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Spatial analysis of fish multi-components biodiversity in the Bay of Biscay: A comparison between environmental DNA and scientific trawling

Master thesis

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Abstract

Environmental DNA (eDNA) metabarcoding is a method to detect taxa in the environment which is increasingly used in marine biodiversity surveys. eDNA is thought to be a more cost-effective and less invasive technique than scientific trawling but it is unclear whether both methods are comparable. In this study, we analysed data provided by both sampling methods from the same scientific survey on Atlantic fishes under the scope of taxonomic, phylogenetic, and functional diversity. We compared performances of both methods and identified spatial patterns of diversity. We found out that eDNA captures more taxonomic and phylogenetic richness than trawling and covers a broader functional space. As trawling surveys, eDNA can also reliably reflect differences in fish community composition along the Bay of Biscay. We found consistent diversity gradients combining both methods but we found no strong evidence to reliably use eDNA for abundance survey. eDNA can thus be implemented as an efficient method in complement to scientific trawling for multi-component biodiversity surveys.

Keywords marine ecology, environmental DNA, biodiversity, Atlantic, taxonomic diversity, functional diversity, phylogenetic diversity

Résumé

Le métabarcoding de l'ADN environnemental (ADNe) est une méthode de détection des taxons dans l'environnement, de plus en plus utilisée dans les études de biodiversité marine. L'ADNe est considéré comme une technique plus rentable et moins invasive que le chalutage scientifique, mais la comparabilité des deux méthodes est encore à déterminer. Dans cette étude, nous avons analysé les données fournies par les deux méthodes d'échantillonnage provenant de la même campagne de mesure sur les poissons de l'Atlantique dans le cadre de la diversité taxonomique, phylogénétique et fonctionnelle. Nous avons comparé les performances des deux méthodes et identifié les répartitions spatiales de diversité. Nous avons découvert que l'ADNe capture une plus grande richesse taxonomique et phylogénétique que le chalutage et couvre un espace fonctionnel plus large. Comme les études par chalutage, l'ADNe peut également refléter de manière fiable les différences dans la composition des communautés de poissons le long du Golfe de Gascogne. Nous avons trouvé des gradients de diversité cohérents en combinant les deux méthodes, mais nous n'avons pas trouvé de preuves suffisantes pour exploiter de manière fiable l'ADNe pour les études d'abondance. L'ADNe peut donc être utilisé comme une méthode efficace en complément du chalutage scientifique pour des mesures multi-composantes de la biodiversité.

Mots-clefs écologie marine, ADN environnemental, biodiversité, Atlantique, diversité taxonomique, diversité fonctionnelle, diversité phylogénétique

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Student's contribution

This report is the result of my master thesis in the unit dedicated to models for halieutics and ecology at Ifremer, to get the master diploma in environmental sciences and engineering at EPFL. I did not contribute to the sampling which was carried out in 2019. PCR and sequencing were performed by SPYGEN company. Marie-Émilie Deschez performed the taxonomic identification of sequences provided by SPYGEN. David Eme compiled the phylogenetic trees. My contribution to this project included *(i)* the collection of functional and taxonomic data *(ii)* merging, cleaning and organizing the dataset *(iii)* the calculation of biodiversity indices (based on Romane Rozanski's pipelines) *(iv)* the data exploration to document and compare patterns of diversity among the different components *(v)* the formal statistical analyses *(vi)* several analytical proposition *(vii)* drawing of figures and writing of this report.

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1 Introduction

Biosphere integrity has been identified as one of the two core "planetary boundaries" with climate change, *i.e.* a critical process for the Earth system with a "safe operating space" which is being exceeded due to anthropogenic perturbation (Steffen et al., 2015). Habitat loss, land use transformations, invasive species, resources exploitation and water pollution are the main identified human activities threatening biodiversity (Tilman et al., 2017). These pressures can result in a rapid loss of species, genes and ecosystem functions which represents a high risk for ecosystem integrity and human well-being (Cardinale et al., 2012; Díaz et al., 2006). Marine regions, especially highly productive coastal areas (Watanabe et al., 2018) are critically threatened by human activities (*e.g.* fishing, nutrient pollution, human population growth, ocean acidification; Halpern et al., 2015) altering ecosystems composition, functioning and services (Worm et al., 2006). Although marine ecosystems are subject to some conservation policies (fisheries international management, marine protected areas), these policies often consider a few valuable species instead of considering the whole ecosystem (Borja et al., 2011). These policies should also consider the ecosystems' mechanisms such as the shifts in response to climate change (Punzón et al., 2016). Marine biodiversity is indeed affected by climate change which notably results in species invasion and turnover in polar and temperate regions, local extinctions in many regions (Cheung et al., 2009). These shifts can impact species composition but also ecosystem functioning. Therefore, a good understanding of the multiple biodiversity components (taxonomic, phylogenetic and functional diversities) is necessary for policy-making in conservation issues (Tucker et al., 2016).

Traditionally, to monitor marine fish abundance and diversity the scientific community has applied several methods such as visual census, video, remote sensing, hydro-acoustics, commercial fishing observation, scientific fishing (Murphy & Jenkins, 2010). Scientific trawling is the most traditional way to monitor marine ecosystem and evaluate fish abundances for stock assessment. However this sampling method is subject to several biases such as variable catch probability according to the fish size and behavior (Benoít & Swain, 2003). Moreover, this method is also costly, polluting, invasive and requires taxonomic expertise to identify fishes which raises ethical concerns (Trenkel et al., 2019). During trawl surveys, scientists sort and identify fishes caught in the net in real time, which requires a lot of resources (see an illustration in the video of the 2019 EVHOE campaign; Lesbats, 2019). In recent years, a novel technique based on environmental DNA (eDNA; *i.e.* traces of DNA left by organisms in the environment through feces, urine, epidermal cells) emerged and has been investigated in ecology (Deiner et al., 2017), including in marine ecology (*e.g.* Fraija-Fernández et al., 2020; Gilbey et al., 2021). The metabarcoding technology related to this sampling method allows detecting species presence through filtration, amplification by PCR from one or several primers and comparison of sequences to a reference database (Fraija-Fernández et al., 2020). This technique has improved thanks to the development of fast and cheap sequencing methods and the implementation of extensive genetic reference databases. eDNA is non invasive (it does not require to kill or injure individuals), time in-

tegrative (it allows detecting species a few hours/days after the individuals left the DNA; Collins et al., 2018) and does not require any external observer (it has therefore less human bias; Yoccoz, 2012). This technique is therefore attractive in ecology with various objectives: detection and mapping of species, including rare or cryptic ones (Nester et al., 2020), study of behaviour of a given species (Takeuchi et al., 2019), deep-water monitoring (Everett & Park, 2018), study of fish diversity, habitat preference (Stoeckle et al., 2017).

