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Disentangling the components of coastal fish biodiversity in southern Brittany by applying an environmental DNA approach

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Abstract

The global biodiversity crisis from anthropogenic activities significantly weakens the functioning of marine ecosystems and jeopardizes their ecosystem services. Increasing monitoring of marine ecosystems is crucial to understand the breadth of the changes in biodiversity, ecosystem functioning and propose more effective conservation strategies. Such strategies should not only focus on maximizing the number of species (i.e., taxonomic diversity) but also the diversity of phylogenetic histories and ecological functions within communities. To support future conservation decisions, multicomponent biodiversity monitoring can be combined with high-throughput species assemblage detection methods such as environmental DNA (eDNA) metabarcoding. Here, we used eDNA to asses fish biodiversity along the coast of southern Brittany (France, Iroise Sea). We filtered surface marine water from 17 sampling stations and applied an eDNA metabarcoding approach targeting Actinopterygii and Elasmobranchii taxa. We documented three complementary biodiversity components—taxonomic, phylogenetic, and functional diversity—and three diversity facets—richness, divergence and regularity. We identified a north/south contrast with higher diversity for the three facets of the biodiversity components in the northern part of the study area. The northern communities showed higher species richness, stronger phylogenetic overdispersion and lower functional clustering compared to the ones in the southern part, due to the higher diversity of habitats (reefs, rocky shores) and restricted access for fishing. Moreover, we also detected a higher level of taxonomic, phylogenetic, and functional uniqueness in many offshore stations compared to more coastal ones, with the presence of species typically living at greater depths (> 300 m), which suggests an influence of hydrodynamic structures and currents on eDNA dispersion and hence sample composition. eDNA metabarcoding can, therefore, be used as an efficient sampling method to reveal fine-scale community compositions and in combination with functional and phylogenetic information to document multicomponent biodiversity gradients in coastal marine systems.

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1 | INTRODUCTION

Human activities constitute major pressures affecting all ecosystems by disrupting interdependent abiotic and biotic factors, threatening biodiversity (Hooper et al., 2012) and causing loss of genes, species and biological function at an alarming rate (Cardinale et al., 2012). Marine species and ecosystems are impacted by increasing anthropogenic pressures such as human population growth that leads to increased demand for ocean space and resources (Halpern et al., 2015). Coastal areas, characterized by high species diversity and high productivity (Watanabe et al., 2018), are affected by human activities (Halpern et al., 2015). Their structural complexity influences the local species composition (Pihl & Wennhage, 2002; Tuya et al., 2019) and provides refuge space and food resources for species spending at least part of their life cycle there (Pihl & Wennhage, 2002; Kovalenko et al., 2012). Factors such as urban expansion, agricultural runoffs, fishing, maritime traffic and industrial pollution alter coastal habitats (Gaylard et al., 2020). All these threats are likely to increase in the next decades (Pereira et al., 2010), stressing the need to understand and monitor how ecosystems respond. Expected changes concern composition, functioning and services and need to be tackled through a holistic approach documenting the three biodiversity components (taxonomic, phylogenetic, and functional) and their three facets (richness, divergence, regularity; Mason et al., 2005; Pavoine et al., 2009). Improved tools should facilitate biodiversity dynamics assessments through the development of more ethical and cost-effective alternatives, such as environmental DNA (eDNA).

Preventing biodiversity declines cannot be based on the sole consideration of the species number and their taxonomic identity, but also needs to include information on evolutionary history and intrinsic biological and ecological features, namely phylogenetic and traits (or functional) components of biodiversity (e.g., Albouy et al., 2015; Safi et al., 2011). Indeed, not all species share the same evolutionary history as some species originate from more recent radiations (Malinsky et al., 2018; Ronco et al., 2021), while others are only distant phylogenetic relatives (e.g., Tuatara species diverged 250 million years ago from its closest snake and lizard extant relative; Gemmell et al., 2020). Phylogenetic diversity quantifies the evolutionary history in a community modeled through a phylogenetic tree derived from morpho-anatomical or genetic differences among taxa. The degree of divergence among taxa and the amount of unique evolutionary history they convey have gained increasing importance in ecology to understand the origin, the distribution and the maintenance of biodiversity (Cavender-Bares et al., 2009; Mouquet et al., 2012; Eme et al., 2020) and in conservation as a unique aspect (i.e., evolutionary history) to preserve biodiversity beyond species richness (Faith et al., 2004; Forest, et al., 2007; Davis et al., 2018; Pollock et al., 2017; Winter et al., 2013; Vane-Wright

et al., 1991). Further, species do not all share the same biological and ecological features and consequently can play different roles in ecosystem functioning (Tilman, 2001; Díaz & Cabido, 2001).

Hence, it is important to consider the functional diversity of a given assemblage, which represents "the value and the range of species and organismal traits that influence ecosystem functioning" (Tilman, 2001) and view organisms as "dynamic entities that interact with their environment" (Calow, 1987). Functional diversity is estimated using species traits, which are morphological, physiological, behavioral or phenological features measurable at the individual level that impact individual fitness via effects on growth, reproduction and survival and thus ultimately ecosystem functioning (Violle et al., 2007). These traits are linked to ecological functions such as mobility, food acquisition, predation, reproduction (Albouy et al., 2011; Villéger et al., 2017). Specialized and functionally rare species can perform unique ecosystem functions, thus making an important contribution to functional diversity (Mouillot et al., 2014). In contrast, functional redundancy, defined as several species performing similar functions, also plays an important role in maintaining functional diversity by ensuring ecosystem functions continuity over time in the face of the potential decline of some species (Mouillot et al., 2014), which is referred to as the "insurance hypothesis" (Yachi & Loreau, 1999).

Regarding the three biodiversity facets, richness refers to the sum of accumulated differences among taxa, divergence represents the difference between taxa within an assemblage and regularity refers to the variability in differences among taxa (Tucker et al., 2017). In taxonomy, the richness and regularity dimensions are, respectively, the species number and the evenness of the abundance distribution among species (Pielou, 1966). However, since all species are considered equivalent, there is no divergence facet. In functional ecology, functional richness is often estimated as the volume in functional space constructed from traits, which is occupied by the species in a community (Villéger et al., 2008). Functional divergence quantifies the distance between species within the functional space whereas functional regularity is the variability of functional distances between species. Documenting the functional divergence and regularity within a community helps to understand the degree of species aggregation in functional space, which directly informs about the level of functional redundancy (i.e., tight packing) or uniqueness within the community and provides insight about resource partitioning (Myers et al., 2021). In phylogeny, the richness dimension corresponds to the overall amount of evolutionary history in a sampled community (PD; Faith, 1992). Divergence refers to the phylogenetic divergence among species while phylogenetic regularity quantifies the variation of phylogenetic distances among species (Tucker et al., 2017). Coupling phylogenetic divergence and regularity offers a better understanding of the influence of old (i.e.,

deep) vs recent (i.e., terminal) phylogenetic divergence on the evolutionary history of a community (Eme et al., 2020). Even though these three facets can be documented at α (within site), β (between sites) and γ (total diversity) biodiversity levels, such a holistic approach is yet to be implemented (Tucker et al., 2017).

Documenting the different components and facets of biodiversity always depends on the appropriate description of the taxonomic composition of communities and thus the reliability of the sampling method. Water environmental DNA (eDNA) metabarcoding is emerging as a method to monitor marine biodiversity and may counteract drawbacks inherent to classical sampling methods (Deiner et al., 2017; Polanco-Fernández, Marques, et al., 2021; Taberlet et al., 2018; Thomsen & Willerslev, 2015). To document marine fish biodiversity, traditional sampling methods are bottom trawl surveys (Rochet et al., 2005), video surveys (Boldt et al., 2018), and underwater visual census (UVC; Mallet & Pelletier, 2014). However, these methods are limited in taxonomic, spatial and temporal coverage (Polanco-Fernández, Marques, et al., 2021) because of their dependence on weather conditions, species specificity (Holderegger et al., 2020), cost/inefficiency and the damages they can cause that raise ethical questions (Trenkel et al., 2019), and importantly, habitat accessibility (bottom trawling is not possible on rocky habitats). eDNA metabarcoding in marine environments is based on the recovery and analysis of DNA traces that may persist from hours to days (Andruszkiewicz Allan et al., 2021; Collins et al., 2018; Holman et al., 2021). These DNA traces are the result of species releasing DNA via feces, urine, and epidermal cells or correspond to entire micro-organisms (Deiner et al., 2016). By collecting water samples, amplifying and sequencing DNA, animal presence can be detected at a given site (e.g., Afzali et al., 2021; Polanco-Fernández, Marques, et al., 2021; Port et al., 2016). This method has several advantages compared to traditional sampling methods, as the sampling gear is independent of the studied species and not sensitive to weather conditions (Holderegger et al., 2020). Furthermore, the use of eDNA should ideally improve (i) the detection of rare species (Balasingham et al., 2018; Wilcox et al., 2013) (ii) the discrimination of morphologically similar species (Holdregger et al., 2020) and (iii) the sampling of difficult-to-access areas such as rocky shores (Jeunen et al., 2020; West et al., 2020; but see Antich et al., 2021). Currently, eDNA metabarcoding is already an effective environmental monitoring tool used to detect species in give area (Yates et al., 2019), but whether it can reveal fine-scale community structure remains to be investigated (Port et al., 2016), especially in open coastal marine systems subject to strong currents (Monuki et al., 2021).

