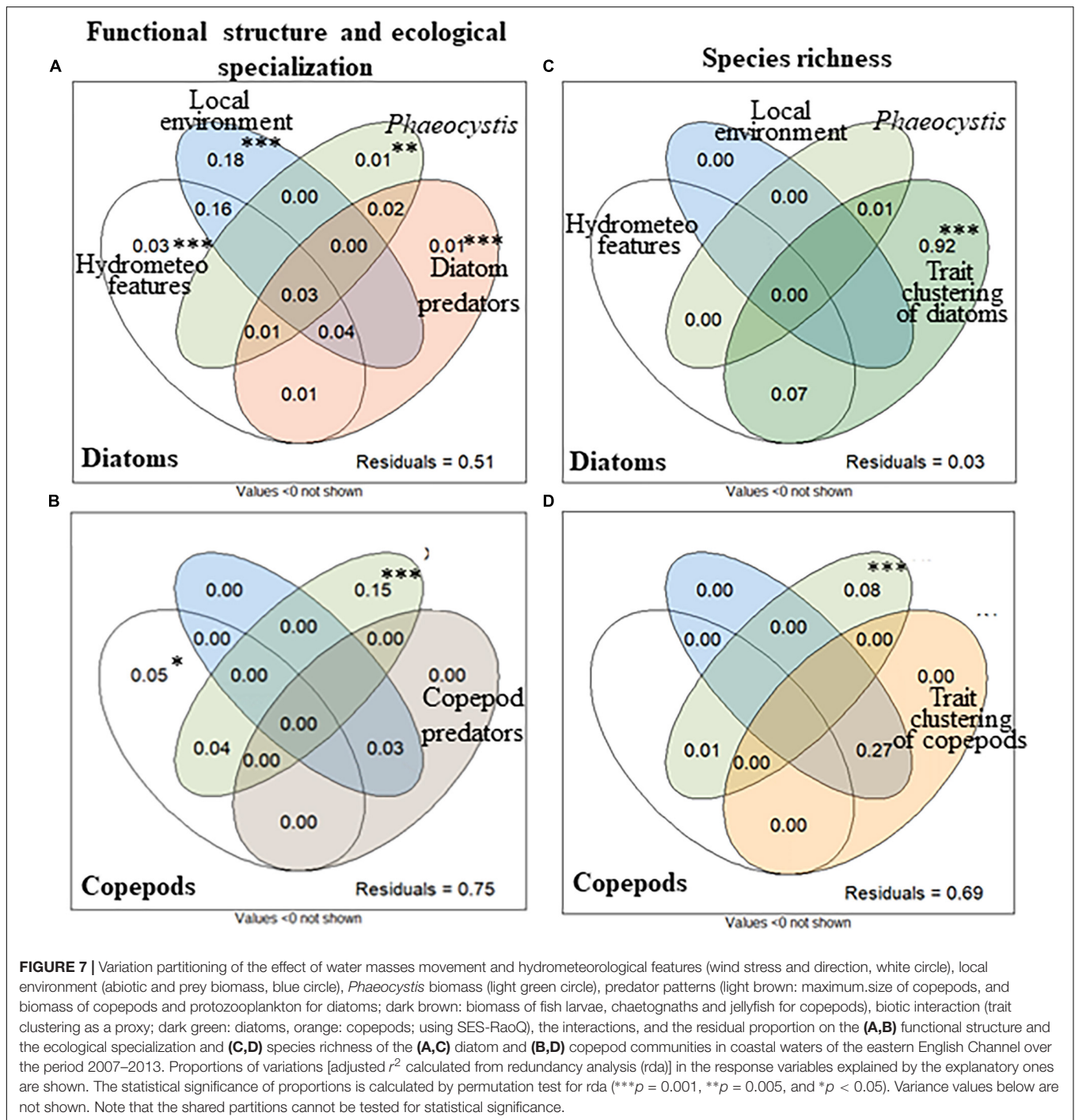
DISCUSSION

In this study, we investigated the challenging questions of linking the seasonal succession of planktonic organisms with resource and defense traits, and the identification of the conditions that shape species richness. The results showed that the diatom and copepod communities of the EEC respond synchronously to varying abiotic and biotic conditions. We highlighted that some environmental drivers acted on some trait combinations, through environmental filtering, leading to temporal succession in species composition. Such a pattern was possible through the expression of several well-established functional trait trade-offs that allowed us to optimize the fitness of a species in a particular environment. The results strongly suggested that the competition-defense trade-off (e.g., Hillebrand et al., 2000; Chase et al., 2002), a mechanism that favors weak competitors, better protected against predation, played a key role, not only in driving diatom and copepod species richness but also in triggering the *Phaeocystis* bloom (as shown below). We also revealed the key role of nutrient levels and competition for nutrients, and of prey-predator interactions in the seasonal succession of diatoms and copepods in the coastal waters of the EEC.

The seasonal succession of trait values within the diatom community along with the seasonal gradient of resource, turbulence, and grazing intensity, resulted from several trait trade-off effects: (i) a trade-off in the competitive ability for light vs. nutrients (i.e., S/V cell ratio, coloniality, and specialization for nutrients in opposition to silicification and specialization for light; as shown in **Figure 4A**; Huisman and Weissing, 1994; Leibold, 1997; Klausmeier and Litchman, 2001); (ii) a defense-competition trade-off (e.g., Hillebrand et al., 2000; Chase et al., 2002); and (iii) an opportunistic-gleaner strategy trade-off (Grover, 1990). We revealed a clear opposition in the