Historically, biodiversity was studied by estimating the taxonomic diversity often measure as species richness (number of species in a community; SR) but also by accounting for species abundances and their regularity in a community.(McIntosh, 1967), once the species are unambiguously defined (Richards, 2013). This regularity facet can be measured with Shannon or Simpson indices or their variant (Villéger et al., 2010) reflecting the dissimilarities in species abundances: a community with species evenly distributed is considered more diverse than a community dominated by a few abundant ones. The number of species detected is highly determined by the sampling effort (*i.e.* the more we fetch, the more we find), a relationship that has been widely studied (Scheiner, 2003) and can be represented with a species accumulation curve (the number of species detected as a function of the sampling effort). This reflects particularly that two different sampling methods performed on the same area have little chance to reveal the same diversity and will only reflect a subset of the actual community. The sampling method provide information on the taxonomic composition of the area, however, the sole consideration of this component (species-neutral diversity) is insufficient to provide an accurate view of the biodiversity in an ecosystem (Rozanski et al., 2022). It is indeed important to take into account species' evolutionary history (Forest et al., 2007) and function in the ecosystems (Mouillot et al., 2013). Therefore considering these aspects requires to also explore two other biodiversity components that are defined as phylogenetic and functional diversity.

The phylogenetic diversity component refers to the evolutionary history among species or individuals within a community. It is relevant since linked to phenomena of extinction and speciation and is known to be undervalued in conservation (Winter et al., 2013). The successful evolutionary material filtered by millions of years of selection is usually represented by phylogenetic trees constructed from a molecular phylogeny. Evolution history between species is estimated from DNA sequences that have accumulated mutations over time since the species diverged. This estimations are calibrated thanks to fossil records that are reliably dated. Trees are thus constructed with statistical inference (Felsenstein, 1983). Phylogenetic diversity can be decomposed into three facets: richness denoting the amount of independent evolutionary history within a community, divergence representing the phylogenetic differences between taxa and regularity representing the variance in these divergences (Tucker et al., 2016). Various measures of these facets exist, all relying on distances measurements between taxa in the phylogenetic tree and based on branch-length segments expressed in units of time. For example the phylogenetic diversity (PD) measures the sum of all branch lengths of the phylogenetic tree formed by a set of species (Faith, 1992), it is the archetypal index documenting the richness facet. Ecologists often make the assumption that high phylogenetic diversity leads to high degree of functional diversity, but a recent study

(Mazel et al., 2017) tends to moderate this hypothesis. Therefore the functional diversity approach is still needed for an integrative assessment of the biodiversity.

Individuals also perform diverse functions within an ecosystem (Villéger et al., 2017) such as reproduction, food acquisition, mobility (Albouy et al., 2011). The functional diversity is defined as the range of these functions and their distribution among individuals: Are some of these functions filled in the same ways by several individuals, are there original species performing unique functions? The study of this biodiversity component is based on functional traits corresponding to any morphological, physiological, behavioral or phenological feature usually measurable at the individual level (Violle et al., 2007) directly influencing organism fitness (Mouillot et al., 2013). In practice, these traits can be ordinal values (values in a discrete set that are ordered but without metric), nominal values (values in a discrete set) or numerical values (Nock et al., 2016) and require a large effort of measurement that is possible for some clades thanks to collaborative data sets (*e.g.* Fishbase). Functional diversity study thus requires to cope with several types of traits (*i.e.* numeric such as the trophic level, nominal such as the habitat. However, traits are often summarized at species level, which is a common approximation neglecting intra-specific variations. These traits are conceptually represented in a multidimensional functional space where organisms occupy a given point (Mouillot et al., 2013). Studying functional diversity is fundamental to identify the amount of species that share attributes within the ecosystem and thus share some biological functions, which is defined as functional redundancy. The degree of redundancy of an ecosystem is associated with the resistance of that ecosystem to extinctions (Borrvall et al., 2000; Elmqvist et al., 2003), since species with overlapping niches may replace each other in case of extinction or collapse of one of them. Exploring the functional diversity allows understanding the ability of communities and ecosystems to persist despite disturbances and to provide ecosystem services (Guilhaumon et al., 2014). For example, a high functional diversity is associated with more productive and more climate-resilient reef fish communities (Duffy et al., 2016).

To represent the complexity of the taxa distribution in the functional space or in the phylogenetic tree, a multi-facet approach has been proposed. The diversity can be decomposed into independent facets called richness, evenness and divergence (Mason et al., 2005; Scheiner et al., 2017). This decomposition allows to numerically measure the complexity of the set of species for each diversity component. For example, considering the phylogenetic and functional components, the richness facet relates how much of the phylogenetic tree or functional space is filled by the taxa and the two other ones represent how the tree is structured or the space is filled (Schleuter et al., 2010). Divergence and regularity facets are homogeneous between both diversity components (functional and phylogenetic) as divergence includes the concept of average distances between taxa and regularity is related to the variability in these distances, where "distance" stands for phylogenetic distance on a tree or distance in a functional space. Considering phylogenetic diversity, regularity characterizes how the phylogenetic tree differs from a star phylogeny (*i.e.* a phylogeny where all species evolved directly from a unique common ancestor, with all pairs of species equally distant) and divergence stands for a mean distance between each pair of species (Tucker

et al., 2016). For functional diversity, regularity denotes the degree of redundancy in the functional space and divergence quantifies the abundance of species far from the center of gravity in the functional space, the so-called specialized species (Rozanski et al., 2022).

We can alternatively measure the three biodiversity components with Hill numbers, a framework proposed to unify several indices with a set of positive indices supposed to reflect the "true diversity" of a community (Chao et al., 2014; Hill, 1973). Depending on the biodiversity component, Hill numbers correspond to an effective number of species (for taxonomic diversity; Jost, 2006), an effective number of unit-branch length segments (for phylogenetic diversity; Chao et al., 2010) and a number of functional groups (for functional diversity, see Figure 1; Chao et al., 2019). Hill numbers are all calculated using a parameter $q \geq 0$ called "order" that quantifies the influence of the most abundant species. For $q = 0$, all species contribute equally to the diversity, regardless of their abundance in the community. A higher order q reduces the diversity by considering only the most abundant species. In this study, as we only considered species occurrence, we used 0-order Hill numbers. Taxonomic 0-order Hill number is equal to the species richness (SR), , the phylogenetic one corresponds to Faith's phylogenetic diversity (PD) and the functional 0-order Hill number (functional diversity, FD) is defined as the number of functional groups:

$$\mathrm{FD} = \sum_{i=1}^{S} v_i$$

with S the number of species and v_i the relative contribution of species i to its own functional group as illustrated on Figure 1.