In this study, we used eDNA metabarcoding to assess the taxonomic, phylogenetic, and functional components of fish biodiversity in an open coastal marine system to the west of Brittany (France; Figure 1). This study area at the crossroad of the Iroise Sea, the English Channel, and the Bay of Biscay offers contrasted environmental and fishing conditions. The northern part represents a biogeographic transition zone between temperate and cold-temperate/boreal marine faunal assemblages (Dinter, 2001). It is one of the richest coastal areas for marine life in the North Atlantic (Benedetti

et al., 2019; Hily & Glémarec, 1999) with a high diversity of marine ecosystems and habitats including rocky bottom, reefs, ridges (Hinschberger & Pauvret, 1968). The Iroise Sea has strong currents caused by important differences in depth and the adjacent English Channel (Figure 1, Dinter, 2001; Muller et al., 2009). The high current speed especially in some areas such as the Raz de Sein, and the presence of rocky shoals and reefs (Hinschberger & Pauvret, 1968) makes it one of the most dangerous seas in Europe that is difficult to access for fishing activities other than with hook and line gears. The Audierne Bay (southern part) has lower habitat diversity than the Iroise Sea and is characterized by a limited sandy stock resting on a very flat bottom (Hénaff et al., 2015). It is a highly productive area, supporting a high level of fishing activity allowing a wide range of gears such as lines, longlines, nets, trawls, pelagic seines, pots and dredges (Boncoeur et al., 2004). For each biodiversity component, we considered the three facets (richness, divergence and regularity) to provide complementary information on biodiversity patterns. Our main objective was to assess how effective eDNA was to document small-scale biodiversity gradients in a coastal marine ecosystem with contrasted environmental conditions. We hypothesized that biodiversity components would be higher in the north of the study area where fishing pressure is reduced and habitat complexity is high. On the contrary, the highly fished Audierne Bay located in the southern part of the study area has less contrasted habitats (Hénaff et al., 2015) and is, therefore, expected to have lower biodiversity, especially for the functional component.

2 | MATERIALS AND METHODS

2.1 | Study area

The study focuses on the southern Brittany coast (Northeast Atlantic), between the Douarnenez and Audierne Bays, in the Iroise Sea and in the Bay of Biscay, respectively. The Iroise Sea (northern part of the study area; Figure 1), extending between the island of Ouessant and the Chaussée de Sein, is a species rich area harboring a wide range of marine ecosystems and habitats (Hinschberger & Pauvret 1968). It became a UNESCO biosphere reserve in 1988 and since October 2007 a total area of 3500 km^2 has been included within the Iroise marine park (PNMI, Parc Naturel Marin d'Iroise). The Iroise Sea has strong north-easterly currents at high tides caused by important differences in depth and the adjacent English Channel (Dinter, 2001). The presence of submerged rocks and reefs (Hinschberger & Pauvret, 1968), makes this a dangerous area restricting fishing activities to hooks and lines. Moreover, the formation of the Ushant tidal front from May to October (Morin et al., 1985)—separating homogeneous coastal waters from the seasonally stratified offshore waters (Schultes et al., 2013)—influences primary productivity and planktonic communities in this area (Brandão et al., 2021). The Audierne Bay (southern part; Figure 1), extends from the Pointe du Raz to the Pointe de Penmarc'h in the Bay of Biscay. In this area, the marine ecosystem is less diverse as
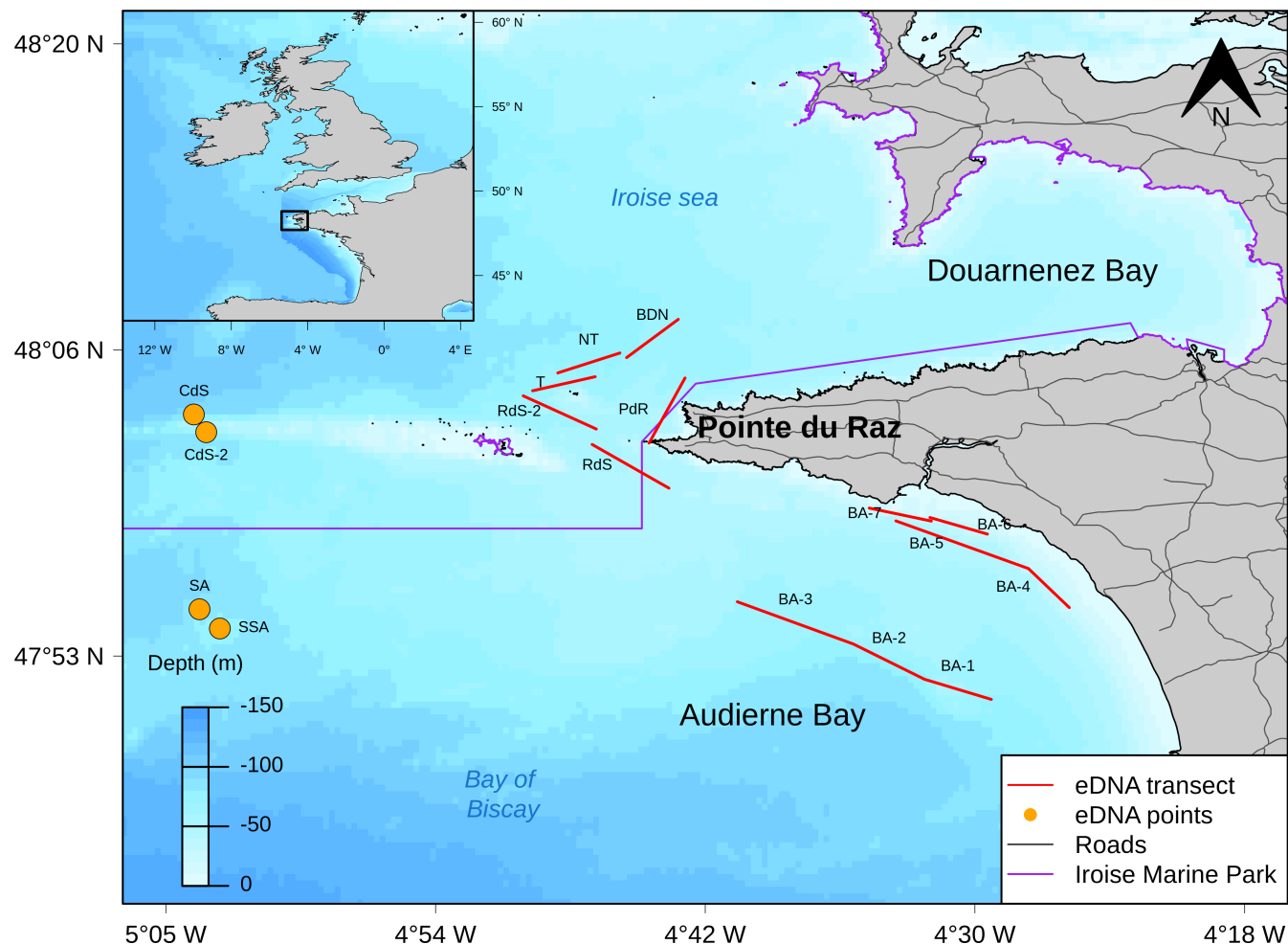
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FIGURE 1 Map of the study area off Brittany with the eDNA sample stations. The abbreviations correspond to station names: BA-1 to 7: Baie Audierne 1 to 7/SA: Sud Armen/SSA: Sud Sud Armen/CdS(−2): Chaussée de sein/RdS(−2): Raz de sein/T: Tévennec/NT: Nord Tévennec/ BDN: Baie Douarnenez Nord/PdR: Pointe du Raz

the habitat is mostly characterized by flat sandy bottoms (Hénaff et al., 2015), while high primary productivity supports a high level of fishing activity. Coastal fishing activities represent a large economic value in this area, which has two main fishing ports (Audierne and Penmarc'h). In 2019 and 2020, the fish auction markets in these harbors sold about 8800 tonnes of fish per year for an average value of 14,000,000 euros per year (FranceAgriMer, 2021).

2.2 | Sampling

During three days in September 2020 (8–10 September) we sampled 17 stations, 13 located near the coast and 4 offshore with greater depths. The coastal stations were sampled along transects, while the strong currents at the offshore stations forced us to sample them at fixed points (Figure 1; Appendix S1). For each station we collected two filter replicates in parallel on either side of the boat, 20–50 cm below the sea surface, corresponding to a total of 34 filters for the whole area. We followed a precise protocol to sample eDNA using a setup composed of an Athena® peristaltic pump

(Proactive Environmental Products LLC; nominal flow of 1.1 L/min), a VigiDNA® 0.2 μm cross-flow filtration capsule (SPYGEN; spygen. com) making it possible to filter 30 L per filter, and separate disposable sterile tubes for each filtration capsule. At the end of filtration, the water inside the capsules was emptied and replaced by 80 ml of CL1 conservation buffer. The capsules were stored at room temperature (Polanco-Fernández, Marques, et al., 2021). To avoid any contamination, we carried out all sampling steps using disposable gloves and single-use filtration equipment.