dominance between r - and K -strategists: species with high maximum growth rate and photosynthetic efficiency adapted to low light but high nutrient and turbulent conditions on the one hand (e.g., diatoms: Armbrust, 2009, and *Phaeocystis* colony: Rousseau et al., 2007; Seuront et al., 2007; Nissen and Vogt, 2021), and species which have low maximum growth rate but high competitiveness for nutrients, such as *Synechococcus* and picoeukaryotes (Stawiarski, 2014), on the other hand. The defense-competition trade-off was deduced from the fact that the diatom communities with the highest proportion of level against predation species matched with periods of (i) high grazing intensity [i.e., late winter/spring (February–March) and late summer/autumn (September–October)] (Gasparini et al., 2000; Stelfox-Widdicombe et al., 2000; Antajan, 2004; Grattepanche et al., 2011b); and (ii) low competitiveness for nutrients (i.e., high silicification but low specialization for nutrients and low S/V cell ratio). The association between the defensive trait and cell biovolume was consistent with this functional trait trade-off (**Figure 4A**). To invest in defensive traits against predation, is generally metabolically costly, in such a way that prey with high defense levels has generally lower maximum growth rate, maximum resource uptake, and/or resource uptake affinity (Pančić and Kiørboe, 2018; Cadier et al., 2019; Ehrlich et al., 2020), all these types of defense costs being related to cell biovolume (Litchman and Klausmeier, 2008; Marañón, 2015).

We observed seasonal successions of copepod species of varying maximum size values, feeding strategies, trophic regimes, and vulnerability to predation along a seasonal gradient of turbulence, food level and composition, and predator abundance (**Figures 2A,B, 3A–D, 4B, 6C**), in line with a competition-defense trade-off. Actively feeding copepods feed more efficiently on non-motile than on motile preys (i.e., competitive specialists), but they are more at predation risk



than ambush feeders (i.e., defense specialists) (Almeda et al., 2018). This suggests that the shift toward the dominance of ambush copepod feeders (i.e., predators) during summer might result from strong predation pressure on active-feeding copepods by zooplanktivorous organisms, especially jellyfish (i.e., Cnidaria and Ctenaria). The increasing abundance of jellyfish during summer (Figure 6C) is known to exert strong top-down control on copepods (Hirst and Kiørboe, 2002). Ambush copepod feeders, mainly carnivores (Figure 4B), were also