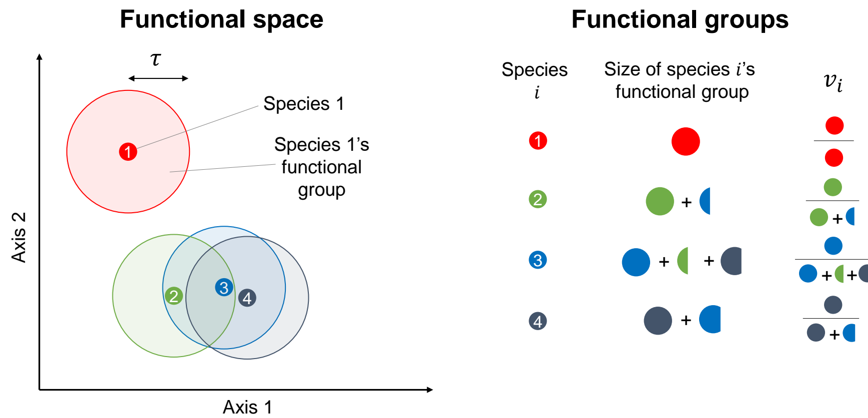

Figure 1: Illustration of the functional groups defined in functional Hill numbers' framework. Each species is associated with a functional group composed of the species at a distance smaller than τ in the functional space. The weight of each species in a functional group is linearly decreasing with the distance to the center of that group and the contribution v_i of each species to its own functional group is used to count the number of effective functional entities ($\mathrm{FD} = \sum_{i=1}^{S} v_i$), taking into account overlapping groups.

Some diversity indices (including Hill numbers with $q > 0$) require abundance or biomass information. However, there is no scientific consensus on the eDNA ability to provide this information using a number of sequence reads as a proxy. Some studies (Liu et al., 2022; Stoeckle et al., 2020) suggested such an approach, but the results are not systematically conclusive. Unknown parameters still remain: eDNA is subject to dilution, transport, deterioration by the environment and the organisms do not release the same amount of DNA. Some studies reported promising results on this relationship in controlled environment (Karlsson et al., 2022), but we still need research on the ability of eDNA approaches to reliably assess abundance in natural environment.

In marine environments, some studies have tried to compare trawling and eDNA monitoring methods, concluding that eDNA detects a higher species richness than trawling with especially good performance for both rare (low abundant) and pelagic species (Afzali et al., 2020; Stoeckle et al., 2020). In general, eDNA is a relevant technique to detect rare species as reported by Weltz et al., 2017 while trawling performs better at monitoring abundance changes according to Afzali et al., 2020. Both studies were able to detect variations in communities with depth or season thanks to eDNA. Very few studies assessed the three diversity components in marine environments with eDNA. Rozanski et al., 2022 reported small scale gradients of taxonomic, functional and phylogenetic diversity associated with protected areas, but did not compare with other monitoring techniques. Considering the functional diversity, a recent study by (Aglieri et al., 2020) revealed that eDNA was less selective than other methods in Mediterranean coastal areas. The authors found out that functional traits were more evenly distributed among species detected by eDNA than among species detected by other methods. Regarding phylogenetic diversity Polanco-Fernández et al., 2020 compared eDNA metabarcoding *v.s.* visual census approaches in tropical reef communities and concluded that eDNA allows detecting a wider range of phylogenetic lineages and taxa while visual census approach is prone to detect species that are preferentially phylogenetically closed (i.e. phylogenetic clustered), and miss distinct phylogenetic lineages. Species detected by visual census are significantly and strongly clustered on a phylogenetic tree which is not the case for eDNA.

Objectives

In this study we compared eDNA and trawling performance in biodiversity monitoring in the Bay of Biscay, a Northeast Atlantic region known to be highly productive. In this region, measures of protection have been settled to protect marine environment and maintain sustainable fish resources therefore several biodiversity studies have been led (Eme et al., 2022; Hily et al., 2008; Rozanski et al., 2022). According to the current knowledge on eDNA metabarcoding, we expect this method to detect more taxonomic richness than trawling, since it has shown to have better performance in the previous studies, and to be able to detect rare species with higher probability (Liu et al., 2022). To our knowledge, no study compared eDNA and trawling method beyond the taxonomic component considering the functional and phylogenetic components. eDNA is more likely to cover a higher spectrum

of functional diversity (as it detects pelagic fishes) than bottom trawling (designed to target demersal fishes) and also detects species that are able to avoid the trawl. Regarding the phylogenetic component, there is no evidence that eDNA or trawling might have better performance in terms of phylogenetic diversity, but this review reported that eDNA detected more phylogenetic diversity than other traditional methods. To test these hypotheses, we explored several biodiversity indicators including taxonomic, functional and phylogenetic diversity indices. We further compared the species compositions dissimilarities and fish abundance in the Bay of Biscay (BoB) where sampling with both eDNA and trawling was carried out. Understanding the relationships between the number of reads and the biomass is currently a major obstacle to the use of eDNA approaches in biodiversity monitoring. To assess this question, we studied the distributions and correlations of fishes abundances (number of individuals) and quantity of eDNA reads from the PCR.