2.3 | eDNAextraction, amplification, sequencing and data processing

DNA extraction, amplification and high-throughput sequencing were performed in distinct dedicated rooms set up with positive air pressure, UV treatment and frequent air renewal. The eDNA capsules were processed at SPYGEN following the protocol proposed in Polanco-Fernández, Marques, et al. 2021. After DNA extraction, we tested the samples for inhibition following the protocol described

in Biggs et al. (2015). If a sample was considered inhibited, it was diluted 5-fold before amplification. DNA amplifications were performed in a final volume of 25 μl, using 3 μl of DNA extract as the template. The amplification mixture contained 1 U of AmpliTaq Gold DNA Polymerase (Applied Biosystems, Foster City, CA), 10 mM Tris–HCl, 50 mM KCl, 2.5 mM MgCl2, 0.2 mM each dNTP, 0.2 μM of each primer, 4 μM human blocking primer and 0.2 μg/μL bovine serum albumin (BSA; Roche Diagnostic, Basel, Switzerland). To perform the amplification, we used the teleo primers (forward: ACACCGCCCGTCACTCT, reverse: CTTCCGGTACACTTACCATG) that amplify a region of 64 base pairs on average (range 29–96 bp) of the mitochondrial 12S region. This primer pair was designed to capture teleost taxa (Valentini et al., 2016) but also captures Elasmobranchii taxa (Polanco-Fernández, Richards, et al., 2021). The "teleo" primers were 5′-labeled with an eight-nucleotide tag unique to each PCR replicate (with at least three differences between any pair of tags), allowing the assignment of each sequence to the corresponding sample during sequence analysis. The tags for the forward and reverse primers were identical for each PCR replicate. The PCR mixture was denatured at 95°C for 10 min, followed by 50 cycles of 30 s at 95°C, 30 s at 55°C and 1 min at 72°C and a final elongation step at 72°C for 7 min. Twelve replicates of PCRs were run per filtration (i.e., 24 per station) to increase the probability of detecting rare species (Ficetola et al., 2015; Valentini et al., 2016). After amplification, the samples were titrated using capillary electrophoresis (QIAxcel; Qiagen GmbH) and purified using the MinElute PCR purification kit (Qiagen GmbH). Before sequencing, purified DNA was titrated again using capillary electrophoresis. We pooled the purified PCR products in equal volumes to achieve a theoretical sequencing depth of 1,000,000 reads per sample. Library preparation and sequencing were performed at Fasteris (Geneva, Switzerland). Two libraries were prepared using the MetaFast protocol (a ligation-based method) and sequenced separately, the paired-end sequencing was carried out using a MiSeq (2 × 125 bp, Illumina, San Diego, CA, USA) on two MiSeq Flow Cell Kit Version3 (Illumina, San Diego, CA, USA) following the manufacturer's instructions. The samples from the different filters were randomly attributed to the two libraries. Two negative extraction controls and one negative PCR control (ultrapure water) were amplified (12 replicates) and sequenced in parallel to the samples to monitor possible contamination.

We analyzed the sequence reads using programs implemented in the OBITools package (http://metabarcoding.org/obitools; Boyer et al., 2016) following the protocol described in Polanco-Fernández, Martinezguerra, et al. (2021). Forward and reverse reads were assembled using the *illuminapairedend* program with a minimum score of 40 and retrieving only the joined sequences. Then we assigned the reads to each sample using the *ngsfilter* program and created a separate data set for each sample by splitting the original data set into several files using *obisplit*. After this step, we analyzed each replicate sample individually before merging the taxon list for the final ecological analysis. Strictly identical sequences were clustered together using *obiuniq*. We removed sequences shorter than 20 bp or with occurrence lower than 10 or labeled "internal" that correspond

most likely to PCR substitutions and indel errors, by applying the *obiclean* program. Taxonomic assignment of the MOTUs was performed using the program *ecotag* with the sequences extracted from release 142 of the European Nucleotide Archive (ENA) database (standard sequences). We assigned sequences at different taxonomic levels: species (match > 98%), genus (96% < match ≤ 98%), family (90% < match ≤ 96%) (Marques et al., 2020). Considering the incorrect assignment of a few sequences to the sample due to tag jumps (Schnell et al., 2015), we discarded all sequences with a frequency of occurrence <0.001 per sequence and per library. We further corrected for Index-Hopping (MacConaill et al., 2018) with a threshold empirically determined using experimental blanks (i.e., combinations of tags not present in the libraries) between libraries. This index removes all reads present in plates where the combination of tags is not present in the library and is later applied for each plate position.

The 34 eDNA filters yielded a total of 13,671,669 reads with an average of 402,108 reads per filter (*SD* = 207,481). Among the 86 taxa detected, 38 were assigned at the species level, 29 at the genus level, 16 at the family level and 3 at even higher level. Next, we removed taxa that were poorly assigned such as at family level or above (e.g., Eupercaria, Carangidae, Clupeocephala) with no representative species detected in our data set, as well as some genera/families of which some representative species had been detected at the species level. For example, the genus *Leucoraja* was removed but remained represented by *Leucoraja circularis*, *Leucoraja naevus* and *Leucoraja fullonica*. We removed the Scyliorhinidae family but remained represented by *Scyliorhinus canicula*. We also removed fish taxa that do not occur in the study area, such as Lutjanidae, which have only tropical and subtropical species (Froese & Pauly, 2021) and the *Oreochromis* genus with only freshwater and brackish water species (Froese & Pauly, 2021). These false-positive detections correspond to species genetically related to Atlantic ones that were missing from the sequence database. We finally retained 52 taxa, including 41 actinopterygians and 11 chondrichthyans. We assigned 37 of them at the species level, 14 at the genus level and one at the family level.

We tested for sample replicability by analyzing the variation in species composition between the two replicates from each station (Appendix S2). To do so, we calculated the Jaccard's (1912) dissimilarity index based on presence–absence (β_{jac}), which represents the proportion of unique taxa within sampling units (here, filters; Baselga, 2010). This index ranges from 0, when the two sampling units are composed of identical taxa, to 1 when they are composed of distinct taxa. Furthermore, the Jaccard's dissimilarity index can be decomposed into two additive and antithetic components, the taxa turnover and the nestedness-resultant dissimilarity, hereafter referred to as nestedness (Baselga, 2012). The taxa turnover corresponds to the replacement of taxa by others between sampling units, while the nestedness quantifies the dissimilarity in taxa composition driven by the richness difference between sampling units when the poorest sampling unit is a subset of the richest sampling unit (Baselga, 2012). A good replication quality would result in a low overall dissimilarity (β_{jac}) between filters, mostly driven by the nestedness component, indicating that the two filters globally detected

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the same species composition. The good dissimilarity results (see results section 3.1) allowed us to pool the two filters for each station and consider a single taxa composition for each station in subsequent analyses.

2.4 | Diversity indices calculation

2.4.1 | Taxonomic indices

Using the filtered taxa table (containing 52 taxa), we captured the taxonomic richness facet -hereafter referred to as species richness- of each sampling station based on taxa presence. However, as the eDNA method cannot yet reliably quantify taxa abundance (Polanco-Fernández, Marques, et al., 2021; Stoeckle et al., 2020; Thomsen et al., 2016), it precludes the regularity facet assessment. Moreover, we computed taxonomic β-diversity indices between the 17 stations based on presence–absence Jaccard's dissimilarity index and its two additive components: taxa turnover, and taxa nestedness (Baselga, 2012).

2.4.2 | Functional traits collection and functional index calculations

To collate functional traits linked to key ecosystem functions, we extracted information for seven traits from the FishBase database (Froese & Pauly, 2021). These traits were average depth, depth range (m) and the position in the water column divided into four modalities (pelagic, bathypelagic, demersal, bathydemersal), which refer to the ecological habitat. These traits can be used as proxies for vertical mobility, space occupation, biotic interactions and physiological responses (Brown & Thatje, 2014, Villéger et al., 2017). The traits trophic level, body shape (flat, short, fusiform, or elongated) and maximum length (four levels: 6–26 cm, 26–79 cm, 79–100 cm, 100–460 cm) are linked to food acquisition, mobility and predation functions. The reproduction trait was divided in seven categories related to reproduction mode (dioecy/protogyny/protandry), fertilization mode (internal/external) and type of parental care (maternal/paternal/none) (see Appendices S3 and S4).

The taxa table contained presence information at different taxonomic levels. For fish identified at genus (14/52) or family (1/52) level, we listed all species belonging to these genera/families that live in the Northeastern Atlantic, based on the literature and "Fishbase". To get a better appraisal of the variability of the functional diversity within and among communities related to taxonomic identification uncertainty, we randomly selected one representative species from the regional species list for each of the 15 (14 genus + 1 family) taxa. Repeating this 100 times resulted in 100 traits tables. We calculated Gower's distance between pairs of species based on the seven functional traits in the 100 traits tables. This distance metric allows mixing different types of traits while giving them equal weights (Gower, 1971; Villéger et al., 2013). Then, we carried out a

Principal Coordinates Analysis (PCoA) on each Gower matrix. To reduce computation time and convergence problems due to numerical instability, while maintaining quality of representation we decided to keep species coordinates for the first five axes for α-diversity indices according to the framework proposed by Maire et al. (2015) and for the first two axes for β-diversity indices. We then computed 100 multivariate functional spaces based on the 100 PCoA.