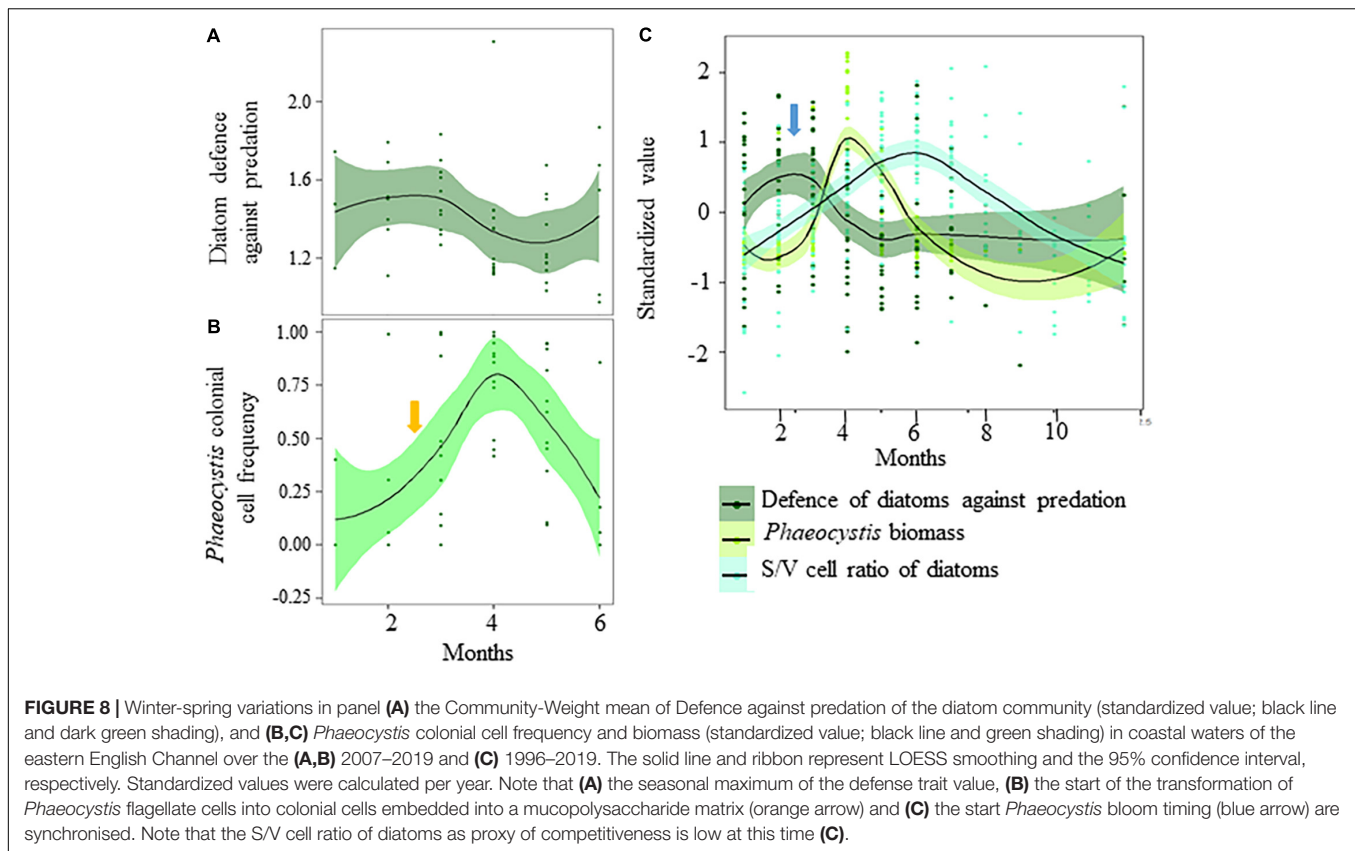
smaller, and with a lower metabolic cost (Kiørboe, 2011 and references therein) than actively feeding copepods. The presumed strong predation pressure of jellyfish on active-feeding copepods, in combination with the shift toward dominance of motile prey, might also explain the shift in maximum size and diet change that we observed for the copepod community from July (Supplementary Figures 6A,C–F). The dominance of active feeding-current feeders observed during the first quarter is consistent with the dominance of non-motile prey of high

food level (i.e., the spring bloom), their higher metabolic needs (Kiørboe, 2011 and references therein), and a lower abundance of zooplanktivore predators (Figure 6C). The prevalence of omnivory in winter and spring, which results from higher detritivory, is consistent with the high quantity of detrital material in winter, and both *Phaeocystis* aggregates and ghost colonies in spring (Becquevort et al., 1998; Mari et al., 2005). The significant decline in the grazing rate of copepods, often reported during a *Phaeocystis* bloom (Gasparini et al., 2000; Nejstgaard et al., 2007 and references therein), might result from a shift in the diet of copepods toward *Phaeocystis* detrital material.