2 Materials and methods

2.1 Study area

The Bay of Biscay (BoB), stretching between the North coast of Spain and Brittany in France, is an intracontinental sea that is largely open to the Atlantic Ocean. The BoB continental shelf (80 000 km^2) is mostly a flat sedimentary area, narrow in the South and broader in the North: At about 200 m depth, the shelf break is found and a steep slope extends down to the Atlantic abyssal plain. The region is influenced by the warmed water of the Gulf Stream (Palter, 2015) and by the freshwater from the Loire and Gironde rivers. Consequently, the Bay of Biscay is a complex and highly productive area, supporting a high level of fishing activities (Hily et al., 2008). In this region, provision of food is the main identified ecosystem service, before regulation and cultural services (Galparsoro et al., 2014), but these services are endangered by anthropogenic pressure altering the regional ecological structure (Borja et al., 2019). In terms of ecosystems, the BoB continental shelf has been identified as a major area of fish spawning and a key migration path (Borja et al., 2019). Since the BoB is located at the transition between two biogeographic regions (Northern and Southern temperate provinces of Northern Atlantic), its ecosystem is under both influences and has therefore higher biodiversity than adjacent areas (Punzón et al., 2016). In the region, annually during autumn, the French international EVHOE bottom trawl survey is carried out to evaluate the demersal fishing resources (Garren et al., 2019). Fifteen sites from the 2019 annual survey were chosen in the BoB for the measurements, all located on the continental shelf except site 5 on upper slope (Figure 2a). Two of them were inside a Marine Protected Area (MPA): sites 10 and 11, in Arcachon's MPA (*Parc naturel marin du Bassin d'Arcachon*) and Gironde's estuary MPA (*Parc naturel marin de l'estuaire de la Gironde et de la mer des Pertuis*) respectively. However, those sites are classified as "poorly protected" in terms of fishing restrictions according to the International Union for Conservation of Nature (IUCN) classification (Claudet et al., 2021; e Costa et al., 2016). Eight sites were deeper than 100 m (mostly less than 170 m except site 5 that was 500 m deep) and 7 sites ranged between 20 and 100 m.

2.2 Data acquisition by trawling

Fishes were sampled during a survey in the BoB called EVHOE (*Évaluation halieutique Ouest de l'Europe*). The trawl is a fishing gear towed by the vessel catching fish and other organisms present on its path unless they actively avoid by swimming or escape through the mesh. The survey trawl was a standard "GOV 36/47" with a 4 m vertical opening and 20 m width and a 20 mm wide mesh. During daylight for each sampling, the operators deployed the trawl during 30 min at a constant speed of 4 knot, to sweep an area of ~ 0.076 km^2. Sampled fishes were identified, counted and weighted by taxonomic experts during the survey (Laffargue et al., 2021). A video of this campaign is available online (Lesbats, 2019).

2.3 eDNA data acquisition

At each of the 15 locations where the trawl was towed we collected 2 eDNA samples for a total of 30 samples, see Figure 2a. The distance between the trawling sampling and the eDNA sampling was lower that 6 km. At each station, we sampled seawater using niskin bottles available on the circular rosette usually deployed during the EVHOE survey. There were 9 bottles on the rosette, each of them containing a volume of approximately 5 L representing an overall sampling volume of 45 L. At each station, the following steps were performed: First the onboard team cleaned the circular rosette and bottles with freshwater; the rosette was lowered open at 5 m above the sea bottom and then triggered from the boat and closed. Once on the boat, the water present into the Niskin bottles was placed into 4 sterilized plastic bags (~ 11.25 L each) and placed into two tanks of 25 L previously disinfected. The onboard team conducted the filtration in a clean laboratory directly on-board dedicated only to the process of eDNA samples. They used two filtration devices composed of 2 Athena® peristaltic pumps (Proactive Environmental Products LLC, Bradenton, Florida, USA; nominal flow of 1.1 L min^{-1}), a VigiDNA® 0.22 µM cross flow filtration capsule (SPYGEN, le Bourget du Lac, France) and disposable sterile tubing for each filtration capsule. Two filtration replicates were performed in parallel in the boat laboratory, at each station. At the end of each filtration, the water inside the capsules was emptied, and the capsules were filled with 80 mL of CL1 Conservation buffer (SPYGEN, le Bourget du Lac, France) and stored at ambient temperature.

2.4 eDNA extraction, amplification, sequencing and data processing

DNA was extracted and amplified with a primer called "teleo", following the protocol described in Polanco-Fernández et al., 2020. The teleo primer amplifies a region of 29 to 64 base pairs on the mitochondrial 12S region and targets fish (Actinopterygii and Chondrichthyes; Polanco-Fernández, Martinezguerra, et al., 2021). The whole protocol is provided in Supp. mat. S1. The sequence reads were analysed using programs implemented in the R package OBITools (Boyer et al., 2015) following the protocol described in Polanco-Fernández, Martinezguerra, et al., 2021. This program was designed to merge the sequences, to remove unaligned sequences and finally to perform taxonomic assignation. These steps are described in details in Supp. mat. S2. Taxonomic assignation was performed by the ecotag program with a genetic reference database previously obtained by combining two genetic libraries: *(i)* the NCBI database (Federhen, 2011) that has been adapted to match with the desired portion of the genome containing 23 000 sequences of animals and *(ii)* a 12S custom reference database built by the host institute from sequenced samples taken on individuals during previous trawling surveys, currently containing 90 sequences of Atlantic fishes.

We assigned sequences at different taxonomic levels: species (match > 98%), genus (96% < match ≤ 98%), family (90% < match ≤ 96%) (Marques et al., 2020). We only kept species and genus from the identified sequences for diversity analyses. We removed rare detections (*i.e.* taxa identified in only 1 filter, in only 1 replicate of the PCR and with a number of reads smaller than 10% quantile of all reads) considering that these detections were

probably associated to PCR or sequencing errors: two genus were removed with this filter (*Pegusa* and *Callionymus*). For each site we calculated the similarity (see paragraph Beta diversity) between the taxa found in both replicates. For the other analyses, we merged both replicates together.

2.5 Data aggregation

In this study, the lowest taxonomic level at which we assigned the sequences was the species level, however in some cases the sequences could only be identified at the genus level. In cases with ambiguity, we chose to aggregate species belonging to the same genus to the genus level when one observation allowed only genus identification (*e.g.* we detected the taxa *Notoscopelus*, *N. elongatus* and *N. kroyeri*, so they were merged to the genus *Notoscopelus*) except when the genus was known to have only one species in the region (*e.g.* we detected *Sardina* and *S. pilchardus*, they were so combined as *S. pilchardus*). The same treatment was performed on taxa detected by trawling and eDNA. Detail of taxa aggregation is provided in Supp. mat. S3. To allow taxa aggregation and analyses based on fish clades, we needed taxonomic classification. We retrieved this classification from the online databases Barcode of Life Data System (BOLD; Ratnasingham and Herbert, 2007) and World Register of Marine Species (WoRMS; Horton et al., 2022) that were queried online through the R package taxize v0.9.99 (Chamberlain & Szöcs, 2013).