We calculated several indices for each of the three facets of functional α-diversity. To document the functional richness facet, we calculated the Fric index corresponding to the volume defined by the convex hull polygon of the species present in the synthetic functional space (Villéger et al., 2008). This metric could be positively correlated with the species richness (SR) in taxonomy. For a given SR, a high Fric value means that species tend to be functionally distinct while a low value indicates that they are more functionally similar (clustered). To measure the divergence and the regularity dimensions we worked directly with the Gower distance matrix to avoid loss of information associated with the dimensionality reduction by the PCoA. For the divergence dimension, we calculated the Mean Pairwise Functional Distance index (MPFD) corresponding to the mean functional distance between all species pairs (Myers et al., 2021). Finally, we measured functional regularity with the Variance in Pairwise Functional Distance (VPFD) index, quantifying the regularity of the functional distances among species (Myers et al., 2021). We then decorrelated the different functional metrics from SR by computing their Standardized Effect Size (SES) values. For this we subtracted the mean metrics value across 1000 random functional associations between species and their traits (null model) and dividing by the standard deviation of these null model metrics values. The SES metrics values helped to identify pairs of sampling stations that were functionally clustered or overdispersed, regardless of their SR. Assuming normality, SES values greater than 1.96 indicate significant overdispersion at a 5% test level, while SES values below −1.96 indicate significant spatial clustering of species with certain traits (Leprieur et al., 2012).

We estimated functional β-diversity indices using the taxonomic equivalent Jaccard dissimilarity index (see part 2.4, Villéger et al., 2013). Functional β-diversity can be decomposed into two additive components: functional turnover, referring to the replacement of functional strategies between communities (stations) within the multidimensional functional space, and functional nestedness defined as one of the communities hosting a subset of the functional strategies presents in the other one (Villéger et al., 2013). Finally, we calculated the mean and the standard deviation of each index for each station across the 100 traits tables (Appendix S5). All diversity indices were computed using the "mFD" package (Magneville et al., 2021) in R software.

2.4.3 | Phylogenetic indices

Phylogenetic diversity estimation is based on phylogenetic trees at the species level. To document the phylogenetic diversity of the 15 taxa identified at the genus or family level in our taxa table, we

chose one representative species belonging to these taxonomic levels. We based our choice on the hypothesis that each genus/family forms a clade (a monophyletic group) whose species have diverged the same amount of time from their common ancestor in the phylogenetic tree. Therefore, the choice of one species over another does not modify the results. We used the recently updated molecular phylogeny for Actinopterygii published by Rabosky et al. (2018) as a backbone tree including 37 species out of the 41 taxa present in our data set. We re-grafted the remaining 4 species on the backbone tree based on their taxonomic affinities and a list of taxonomic constraints by using the recent phylogenetic classification of bony fishes (Betancur et al., 2017). We randomly sampled the waiting time (i.e., branch length) for the four species from an exponential distribution based on the birth-death model parameters estimated by maximum likelihood from a larger tree (Nee et al., 1994). This tree was extracted from the molecular phylogeny of Rabosky et al. (2018) and includes 176 species found in the Bay of Biscay and Celtic Sea. We repeated this procedure 100 times to generate a distribution of fully sampled phylogenetic trees including 41 species to account for the phylogenetic uncertainty related to the re-grafting procedure. This procedure avoided spurious branching of several re-grafted species found in the collection of mega-phylogenies published by Rabosky et al. (2018). For the 11 chondrichthyans, we used a subset of 100 trees of the recent mega-phylogeny published by Stein et al. (2018). Finally, we built a single set of 100 phylogenetic trees including both clades (i.e., Actinopterygii and Chondrichthyes) and 52 species using a conservative and young divergence estimate between the clades of 420.7 Ma (Benton et al., 2015, Stein et al., 2018).

We calculated three indices to assess the three facets of phylogenetic diversity (Appendix S6). To document the richness facet, we used Faith's phylogenetic diversity (PD, Faith, 1992), which represents the sum of branch lengths linking all observed species in the phylogenetic tree. As this metric is positively correlated with species richness (SR; Tucker & Cadotte, 2013), a community with many species could lead to a high PD value, even if the species were phylogenetically clustered. Thus, for a given SR, higher PD indicates that the species are more phylogenetically dispersed, while a lower PD indicates that they are phylogenetically more clustered (Davies et al., 2007). We computed divergence using the phylogenetic Mean Pairwise Distance (MPD) metric corresponding to the average phylogenetic distance among species (Tucker et al., 2017). MPD is influenced by ancient diversification events meaning if some processes have produced a basal clustering/overdispersion in the phylogenetic tree, the MPD would reveal it (Mazel et al., 2016). We assessed the regularity dimension by applying the Variance in Pairwise Distance (VPD) measuring the variance in phylogenetic distances among species (Clarke & Warwick, 2001; Eme et al., 2020), an index capturing more complex phylogenetic structure such as the presence of distinct old lineages with recent clusters of closely related species (Zintzen et al., 2011; Eme et al., 2020).

We decorrelated the phylogenetic indices from SR by the computation of SES values based on a null distribution of 1000 trees, shuffling the species names at the tips of the phylogenetic trees. We used the 95% percentile interval of a normalized Gaussian distribution to detect significant phylogenetic clustering or overdispersion (see part 2.5.2). We then carried out a normalized PCA on all seven taxonomic, functional and phylogenetic alpha indices and computed the pairwise non-parametric Spearman's correlation coefficients to determine their dependence (Appendix S7).

At the regional scale (β-diversity), we computed the UniFrac dissimilarity index, which is equivalent to the taxonomic Jaccard index (Leprieur et al., 2012; see part 2.4). As such, it also varies between 0 (all species of the two communities share the same phylogenetic history) and 1 (the species of the two communities do not share any phylogenetic history). The UniFrac index can be decomposed into two additive components. The UniFrac Turnover (UniFracTurn) quantifies the relative proportion of unique phylogenetic lineages between communities that is not attributable to their difference in Phylogenetic Diversity (PD, Leprieur et al., 2012). The UniFrac Phylogenetic Diversity (UniFracPD) component measures the amount of phylogenetic differences between phylogenetically nested communities (i.e., communities sharing at least one branch within a rooted phylogeny; Leprieur et al., 2012). We computed all β-diversity indices using the *"Betapart"* package in R (Baselga et al. 2021). Finally, we calculated the mean and the standard deviation of each index across the 100 phylogenetic trees (Appendix S6).

2.4.4 | Hill numbers

We used the unifying concept of Hill numbers (Hill, 1973; Jost, 2006) to document the richness facet of the three biodiversity components. Hill numbers measure the effective number of units in a sample, either species number in taxonomy, or branch-length segments in phylogeny, or functional distances in functional diversity, and account for species occurrence and/or abundance within a single framework (Chao et al. 2014). Hill numbers are based on the parameter q that determines the sensitivity of the measure to the relative abundance of the diversity unit used, as follows: $^qD = \left(\sum_{i=1}^{s} p_i^q\right)^{\frac{1}{1-q}}$

where S is the number of diversity units in the assemblage and p_i the relative abundance of this unit. If q equals 0, abundances are not accounted for. If q equals 1 or 2, abundances are accounted for but with different weights for common vs. rare units (Chao et al., 2014). Our study was only based on taxa occurrences, as such, we only used Hill numbers with $q = 0$ to capture functional and phylogenetic diversity. Note that for $q = 0$, the taxonomic Hill number corresponds to species richness (Chao et al., 2014). We calculated the functional Hill number that measured the effective number of paired species distance units (Chao et al., 2014) from the Gower distance matrix, which offers the advantage to consider the whole functional space and not only a synthetic functional space as for the Fric index. Moreover, we calculated the phylogenetic Hill number that represents the effective number of unit-branch length segments of a phylogenetic tree (Chao et al., 2014). As for traditional phylogenetic and functional indicators, we decorrelated the phylogenetic indices from SR by the computation of SES values.

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2.5 | Regional β-diversity comparison

To identify the degree of uniqueness of each station in terms of taxonomic, phylogenetic or functional diversity, we used a β-diversity approach. We considered the average values of taxonomic, phylogenetic, and functional β-diversity (and its two components) for each sampling station by computing the mean of the pairwise comparison between each station and the 16 others weighted by the inverse of the geographic distance between stations. This weighting gave more importance to changes occurring between the focal station and the nearest neighbors compared to more distant ones (Leprieur et al., 2011; Villéger et al., 2013). We performed a sequential K-means approach for identifying the number of station groups (2–16 groups tested). We computed several indices to choose the most probable number of groups by using the "NbClust" R package (Charrad et al., 2014) and retained as optimal four groups. We then performed a non-normalized Principal Component Analysis (PCA) using the six turnover and nestedness-resultant components linked to taxonomy, phylogeny and functional diversity. The four groups were highlighted on the first two axes of the PCA.

3 | RESULTS

3.1 | Variation in species composition between replicates

When analyzing the variation in species composition between the replicate filters collected at each station, we noticed that the overall dissimilarity β_{jac} rarely exceeded 0.2, meaning filters from the same station were on average more than 80% similar (Appendix S8). However, some stations showed higher values such as Baie Audierne 3 (BA-3) and Nord Tévennec (NT), respectively, reaching 0.37 and 0.42, indicating approximately 40% difference in species composition between the replicates. Nevertheless, these differences were mainly driven by nestedness (β_{jne}) accounting for 66% for BA-3 and 100% for NT, meaning that the poorer filter mostly contained a subset of species present in the richer filter, which is in agreement with a good replication level. For several other stations, the low dissimilarities observed between replicate filters were mainly explained by the species turnover component β_{jtu} (e.g., BA-1, BA-2, CdS, CdS-2) indicating a replacement of species. However, all replacement rates were low, with a maximum value of 20% reached at the Chaussée de Sein (CdS). Due to the good replication level, we pooled the results of both filters for each station into a single species list.