We hypothesize that the increase in diatom species richness in early spring and autumn resulted from high grazing pressure by generalist copepods, which grazed the dominant highly competitive diatoms that displayed weak defensive traits. Annual maxima of diatom species richness (Figure 5A and Supplementary Figure 7A) matched with periods of annual maxima of defense level (Figure 6B and Supplementary Figures 4O,P) and high grazing pressure occurred at this time of the year (Gasparini et al., 2000; Antajan, 2004). Seasonal variations in diatom species richness were inversely related to functional divergence linked to resource and defense (SES-RaoQ and SES-RaoQdef) (Figures 5A,E,F and Supplementary Figures 7A,D,E). This indicates that species richness increased as the diatom community converged toward species of similar traits for resource and defense. Trait convergence, which results from abiotic stress (Cornwell and Ackerly, 2009) and/or competitive dominance and ensuing species exclusion (Mayfield and Levine, 2010), is unlikely given the increase in diatom biomass and species richness in early spring and autumn. Cavender-Bares et al. (2009) demonstrated that generalist consumers are expected to cluster prey communities toward species with high defense levels. Although we observed a pattern in line with Cavender-Bares et al. (2009) during the spring period, the autumnal peak in diatom species richness that we observed in the data was associated with specialist ambush and carnivore feeders: such a discrepancy may result from the high predation pressure exerted by jellyfish on generalist and actively feeding copepods (Figure 6C), which are more vulnerable to predation in comparison to passive ambush feeders (Kiørboe, 2011 and references therein). Copepod species richness also peaked in autumn, when the copepod community converged toward species of the similar maximum size, trophic preference, and feeding mode (Figure 6C) and when we observed dominance of copepod species less vulnerable to predation (i.e., passive ambush feeders; Kiørboe, 2011 and references therein, Almeda et al., 2018; refer also “feeding mode” in Figure 6C and Supplementary Table 6). However, the seasonal succession of copepod species was by far less evident than for diatoms. The lack of identification of the different copepodite stages, with sizes varying by one order of magnitude between the different copepodite stages (i.e., CI–CVI, Durbin and Durbin, 1978; Cohen and Lough, 1981), probably explained the result. Moreover, copepods live much longer than diatom cells (several months/up to 1 year for copepods, but a few days for diatoms) and their traits enable them to survive in unfavorable conditions. Large unexplained variance (>50%), as we quantified in the VP analysis, is common in ecological studies (Brasil et al., 2020 and references therein) and is often the result of (i) unmeasured

environmental drivers, such as trace metals (Chappell et al., 2019); and (ii) potential antagonistic responses among species within a community (Brasil et al., 2020). Brasil et al. (2020) have also recently provided evidence that the assessment of biodiversity and FD is influenced by the presence/lack of rare species: rarity can contribute to large residuals when varpart models are computed. The uncertainty in plankton counts [estimated to be 10% for diatoms based on the table of Lund et al. (1958), and 3–40% for zooplankton (Mack et al., 2012; Kwong and Pakhomov, 2021) with an average of 30% (Frontier, 1969)] could have contributed to the large unexplained discrepancies found in the VP analyses (Brasil et al., 2020). Uncertainty in the species carbon conversion factors that we used for the calculation may have also influenced the estimations and the initial assumptions on how to capture the biological responses, such as linearity of the relationships between the response and explanatory matrices or statistical normality.