2.6 Fish data

Functional traits

We measured functional diversity using a set of available and unambiguous functional traits, measurable at individual level. We chose 9 traits associated with several functions of the individuals (habitat, feeding, reproduction and mobility): maximum length, average and range depth, trophic level, position in the water column, body size, reproduction mode, fertilisation mode and parental care. We retrieved 88.9% of the traits from the online *Fishbase* database (Froese & Pauly, 2022) and completed missing traits with information from experts and from the reference guide (Quéro et al., 2003) to get a traits table filled at 94.5%. In order to build a functional Euclidian space, we used Gower distance that allow to acocunt for different types of traits and missing data (Gower, 1971), the distance between species i and j is defined as:

$$G_{i,j} = \left(1 - \frac{\sum_{k=1}^{v} s_{i,j,k}}{\sum_{k=1}^{v} \delta_{i,j,k}}\right)^{1/2}$$

with v the number of traits, $\delta_{i,j,k}$ a weight with value 1 if the k-th trait is measured for species i and j, 0 otherwise, $s_{i,j,k}$ the similarity between species i and j for the k-th trait. This similarity is defined as 1 if both species have the same trait value, 0 if they have a different one (in case of nominal traits) or linearly dicreasing with the difference between the two traits values (in case of numerical traits) or 0 for missing values. Gower showed that the distance is Euclidian when no data is missing, therefore we tried to have as little blanks

in this trait table as possible. The obtained distance matrix allowed the construction of a new Euclidian numerical functional space using principal coordinates analysis (PCoA; Maire et al., 2015). We centered and normalized all quantitative traits before analysis. For taxa detected or merged at genus level, we randomly selected one species of that genus occurring in the Eastern Atlantic from the reference guide (Quéro et al., 2003). The exhaustive list of species is provided in Supp. mat. S4. We repeated this random draw 100 times to provide an average and standard deviation of functional indices.

Phylogenetic data

To measure phylogenetic diversity indices we used recent phylogenetic trees delineated at the species level that were built before this study. For the Actinopterygii we used Rabosky's molecular tree (Rabosky et al., 2018) as a backbone containing 204 species known to be present in the Bay of Biscay and the Celtic Sea. 21 missing species were re-grafted based on a Yule model parameter of speciation (Nee et al., 1994). For Elasmobranchii, we extracted 100 trees from the posterior distribution of the molecular phylogenies published by Stein et al., 2018 and selected the 28 species present in the area. Finally, we built a single set of 100 trees grouping both Actinopterygii and Elasmobranchi taxa including a total of 253 species and we considered an estimated divergence time between the two clades between 421 and 468 Ma (Benton et al., 2015). To account for the phylogenetic uncertainties in the downstream analyses, we computed the phylogenetic diversity indices on each of the 100 trees and we reported the average (and standard deviation). For detected genus, we arbitrarily selected one species of that genus, making the assumption that the genus form a clade (*i.e.* a monophylethic group) and thus that species from a specific genus have diverged the same amount of time from their common ancestor and thus have the same phylogenetic distances, as in Rozanski et al., 2022.

2.7 γ and α diversity indices

We studied the three components of the fish biodiversity in the BoB at different spatial scales. γ diversity refers to the diversity over the whole study area and α diversity denotes the diversity at a local scale within a given site of the study area (Marcon, 2018). We divided functional and phylogenetic biodiversity components into three facets. The richness facet represents an extensive measure of a number of groups or total evolutionnary history. The divergence facet represents the average distance between species. Finally the regularity facet represents the variability of that distance.

Taxonomic diversity

We measured taxonomic richness with species richness (SR) index, *i.e.* the number of taxa in a given site. To evaluate the impact of sampling effort for eDNA and trawling on the number of detected taxa, we built a species accumulation curve fitted with an asymptotic

model using the package vegan v2.5-7 (Dixon, 2003):

$$\mathrm{SR}(n) = \mathrm{SR}_{\max} + (\mathrm{SR}_0 - \mathrm{SR}_{\max})\mathrm{e}^{-kn}$$

with n the number of sites, k an accumulation rate and $\mathrm{SR}_{\max}$ the asymptotic species richness. We thus estimated an accumulation rate and asymptotic richness for each method. Since all species are considered equivalent in taxonomic framework, there is no facet of divergence. In our study we accounted for incidence data (*i.e.* only accounting for taxa presence or absence) for biodiversity analysis, we did not consider any notion of taxonomic regularity either.

Phylogenetic diversity

We measured phylogenetic richness by calculating the Faith's index of phylogenetic diversity (PD; Faith, 1992), corresponding to the sum of all branch lengths in the phylogenetic tree associated with a given community. We measured phylogenetic divergence through Mean Pairwise Distance (MPD) index, defined as the average phylogenetic distance between all pairs of species in a community (Tucker et al., 2016). We measured phylogenetic regularity by computing the Variance in Pairwise Distance (VPD) between pairs of species in a community. We used the package PhyloMeasures v2.1 to calculate these indices (Tsirogiannis & Sandel, 2015). We also needed to quantify the degree at which a set of species is spread or clustered on the phylogenetic tree. To test for the dispersion of species on a tree, we quantified clustering of species on phylogenetic tree (phylogenetic signal) by computing the D-value, a statistics to calculate whether the detectability by eDNA/trawling is significantly dispersed or clustered in a phylogenetic tree (Fritz & Purvis, 2010). This statistics is useful because it is simply defined and measures both strength and significance of the phylogenetic signal. The D statistics is defined as follows:

$$D = \frac{\sum d_{\mathrm{obs}} - \mathrm{mean}\left(\sum d_B\right)}{\mathrm{mean}\left(\sum d_R\right) - \mathrm{mean}\left(\sum d_B\right)}$$

with $\sum d_{\mathrm{obs}}$ the observed sum over the tree branches of differences of frequencies of the detectability between the descending branches, $\sum d_B$ the distribution of the same value for a tree where detectability follows a Brownian evolution model and $\sum d_R$ the distribution of the same value for a tree where detectability is randomly distributed with the same probability as in the observed data set. We calculated the D statistics with the package caper v1.0.1 (Orme et al., 2013) with 1000 random permutations. In this framework, small D correspond to more clustered taxa: $D = 0$ corresponds to taxa as phylogenetically conserved as expected under a Brownian threshold model and $D = 1$ corresponds to taxa as dispersed as if they were randomly drawn on the phylogenetic tree, but D can go beyond the range $[0, 1]$. The $\sum d_{\mathrm{obs}}$ value is compared to the distributions of $\sum d_B$ and $\sum d_R$ for significance test to obtain a pseudo p-value.