3.2 | α-Diversity indices

The map of the three facets of the biodiversity components and richness revealed a clear spatial pattern (Figure 2). Stations in the Iroise Sea had higher species richness, divergence and regularity indices for each component compared to stations in the southern part (Figure 2a,b).

Considering the richness facet, the stations with the highest number of species were Tévennec (T) and Raz de Sein 2 (Rds-2; SR = 25 for both), followed by Raz de Sein (RdS; SR = 24) and both station on the Chaussée de Sein (CdS; SR = 22 for both; Figure 2a,c). The same stations displayed the largest evolutionary history with SES values of phylogenetic diversity (SES.PD) highest in these communities regardless of their high SR. Although none of the diversity values supported a significant phylogenetic overdispersion (Figure 3), we still noticed a contrast between northern and southern stations. The highest values of SES.PD were found in the Iroise Sea at the Raz de Sein (SES.PD = 1.11) followed by CdS (SES.PD = 0.99) and Tévennec (SES.PD = 0.80; Figure 2c, Figure 3). In contrast, the stations containing the lowest number of species were Baie Audierne 2 (BA-2, SR = 7) and 3 (BA-3, SR = 9) and Sud Sud Armen (SSA, SR = 13; Figure 2; Appendix S9), all located in the southern part of the study area. These stations also had a low SES.PD (SES.PD$_{BA-2}$ = −0.47, SES.PD$_{BA-3}$ = −0.47, SES.PD$_{SSA}$ = −1.03; Figure 3), reflecting the lower amount of evolutionary history represented by the species present, but any such phylogenetic clustering remained non-significant (Figure 3). The alternative measure of richness based on the SES phylogenetic Hill number (SES.HillP_q0) showed the same spatial trend as SES.PD (Figure 3).

Considering functional richness, in the Iroise Sea, Tévennec (T) had the highest SES.Fric (Figure 2a,c) with the highest functional volume and richness, significantly higher than under the null model thus indicating functional overdispersion, compared to all other stations (SES.Fric = 7.82; Figure 3). Conversely, the stations in the Audierne Bay, BA-4 and BA-6, had the lowest functional richness measured with SES.Fric (Figure 2a,c; Appendix S9) which indicated significant clustering (SES.Fric$_{BA-4}$ = −3.51 and SES.Fric$_{BA-6}$ = −6.71; Figure 3). Even if the SES.Fric was slightly higher in the Iroise Sea (mean SES.Fric = −0.75) than in the southern area (mean SES.Fric = −1.54), functional richness revealed clustering for most of the station throughout the study area (Figure 3); such clustering was even stronger for the SES of the functional Hill number (SES.Hillf_q0).

We assessed the divergence and regularity facets using two couples of SES metrics that are strongly correlated (SES.MPD and SES.VPD for the phylogeny component: $\rho = 0.99$, $p = 8.68 \times 10^{-6}$, S = 10, df = 15; SES.MPFD and SES.VPFD for the functional component: $\rho = 0.88$, $p = 2.2 \times 10^{-16}$, S = 102, df = 15; Appendix S7). The functional divergence (based on Mean Pairwise Functional Distances: SES.MPFD) and regularity (based on the Variance of Pairwise Functional distance: SES.VPFD) showed clustering values (Figure 3). These stations contained species that were closely related and regularly spaced (i.e., low SES.VPFD) in the functional space. The stations Tévennec and Raz de Sein 1 and 2, in the Iroise Sea and the site Sud Armen (SA) all presented slight overdispersion for SES.MPFD with values reaching 0.50, 0.09, 0.16 and 0.51, respectively, but none of them was significant (Figure 3). In terms of regularity, the same stations exhibited some overdispersion: the three in the Iroise Sea were also non-significant (SES.VPFD
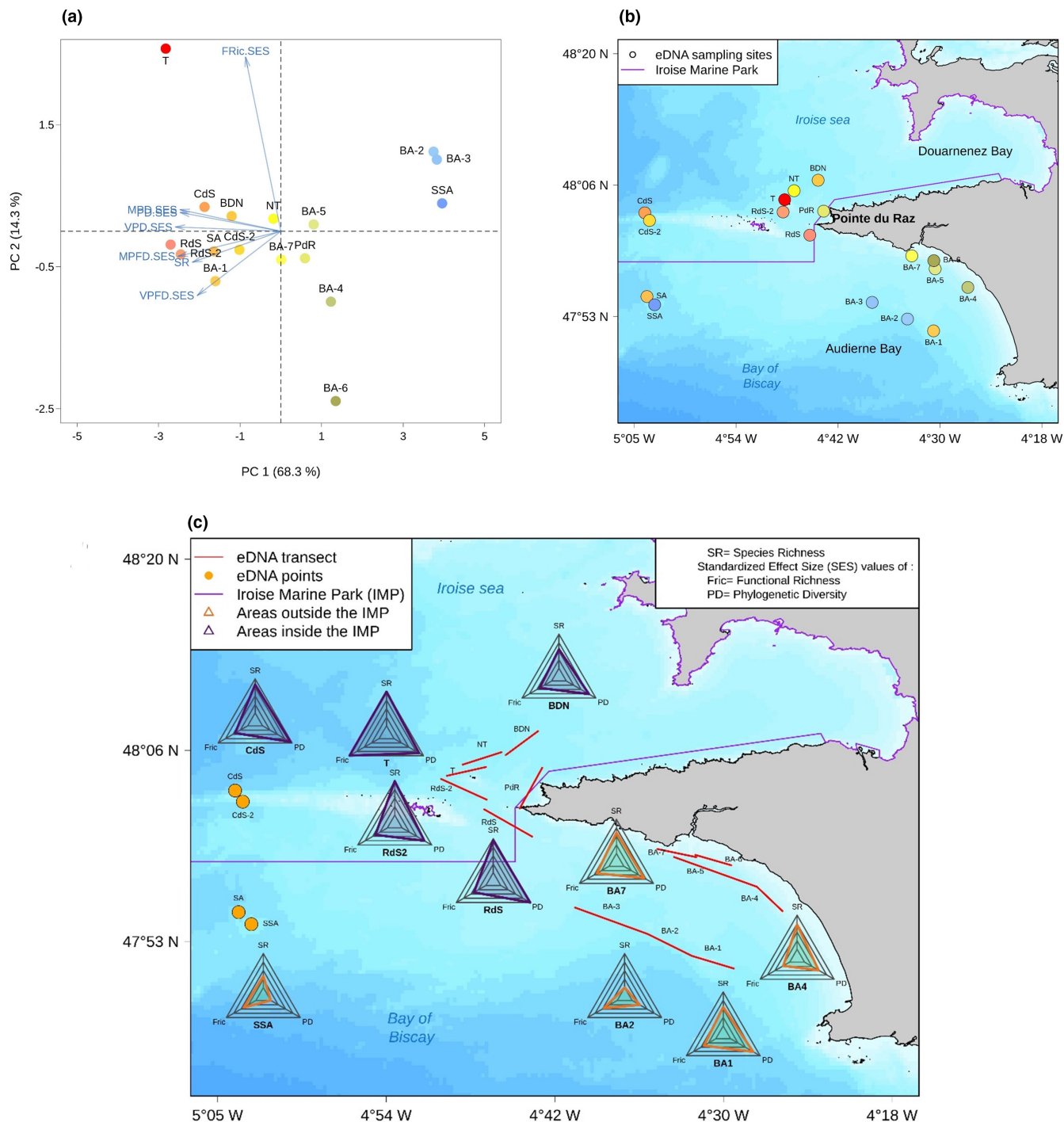
FIGURE 2 Overview of the spatial distribution of standard effect size (SES) values of richness, divergence and regularity indices for each biodiversity component in the study area. The abbreviations correspond to station names: BA-1 to 7: Baie Audierne 1 to 7/BDN: Baie Douarnenez Nord/CdS(−2): Chaussée de sein/NT: Nord Tévennec/PdR: Pointe du Raz/RdS(−2): Raz de sein/SA: Sud Armen/SSA: Sud Sud Armen/T: Tévennec. (a)—PCA of SES values of α-diversity indices. The color gradient represents the α-diversity indices range, from blue (minimum) to red (maximum). Arrows represent SES values of functional richness (FRic), phylogenetic diversity (PD), species richness (SR), mean pairwise phylogenetic distance (MPD), mean pairwise functional distance (MPFD), variance in pairwise phylogenetic distance (VPD) and variance in pairwise functional distances (VPFD). (b)—spatial distribution of the α-diversity gradient in the study area based on PCA colors. (c)—spatial distribution of richness facets for each component (we displayed a subset of the most representative stations, radar charts of all stations are availables in Appendix S9). The radarcharts range from 0 (center) to 1 (vertices)

between 0.49 and 0.56) while SA and BA-1 in the south were significantly overdispersed, with SES.VPFD, respectively, reaching 2.13 and 3.30 (Figure 3). In the south, 88.9% of the station, mostly

located in the Audierne Bay, were clustered in terms of SES.MPFD, among those 71% significantly: BA-2 to BA-6 (SES.MPFD between −4.98 and −1.30) and SSA (SES.MPFD = −5.17). Furthermore, all