Despite potential shortcomings inherent to both the nature of the data and methodological assumptions, we characterized the important role of prey-predator interaction in shaping autumnal copepod community as a consequence of a strong predation pressure by jellyfish on the actively feeding copepods, which in turn induces relaxation of prey-prey competitive interactions. Because of the dominance of phytoplankton *r*-strategists in spring and autumn, generalist consumers might have grazed mainly on the dominant diatom species that displayed higher growth rates than diatom species with strongly defended cells. Several studies have suggested that species coexistence is possible only under both high grazing pressure and nutrient level conditions to allow the strongly grazed species to regrow after grazing (e.g., Proulx and Mazumder, 1998; Leibold, 1999; Worm et al., 2002). This could explain why diatom species richness declined in summer when nutrients are growth-limiting and the grazing pressure much lower than in spring and autumn (Gasparini et al., 2000; Stelfox-Widdicombe et al., 2000; Antajan, 2004; Grattepanche et al., 2011b). The defense-competition trade-offs could have reduced the frequency of well-defended, but poor-competitive, species and reduced diatom species richness in nutrient-limiting conditions that favor competitive exclusion. The relatively high S/V cell ratio and chain length values, but lowest silicification and defense level, observed in summer, reinforce this idea of the prevalence of competitive exclusion during this period. The concomitant shift toward niche differentiation through the tendency toward a decrease in functional divergence (e.g., Cornwell and Ackerly, 2009), according to the principle of limiting similarity (MacArthur and Levins, 1967), also suggested competitive exclusion. Such shift toward niche differentiation, paralleled by a decrease in species richness, started in April from the maximum of the *Phaeocystis* bloom. It suggests that the unbalancing of the defense-competition trade-off toward competitive exclusion began at the time *Phaeocystis* is a poor competitor for nitrate (Lancelot et al., 1998), has, in average, a lower maximum growth rate than diatoms (e.g., Breton et al., 2017 and reference therein), but strong protection against grazing by forming colonies that grow larger in the presence of predators (Jakobsen and Tang, 2002; Long et al., 2007; Nejstgaard et al., 2007, and references therein). *Phaeocystis* might have consequently benefited from the grazing



preference of generalists toward poor-defended, but highly competitive, species (Figure 8). The seasonal maximum of the defense trait value (Figure 8A), the start of the transformation of *Phaeocystis* flagellate cells into colonial cells embedded into a mucopolysaccharide matrix (Figure 8B, orange arrow), as well as the timing of bloom initiation of *Phaeocystis* (Figure 8C, blue arrow), were synchronized. The results highlight the potential key role in the defense-competition trade-off besides nutrient level in triggering the *Phaeocystis* bloom, and more generally, the cardinal role of generalist consumers in the initiation of the bloom. As observed for other ecological communities [Chihoub et al., 2020 (copepods); Wengrat et al., 2018 (diatoms); Villéger et al., 2014; Menezes et al., 2015; Alexander et al., 2017 (fish); Rogalski et al., 2017 (daphniids); Donohue et al., 2009; Zhang et al., 2019 (benthic invertebrates)], eutrophication favors biotic homogenization, which in turn may favor blooms of inedible species such as *Phaeocystis*. We did not detect any negative effect of the *Phaeocystis* bloom on the plankton community (Supplementary Figure 9), but a shift of the copepod community toward biotic homogenization was detected.

CONCLUSION

The application of a trait-based approach, combined with the assessment of ecological specialization, has made possible a better understanding of seasonal succession and biodiversity patterns in plankton along gradients of resources, turbulence,

and grazing pressure. We have shown that species succession is driven by different trade-offs among functional traits, under the functional constraints dictated by the environmental pressure encountered by plankton communities across the seasons. We suggest that the competition-defense trade-off plays an important role in promoting plankton species richness and in triggering the *Phaeocystis* bloom in coastal waters of the EEC. By successively favoring species with ecological strategies that match environmental conditions, the diatom and copepod communities in coastal waters of the EEC respond synchronously to varying resources and biotic conditions.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article are available by the authors in **Supplementary Data**.

AUTHOR CONTRIBUTIONS

EB, BS, and EG conceptualized the study. EB and EG performed the investigation on methodology. EB, BS, D-IS, DP, CS, MC, SF, J-MB, and AL provided the abiotic and biological data. EB, AP, OD, and EG performed the data analysis. EB, UC, EG, BS, LK, GB, and LS contributed to the manuscript writing. All authors contributed to the article and approved the submitted version.

FUNDING

This work was a contribution of the project EVOLECO-NUPHY supported by the French National program LEFE (Les Enveloppes Fluides et l'Environnement).

ACKNOWLEDGMENTS

We acknowledge the three reviewers for their constructive comments, which allowed us to greatly improve the manuscript. We thank the crews who helped during long-term monitoring downstream of the Gironde estuary (2001–2017) and in coastal waters of the eastern English Channel (1996–2019), and the SOMLIT teams for sampling and physicochemical measurements

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