Functional diversity

We quantified functional diversity from indices measured on the built functional space with the method explained in Functional traits. We assessed the richness facet through the 0-order functional Hill number (FD), denoting the number of equivalent functional entities in a site or in an assemblage (see Figure 1 for the definition of FD). We also measured the FRic index denoting the volume of the convex hull formed by species in the functional space which is an alternative measure of functional richness (Mouillot et al., 2013). When we refer to "functional richness", we denote only FD. We estimated the functional regularity with an indicator denoted functional evenness (FEve) as the size of the minimum spanning tree linking all species in the functional space. We assessed the functional divergence (FDiv) by computing the mean distance of detected taxa from the center of gravity of the functional space. We made the calculations with the package `mFD` 1.0.1 (Magneville et al., 2021). We compared distributions of functional traits with Pearson's χ^2-test. We calculated and plotted distributions densities by computing Kernel density estimation with a Gaussian window.

Standardized effect size

Species richness influences both phylogenetic and functional richness (Tucker & Cadotte, 2013). However, to compare the three biodiversity components, the independence of these indices is crucial. Therefore, we decoupled phylogenetic and functional measures of diversity (PD, MPD, VPD, FD, FEve, FDiv) from the species richness by calculating the standardized effect size (SES) based on a null model (Leprieur et al., 2012). We obtained null models by generating 99 random permutations of the species in the phylogenetic trees and in the trait table. We then applied the following formula for each indice X:

$$\text{SES}_X = \frac{X_{\text{obs}} - \text{mean}(X_{\text{null}})}{\text{sd}(X_{\text{null}})}$$

where X_{obs} is the observed indice value, $\text{mean}(X_{\text{null}})$ and $\text{sd}(X_{\text{null}})$ are the mean and standard deviation of the random indices under null model. A positive (resp. negative) SES means that the considered index is higher (resp. lower) than the null model, *i.e.* the distribution of the index if the same number of taxa were randomly drawn from the total community. For each SES, we estimated their significance based on the probability $p(|X| > \text{SES})$ where X follows a standard normal distribution, under the assumption than SES from null model follows normal distribution. We first considered the set of taxa obtained by eDNA and by trawling in each site as different communities. We then calculated the same indices with combined communities (adding the species detected by eDNA and by trawling in each site).

Table 1 summarises indices used for three facets and three components of diversity.

We finally selected 4 particular sites to display their taxonomic composition, phylogenetic tree and functional space with both methods for illustration in this report. We chose to represent site 2 (offshore, high phylogenetic richness), site 5 (offshore, high functional

Table 1: Indices of diversity used in this study.

Component	*Facet*		
	Richness	*Evenness*	*Divergence*
Taxonomic	SR	-	-
Phylogenetic	PD	VPD	MPD
Functional	FD	FEve	FDiv

richness in trawling, some rare species detected), site 8 (closer to the coast, high taxonomic diversity, trawling included in eDNA) and site 15 (coastal, low functional diversity).

2.8 β diversity indices

To detect spatial structures and identify communities based on dissimilarities, we used a β-diversity approach by comparing pairwise communities *i.e.* set of fishes detected in one site with one method. To do so we calculated the Jaccard dissimilarity index (β_{jac}):

$$\beta_{\text{jac}} = 1 - \frac{|A \cap B|}{|A \cup B|}$$

with A et B the communities and $|\cdot|$ denoting the size of a community. Jaccard dissimilarity index can be decomposed in two additive components: the species turnover (β_{jtu}) corresponding to the replacement of taxa by others between sites/detection methods, and the nestedness that (β_{jne}) quantifies the richness difference between the two sites/detection methods when the poorest sites/detection methods is a subset of the richest one (Baselga, 2012). To perform these calculations with used the betapart v1.5.4 R package (Baselga & Orme, 2012). We then categorised the communities to identify patterns according to space and method.To do so we performed a principal coordinates analysis (PCoA) on the different matrices of β diversity from the Jaccard distance, using the R package ade4 v1.7.18 (Dray & Dufour, 2007). To detect spatial patterns, we split sites according to their depth (above or below 100 m depth) and drew ellipses of dispersion with width equal to 1.5 times the standard deviation to identify if sites with similar depth were similar in species composition.

2.9 Hotspots and coldspots of diversity

To identify coldspots and hotspots of diversity we calculated the local spatial autocorrelation of diversity indices with the Getis-Ord statistics (G_i^*; Getis and Ord, 1992). The Getis-Ord statistics is a measure of local average on a numerical measure. This measure allows identifying high-high and low-low clusters, for spatial variables *i.e.* locations where the local average of that variable is higher or lower than expected from a null model of spatial random distribution of that variable. In this analysis we built a neighbourhood around each point. Two points are considered neighbour if their Thiessen polygons are adjacent (see Supp. mat. S5 for the connectivity graph). The Getis-Ord statistics calculates the rela-

tive sum of richness indices over each point's neighbourhood:

$$G_i^* = \frac{\sum_j w_{ij} x_j}{\sum_j x_j}$$

with (w_{ij}) a weight matrix indicating if points i, j are neighbours and x_j the value of the considered diversity index. This statistics is then compared through a distribution of a null model's statistics obtained by 10^5 permutations. A cluster of high/low indices is identified when the Getis-Ord at this point is higher/lower than 5% of the obtained randomized statistics. We performed the calculations with rgeoda v0.0.9 (Anselin et al., 2009) according to the developers' specifications. We analysed autocorrelation separately for eDNA and trawling points, then on merged communities.

2.10 Qualitative comparison of abundance

For the comparison of both methods in terms of abundance study, we did not directly compare the number of reads by eDNA and the number of individuals because they did not have a similar distribution. We thus transformed the number of individuals caught by trawling and number of reads by eDNA to best fit an exponential distribution. We transformed the distributions of abundance and estimated their parameters with fitdistrplus v1.1-8 package (Delignette-Muller & Dutang, 2015). We then calculated correlation using linear least squares regression between obtained transform abundances and transformed number of reads of the same taxa caught by same sites.

All calculations were performed with R v4.1.2 (R Core Team, 2021) and the cited packages.

3 Results

3.1 γ diversity

Taxonomic diversity

The taxonomic assignation of eDNA sequences resulted in the identification of 1039 different sequences at family rank or lower (33.1% at species level, 33.7% at genus level and 33.1% at family level) corresponding to 202 different taxa (128 genus or species). After taxonomic homogenization we identified 92 taxa among which 79 Actinopterygii (27 different orders), 12 Elasmobranchii (6 different orders) and 1 Holocephali (*Chimaera monstrosa*). In each sampling site we detected between 33 and 55 taxa (42.2 on average). In each site, we detected taxa with 31 300 reads on average.