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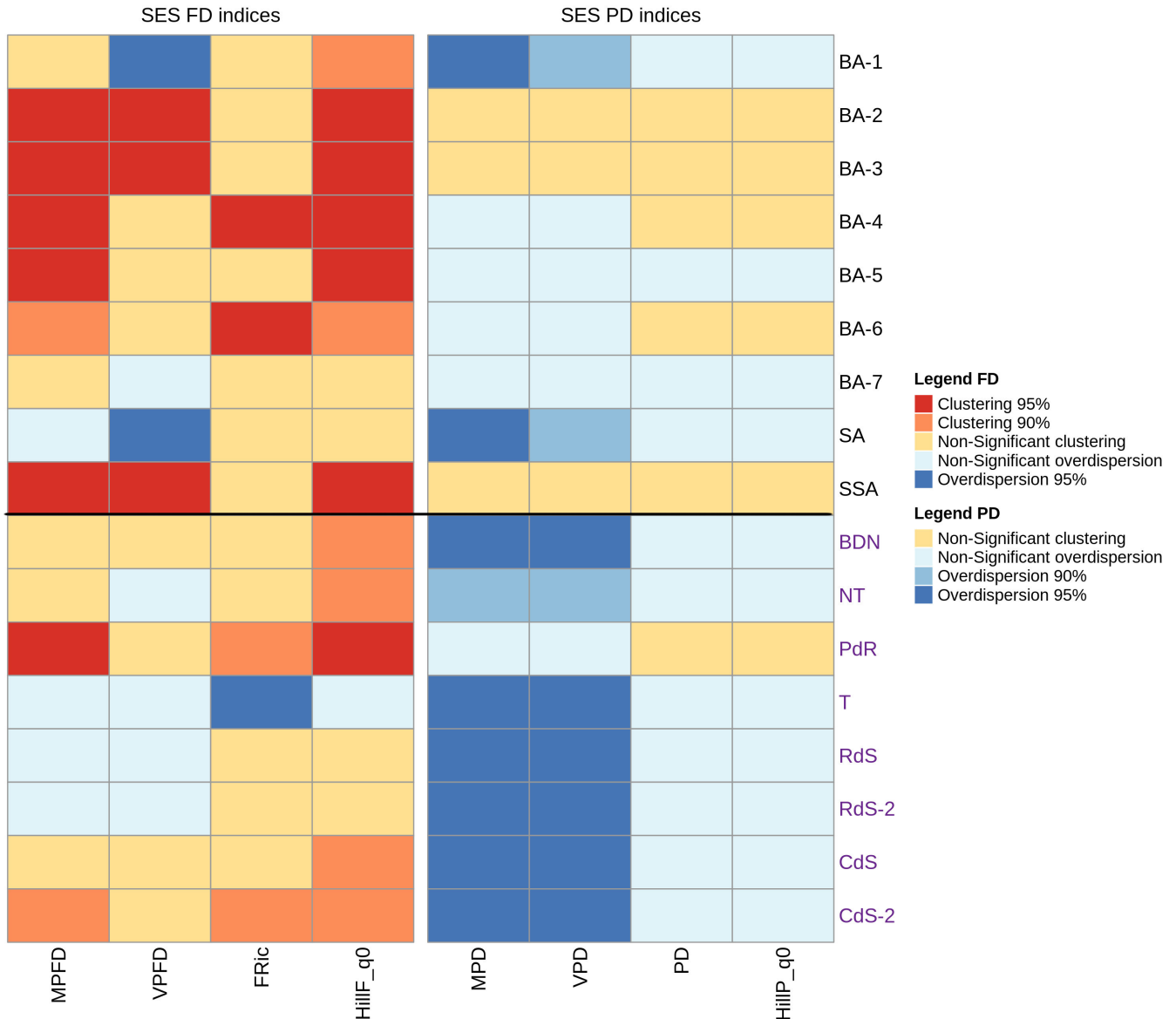Open Access

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FIGURE 3 Comparative heatmaps of functional and phylogenetic standard effect size (SES) values of α-diversity indices. The bold line separates the two groups of stations: the names in black correspond to southern stations while the purple ones correspond to northern stations (inside the Iroise Marine Park). The levels of clustering and overdispersion were displayed using thresholds of 95% and 90% for SES values. Significant clustering (or overdispersion) means that the observed values are significantly lower (higher) than under the null distribution. The metric names correspond to: MPFD = mean pairwise functional distance; VPFD = variance in pairwise functional distance; FRic = functional richness; HillF_q0 = Functional Hill numbers of order 0 (number of species-pair distance unit); MPD = mean pairwise (phylogenetic) distance; VPD = variance in pairwise (phylogenetic) distance; PD = phylogenetic diversity; HillP_q0 = Phylogenetic Hill numbers of order 0 (number of unit-branch-length segments)

these stations showed significant clustering for SES.VPFD, notably BA-2, BA-3 and SSA (SES.VPFD, respectively, reaching −3.53, −3.19 and −2.24, Figure 3).

Considering the phylogenetic diversity components, the SES. MPD and SES.VPD metrics presented similar results for all stations with 82.5% of stations showing overdispersion for both indices, among which 60% were significant (Figure 3). The pairwise distances between species in the phylogenetic tree were high on average and variable, implying the presence of species belonging to very distinct phylogenetic lineages as well as of several species phylogenetically

closely related (belonging to the same lineage). The stations maximizing SES.MPD and SES.VPD were significantly overdispersed and mostly located in the Iroise Sea, such as CdS (SES.MPD = 3.65, SES. VPD = 2.51), RdS (SES.MPD = 3.69, SES.VPD = 2.62), RdS-2 (SES. MPD = 3.75, SES.VPD = 2.65). The lowest values of SES.MPD and SES.VPD were found in the south, in SSA (SES.MPD = −0.73, SES. VPD = −0.72), BA-3 (SES.MPD = −0.22, SES.VPD = −0.71) and BA-2 (SES.MPD = −0.21, SES.VPD = −0.57), with none being significantly clustered (Figure 3). Maps of observed indices are available in Appendix S10.

3.3 | β-Diversity indices

Comparisons between the taxonomic, functional and phylogenetic β-diversity indices highlighted four groups of stations (Figure 4). In group 1, four stations showed strong overall dissimilarities and had maximized turnover components (group 1; Figure 4, Appendix S11). Most stations in this group (75%) were in deeper waters near the Chaussée de Sein (CdS, CdS-2 and SA). These stations contained the most unique species, functional strategies and phylogenetic lineages compared to the other groups. Group 2 and 3 minimized dissimilarities compared to group 1, but they did so differently for the two dissimilarity components. Group 2, composed of four neighboring stations (T, RdS-1, RdS-2, PdR) in the Iroise Sea, had species and functional turnover minimized, reflecting that species and functions from this area were also found in most other stations (yellow; Figure 4). Group 3 showing intermediate values

of turnover and minimum nestedness was composed primarily of Audierne stations (BA-1, BA-5, BA-6, BA-7, NT, BDN), indicating that these stations had few different species, lineages and functions (red; Figure 4). Lastly, the three stations making up group 4, all located in the southern part of the study area, had the highest nestedness component especially for the functional index (SSA, BA-2, BA-3), thus containing subsets of species, phylogenetic lineages and mostly functional strategies that were also found in other stations (purple; Figure 4).

4 | DISCUSSION

In this study, we showed that environmental DNA (eDNA) is an efficient alternative method for detecting fine-scale multicomponent diversity patterns for fish in an environmentally contrasted coastal
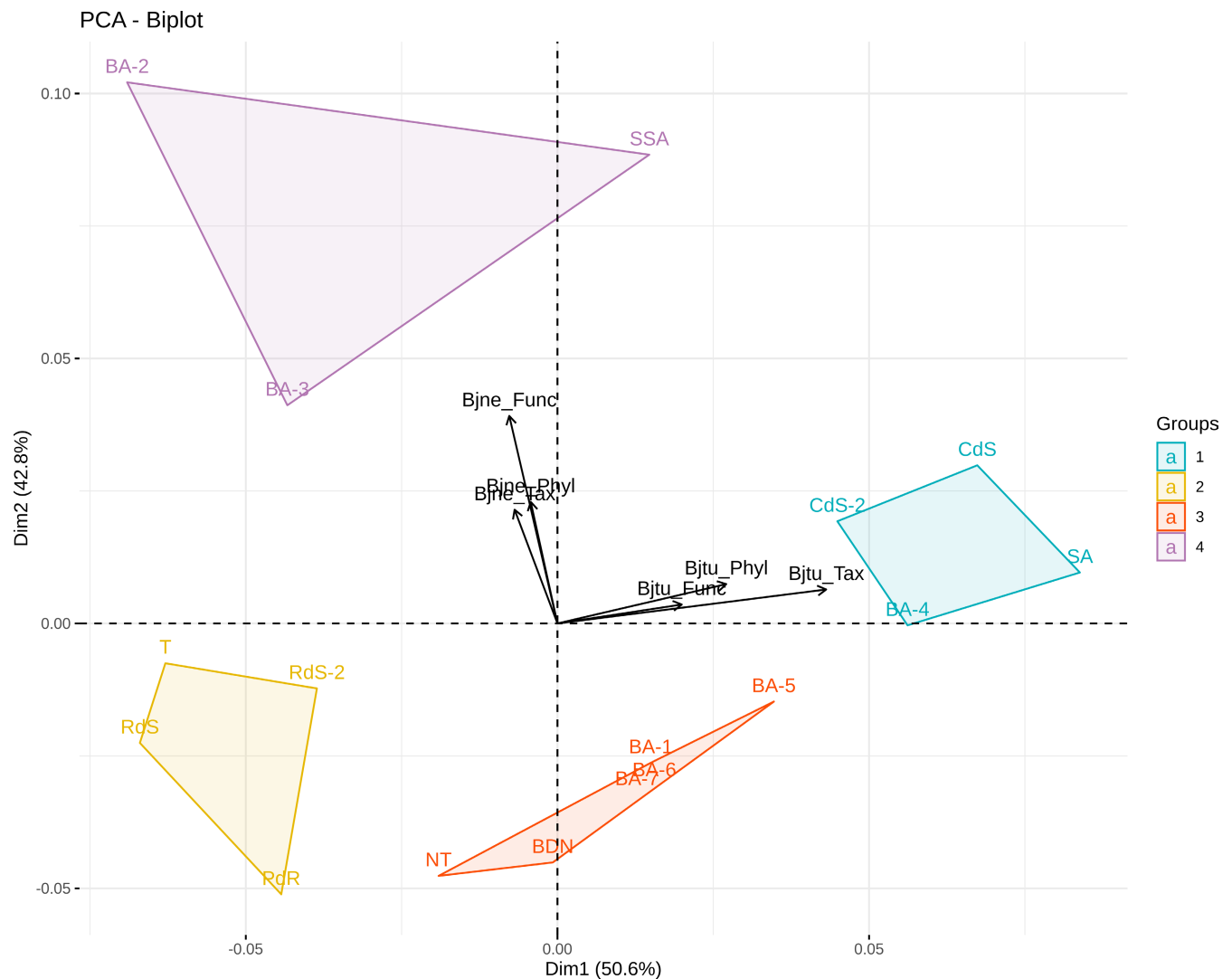

FIGURE 4 Principal component analysis (PCA) of taxonomic, functional and phylogenetic β-diversity respective turnover and nestedness-resultant components ($\beta_{jac} = \beta_{jtu} + \beta_{jne}$) for the 17 stations. The first two axes are accounting for 93.4% of total inertia. The abbreviations correspond to station names: BA-1 to 7: Baie Audierne 1 to 7/BDN: Baie Douarnenez Nord/CdS(–2): Chaussée de sein/NT: Nord Tévennec/ PdR: Pointe du Raz/RdS(–2): Raz de sein/SA: Sud Armen/SSA: Sud Sud Armen/T: Tévennec

marine area off Brittany. The use of water eDNA metabarcoding combined with functional and phylogenetic information enabled detecting sharp biodiversity variations over small spatial distances and discriminating between two distinct areas, the Iroise Sea and the Audierne Bay. In the Iroise Sea, taxonomic, phylogenetic, and functional biodiversity components were generally larger compared to southern stations. The use of three complementary biodiversity facets—richness, divergence and regularity—revealed contrasted patterns for phylogenetic and functional biodiversity components. Fish communities in the Iroise Sea had higher species richness, showed stronger phylogenetic overdispersion and lower functional clustering for the three facets than communities in the Audierne Bay. Therefore, the eDNA approach enables detection of multicomponent diversity gradients based on species occurrences in coastal marine ecosystems.

4.1 | Fine-scale diversity patterns

Our results showed that the eDNA metabarcoding method can reveal fine-scale (i.e., 5–30 km) diversity contrasts in an open coastal marine ecosystem. We detected higher α-diversity for the three biodiversity components for the sampling stations located in the Iroise Sea compared to the stations located a few kilometers further south in the Audierne Bay. The sensitivity analyses for α-diversity estimates showed that the observed patterns were robust to the removal of elasmobranchs (for actinopterygian patterns see Appendix S12) and the variability in species detection rates between replicates within stations (Appendix S13). Our results agree with previous studies showing the efficiency of the eDNA method to detect fine-scale variations in species richness and taxonomic composition of marine vertebrates along a 2.5 km transect in a kelp forest ecosystem (Port et al., 2016), and within a 11 km^2 coastal area in Maizuru Bay (Yamamoto et al., 2017). The ability to detect such fine-scale diversity patterns, at least in temperate regions, indicates that organismal DNA excretion for macro-organisms such as fish overcomes degradation and transport forces (Port et al., 2016), which could open the way to routine use of eDNA to monitor marine ecosystems (Polanco-Fernández, Martinezguerra, et al., 2021; Stat et al., 2017). Contrary to previous studies focusing on taxonomic diversity alone, we used the eDNA approach to develop a more holistic perspective on biodiversity by documenting the three facets of functional and phylogenetic diversity components.

The higher levels of taxonomic, functional and phylogenetic α-diversity observed in the Iroise Sea can be explained by the presence of several chondrichthyan species (e.g., the Blonde ray, *Raja brachyura*, the Shagreen ray, *Leucoraja fullonica*), the widespread diversity of actinopterygian lineages (e.g., Clupeiformes, Labriformes, Perciformes), and the significant phylogenetic signal of functional traits associated with reproduction, body shape and habitat (i.e., depth; Appendix S14). For example, the high level of phylogenetic

divergence and irregularity in phylogenetic distances among species within the Iroise fish communities were influenced by the divergence between actinopterygians and chondrichthyans dating back from, at least, 421 Myr (Benton et al., 2015; Stein et al., 2018), and the presence of several species phylogenetically closely related belonging to the same families (e.g., the sandy ray—*Leucoraja circularis*, the shagreen ray—*Leucoraja fullonica* and the blonde ray—*Raja brachyura* from the Rajidae). Most of the chondrichthyans were detected near the Sein Island at both stations of the Raz de Sein (RdS, RdS-2) and Tévennec (T). These stations also contained communities with the highest level of functional richness, divergence and irregularity, especially Tévennec (Figure 3) compared to the rest of the area. Although elasmobranchs seemed to drive the diversity patterns for the three biodiversity components, these patterns were also observed, to a lesser degree, with actinopterygian taxa only (Appendix S12).

The lower α-diversity detected in the southern part of the study area (including Audierne Bay and both Armen stations; Figure 1), is mainly due to the presence of many small and medium-sized pelagic species (e.g., *Sardinus pilchardus*, *Engraulis encrasicolus*, *Sprattus sprattus*, *Alosa fallax*, *Scomber scombrus)* and a low proportion of chondrichthyans (22.2% vs. 77.8% in the Iroise Sea). These species belong to two main lineages (Clupeiformes, Scombriformes), which explains the lower level of phylogenetic divergence and irregularity in phylogenetic distances compared to the Iroise Sea. Moreover, the functional clustering is stronger in the southern stations, indicating that more species perform similar functions, which increases functional redundancy. For example, 66% of the species in the southern area share the same reproduction mode with dioecy, external fertilization and no parental care, compared to only 36% in the Iroise Sea. The south also included 57% of fusiform species (e.g., *Alosa fallax*, *Sprattus sprattus)* against 45% in the north. Identified biodiversity gradients were robust to sampling and sample treatment uncertainty, since station replicates (use of 2 filters of 30 L) showed good level of agreement (dissimilarity β_{jac} mean = 0.183±0.092) with detection of similar species among paired filters. Moreover, the analysis performed using a randomly selected filter for each station instead of pooling the two filters also showed strong North/South differences supporting the robustness of our results (Appendix S13). However, replication quality and sampling effort may vary according to the studied environment because biotic and abiotic conditions can influence degradation, deposition and detection of eDNA (Stewart, 2019). For example in highly diverse tropical marine ecosystems where eDNA shedding and decay rates tend to be higher, partially due to higher water temperature (Jo et al., 2019), a study by Stauffer et al. (2021) highlighted strong dissimilarity in species composition between filtration replicates (e.g., dissimilarity β_{jac} mean = 0.729±0.102 in the West Indian Ocean; β_{jac} mean = 0.528±0.146 in the Caribbean Sea, with a major contribution of the turnover component for both sampling areas) and required additional sampling efforts to ensure robust biodiversity estimates.

4.2 | Influence of habitat and fishing

The higher α-diversity observed in the Iroise Sea may be related to its habitat complexity and diversity with the presence of rocks and reefs (Hinschberger & Pauvret, 1968) as well as strong currents (Dinter, 2001; Muller et al., 2009), which constrains fishing activities. These factors can explain the presence of chondrichthyans in the Iroise Sea by potentially providing refuges and increasing the abundance of their prey (Bornatowski et al., 2014). As chondrichthyans have a distinct evolutive history separate from actinopterygians, they inherited some specific functional traits (e.g., reproduction with internal fertilization) through their lineage, which could partially explain the slightly higher functional diversity detected in the Iroise Sea. A high diversity of habitats may increase functional diversity within communities by increasing the possibility for resource partitioning and specialization (Evans et al. 2005). Habitat heterogeneity provides more diversified resources (Evans et al., 2005; La Mesa et al., 2011) that can be used by a wider range of functionally distinct species performing specific key functions in the ecosystem (Mouillot et al., 2013). Moreover, the proximity of the Ushant tidal front offshore the Chaussée de Sein, occurring in summer in the Iroise Sea (Schultes et al., 2013), leads to phytoplankton and mesozooplankton diversity hotspots (Brandão et al., 2021; Ramond et al., 2021), which may, therefore, represent abundant trophic resources for planktivorous fish species (e.g., anchovies, pilchards; Brandão et al., 2021).