Scientific trawling catches included 250000 fish individuals, with an average of 17000 per sampling site. We identified 84 species and we kept 70 taxa after aggregation: 60 Actinopterygii (belonging to 22 orders), 9 Elasmobranchii (5 orders) and 1 Holocephali (*C. monstrosa*).

We detected 56 common taxa between eDNA and trawling methods (see Venn diagrams Figure 2b). We found that 4.2 trawling sites caught the same SR as a single eDNA site (see species accumulation curves Figure 3). The asymptotic richness SR_{max} was 93, 75 and 108 for eDNA, trawling and the two data sets combined respectively.

eDNA and trawling detections among orders were significantly different ($\chi^2 = 71, \mathrm{df} = 35, p = 0.00034$). eDNA detected relatively less Pleuronectiformes, Gadiformes, Carangiformes and Callionymiformes and more Spariformes and Beloniformes compared to trawling catches. Detailed distribution of orders by detection method is provided in Supp. mat. S6.

Phylogenetic diversity

The detected species have an estimated common ancestor dating back to 446 ± 14 Ma (see phylogenetic tree Figure 2c). The total PD is 10040 ± 250 Ma (9180 ± 220 Ma when restricted to eDNA and 7060 ± 150 Ma when restricted to trawling). Considering the phylogenetic richness facet, eDNA results showed a significant overdispersion regardless of the number of taxa for the whole area ($SES_{PD} = 3.56, p = 0.00036$) compared to the trawling for which SES was not significant ($SES_{PD} = 1.49, p = 0.14$). SES values of γ phylogenetic divergence (MPD) and regularity (VPD) were similar for both methods, showing a non-significant overdispersion for these indices ($SES_{VPD} = 0.95$ for eDNA and 0.90 for trawling and $SES_{MPD} = 1.46$ for eDNA and 0.84 for trawling).

The D clustering statistics indicated that taxa detected by eDNA were more dispersed on the phylogenetic tree ($D = 1.10 \pm 0.01$) than taxa detected by trawling ($D = 0.84 \pm 0.01$). Distributions of the taxa detected by eDNA or trawling on the phylogenetic tree significantly differed from the distribution obtained by Brownian model ($p = 0.002$ for both) but they did not significantly differ from a random distribution ($p = 0.66$ and 0.19 for eDNA

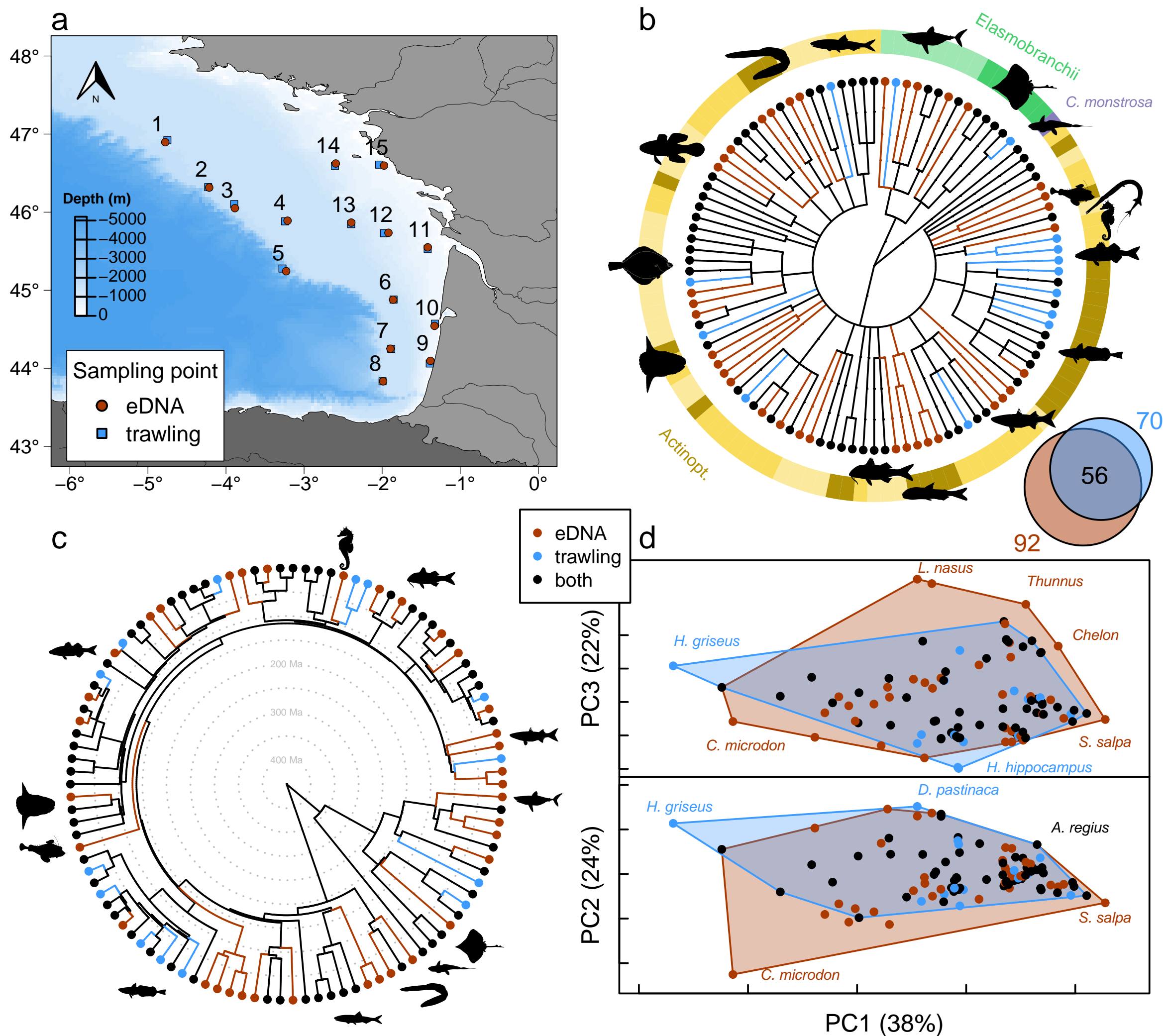

Figure 2: (a) Map of the sampling points in the Bay of Biscay, the circles represent the locations of the eDNA samples and the squares represent the trawling hauls. (b) Taxonomic tree of the detected taxa at the regional scale, each taxa is represented by a tip and the branches correspond to the taxonomic clades (genus, family, order and class). Tip and branch colors represent the detection method that allowed to detect the taxa (*e.g.* a red branch indicates that descending taxa were only detected by eDNA). Colors on the outer ring correspond to infraclass for Elasmobranchii and to orders for Actinopterygii. The Venn diagram shows the number of taxa detected by each method after aggregation. (c) Phylogenetic tree with detection method at the regional scale, each tip correspond to a detected taxa, with color indicating how this taxa was detected and same branch colors as for b. Branch lengths are proportional to the evolutionary history shared by the descending taxa. (d) Functional space obtained by PCoA (axes 1-2 and 1-3) at the regional scale. Each point indicates a taxa, the distance between taxa reflects the Gower distance between species based on their functional traits. Points colors indicate how the species was detected across all sites. The colored polygon is the convex hull of all taxa detected by a given method (eDNA in red, trawling in blue). For b,c and d taxa are colored in black if they were detected by both methods in same or in different sites.