Although functional diversity is slightly higher in the Iroise Sea, communities across the whole study area tended to be functionally clustered indicating that despite species belong to very distinct phylogenetic lineages in the Iroise Sea (i.e., phylogenetic overdispersion; Figure 3) they shared common functional traits and performed similar key functions than those present in the southern part. The number and the choice of traits to document the different functions (e.g., mobility, food acquisition, reproduction, predation, habitat use) are known to influence functional space and functional diversity patterns (Zhu et al., 2017), especially functional richness, while divergence and regularity estimates are more robust (Legras et al., 2020). In addition, only few modalities characterized some functional traits (e.g., the reproduction mode) despite a long evolution among distinct clades, which can quickly create a "trait saturation" effect due to oversimplification that does not reflect real evolutionary convergences (Kohli & Jarzyna, 2021). However, we do not believe that the detected patterns were caused by a loss of information in the five dimensional functional space, as most studies agree that three to six dimensions are sufficient to provide an operational trait-space capturing most of the variability (Maire et al., 2015; Mouillot et al., 2021). Furthermore, the functional clustering detected by the Fric index based on this reduced functional space was confirmed by the functional Hill number (Figure 3), an alternative measure of functional richness based on the whole functional space.

The lower α-diversity for the three biodiversity components in the southern part of the study area is probably due to lower habitat complexity (flat bedrock) and higher fishing pressure in the exploited Audierne Bay (Hénaff et al., 2015). At almost all southern stations, we noticed the presence of small pelagic species such as European anchovy (*Engraulis encrasicolus*), European pilchard (*Sardina pilchardus*), or sprat (*Sprattus sprattus*) that share a common evolutive history (Clupeiforme order) and functional trait modalities specific to an r-selected reproductive strategy (e.g., small size, external fertilization, no parental care) favoring offspring quantity (Stearns, 1977) and dispersal. The size-selective pressure of fishing may have favored species with such traits enabling quick recolonization for areas constantly under pressure from which larger and rarer fishes have been removed (Farriols et al., 2017; Pauly et al., 1998). Moreover, lower habitat complexity might prevent high resource partitioning and specialization and may require a smaller range of ecological functions.

4.3 | Functional and phylogenetic uniqueness patterns

Our multicomponent β-diversity approach revealed the uniqueness of several offshore stations and the strong nestedness of some stations in the Audierne Bay. Higher levels of taxonomic, phylogenetic, and functional turnover have been detected on the Chaussée de Sein (CdS, CdS-2) and at Armen stations (SA; Figure 4). Such singularities were mostly due to the presence of DNA from John Dory (*Zeus faber*, Zeiforme), boarfish (*Capros aper*, Acanthuriforme) and blackbelly rosefish (*Helicolenus dactylopterus*, Perciforme), that were only detected at these stations. These species belong to distinct phylogenetic lineages and exhibit different functional trait modalities (e.g., maximum length possibly reaching 30 cm for boarfish, 50 cm for blackbelly rosefish and 90 cm for John Dory; Froese & Pauly, 2021) providing them both unique phylogenetic histories and functional strategies. However, the presence of DNA from some of these species supposed to live primarily at deeper depths such as the blackbelly rosefish (average depth: 575 m, usual range: 150–600 m, Froese & Pauly 2021; Mendonça et al., 2006) at the offshore stations (60–75 m) could be due to eDNA persistence and transport in the marine environment (Andruszkiewicz et al., 2019; Barnes & Turner, 2016). Indeed, the strong tidal currents in this area probably increased vertical mixing caused by bottom friction (Dinter, 2001; Muller et al., 2009; Ramond et al., 2021), which could have generated physical dispersion of eDNA fragments from deeper areas located around these sampling stations, possibly questioning the actual presence of these species and the uniqueness of these stations. Interestingly, despite the strong tidal currents, we could not detect these species in the coastal stations, which suggests that eDNA molecules could be too diluted and degraded to be detected if sampled far from their source. Additional studies will be needed to refine our understanding of the spatial scale of eDNA transport and the spatial accuracy of species detection. The strong nestedness recovered for the three diversity components for the stations mostly located in the Audierne Bay (SSA, BA-2, BA-3) was caused by the presence of a subset of small pelagic species belonging to Clupeiformes that are widespread in the area and which share similar functional traits.

4.4 | Limitations and perspectives

Although the water eDNA metabarcoding method is promising and already showing results at a regional scale, it is necessary to reduce several sources of uncertainty before using it routinely as a new biomonitoring approach (Polanco-Fernández et al., 2021). First, it remains unclear how long and how far eDNA molecules can travel before they become too degraded to be detected (Andruszkiewicz et al., 2019; Andruszkiewicz Allan et al., 2021; Fukaya et al., 2021; Thomsen et al., 2012). Fine-scale hydrodynamic structures (local currents, eddies) might blur the signal between the observed spatial pattern of DNA distributions and the location of the excreting individuals if the transport forces overtake DNA excretion and degradation (Thomsen et al., 2012, but see Port et al., 2016). However, in our study the spatial distribution of species' eDNA is consistent with the spatial distribution of species based on local knowledge from fishermen, (Laurent Maréchal, personal communication), differences in habitat complexity and fishing pressure, and species ecological traits. For example, we preferentially detected *Chelon* sp., an estuarine taxon (Froese & Pauly, 2021), at the coastal stations in the Audierne Bay close to the Goyen estuary (Appendix S2). Second, we may not have detected all species potentially present in the study area because we carried out sampling at the water surface and thus may have missed some benthic species. The use of a single marker could have also reduced the range of species detected (Cilleros et al., 2019). A multimarker metabarcoding approach could widen the species detection range and help discriminate between closely related taxa by combining the qualities and specificities of each marker for more complete biodiversity surveys (Polanco-Fernández, Richards, et al., 2021; Stefanni et al., 2018). Another source of uncertainty in species detection comes from the lack of species sequences available in genetic databases that also may considerably reduce the breadth of detected biodiversity (Marques et al., 2021). In addition, the presence of DNA sequences belonging to distant relative species in genetic databases and the remaining sequence annotation problems may lead to false-positive detections, which require careful curation (Cilleros et al., 2019; Yamamoto et al., 2017). To address these issues, sustainable data quality management requires implementing quality assurance measures when developing the reference library, based on valid taxonomy and formally correct barcode sequences, as well as quality control to detect contamination or recent taxonomic changes (Weigand et al., 2019). In addition, alternative approaches by-passing the use of universal primers and the error prone PCR step, such as capture enrichment, are being developed to improve the taxonomic accuracy of species identification (Gauthier et al., 2020).

Reliably quantifying the relative species abundance through eDNA concentration will be a milestone that will greatly improve biodiversity assessment (Spear et al., 2021). The correlation between species abundance and DNA concentration remains inconsistent in situ (Fraija-Fernández et al., 2020). Positive correlation have been mostly demonstrated in laboratory controlled conditions (e.g., Doi et al., 2015; Lacoursière-Roussel et al., 2016; Yates et al., 2019), but results were contrasted in the marine environment, with studies detecting a significant correlation (Afzali et al., 2021; Evans et al., 2016; Pont et al., 2018; Stoeckle et al., 2021; Thomsen et al., 2016) while others only detected a correlation for some species and not for others (Fraija-Fernández et al., 2020; Yates et al., 2019). Refining techniques used to determine species abundance from eDNA represents an area of active research (Doi et al., 2015; Fukaya et al., 2021; Yoshitake et al., 2021) that will help to fulfill the full potential of multicomponent and multifacet biodiversity assessments (e.g., full use of the unifying framework of Hill numbers; Chao et al., 2014).

5 | CONCLUSION

We showed how combining functional and phylogenetic information with eDNA metabarcoding was efficient to recover the multiple components of biodiversity at regional scale, highlighting a north/south diversity gradient. Water eDNA metabarcoding revealed a greater diversity in the Iroise Sea, an ecosystem including a higher diversity of habitats and more difficult to access areas for fishing compared to the Audierne Bay. This multicomponent biodiversity assessment investigating three diversity facets using eDNA metabarcoding represents a promising avenue to determine conservation prioritization by providing a more holistic view on diversity. The eDNA approach offers new perspectives to increase spatial and temporal sampling in order to better monitor community dynamics and understand responses to current changes (Seymour et al., 2021). The application of such an analytic framework from eDNA metabarcoding to multicomponent biodiversity assessment will help to refine policy management and thus to conserve biodiversity in all its complexity (Pollock et al., 2020) by integrating more quickly marine ecosystem changes into conservation planning (Ferrier & Wintle, 2009).

CONFLICT OF INTEREST

The authors declare there are no conflicts of interests.

AUTHOR CONTRIBUTIONS

RR, DE, VT and CA jointly designed this study, DE and CA participated in the field work. RR, AV, CA and DE analyzed and interpreted the data. All the authors RR, VT, PL, AV, TD, LP, DE and CA contributed to the writing and the improvement of the manuscript.

DATA AVAILABILITY STATEMENT

Summary data are presented in the Supplementary Material. All the raw reads are available at https://doi.org/10.6084/m9.figshare.16709482.v2.

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