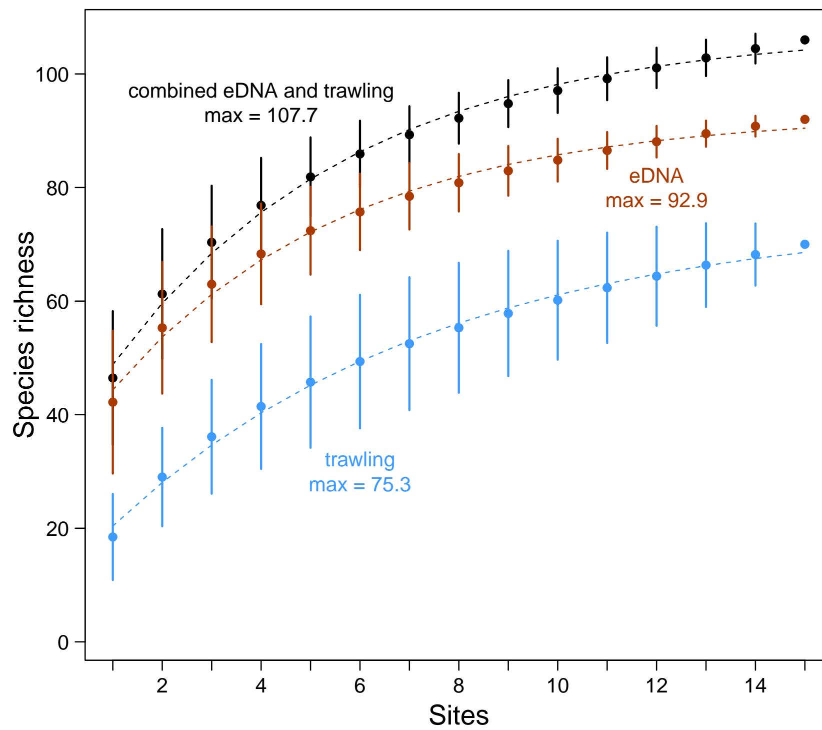

Figure 3: Species accumulation curve of taxa collected by eDNA and trawling. The dotted lines correspond to a fitted asymptotic model (sum of squared residuals 19.86, 14.25 and 23.81 for eDNA, trawling and both respectively, rate of accumulation 0.213, 0.150 and 0.203, initial SR_0: 32.9, 11.5 and 35.6) and the asymptotic richness is indicated for each method.

and trawling respectively).

Functional diversity

Considering functional diversity, PCoA on traits values allowed to explain 84% of the variation of the traits with 3 axes (38, 24 and 22%). From this functional space, the measured functional richness (FD) was 9.46 ± 0.12 functional entities (8.78 and 9.36 when restricted to eDNA and trawling respectively). Both methods showed an overdispersion of the richness facet, however only the trawling FD value was significantly higher than under a null model ($SES_{FD} = 2.69, p = 0.0071$ for trawling while $SES_{FD} = 0.85, p = 0.40$ for eDNA). The filled volume (FRic, another measure of richness) corresponding to the convex hull of each method represented 81% of the total functional space for trawling and 78% for eDNA. Figure 2d represents the functional space filled by detected taxa and these convex hulls. In terms of divergence (FDiv) both method revealed a clustering trend for the whole area, nevertheless, the trawling trend was stronger ($SES_{FDiv} = -1.65, p = 0.099$) compared to the eDNA trend ($SES_{FDiv} = -0.43, p = 0.67$). Finally, the SES values of regularity (FEve) showed a slight non-significant clustering trend regardless of the method used ($SES_{FEve} = -0.015, p = 0.99$ with eDNA and $SES_{FEve} = -0.28, p = 0.78$ with trawling).

Fishes detected by eDNA significantly differ in habitat compared to those caught by trawling: eDNA captured more pelagic and bathypelagic species and less demersal species than trawling ($\chi^2 = 14, \text{df} = 4, p = 0.006$; Supp. mat. S7 top) in relative distribution. In terms of body size, eDNA captured more fusiform and elongated fishes and less flat fishes than trawling ($\chi^2 = 18, \text{df} = 6, p = 0.0065$; Supp. mat. S7 bottom). Moreover, eDNA method detected more fishes of low trophic level (< 3) and less fishes of intermediate trophic level ($3 - 4$) than trawling ($\chi^2 = 32, \text{df} = 8, p = 8 \cdot 10^{-5}$; Supp. mat. S8). Other traits (depth, reproduction, length) showed no difference in distributions with the detection method.

3.2 α diversity

eDNA captures systematically more taxonomic, phylogenetic and functional richness than trawling for each site (see Figure 4 and Table 2). For eDNA, 2 sites out of 15 showed a significant higher PD than the null model (sites 2 and 8, see Figure 4a), the others detected no significant difference in PD whereas for trawling, 2 sites had a lower PD than the null model (sites 11 and 15), the others being not significantly different. Regarding the absolute value of PD, there were some contradictions in α diversity between eDNA and trawling. Sites 8 and 9 for example showed high values of phylogenetic richness (PD $> 5\,500$ Ma) compared to other sites in eDNA and showed low values of PD in trawling ($< 1\,700$ Ma). Considering functional richness, 4/15 sites showed a significant clustering trend for SES_{FD} in eDNA, while 10/15 in trawling. Only one site (8) showed a significant low SES_{FD} with both methods. The details of detected taxa by method and by site is provided in Supp. mat. S9 and species richness are summarised on Venn diagrams by site in Supp. mat. S10.

When merging both methods for each site (see Figure 5a), we found that offshore sites

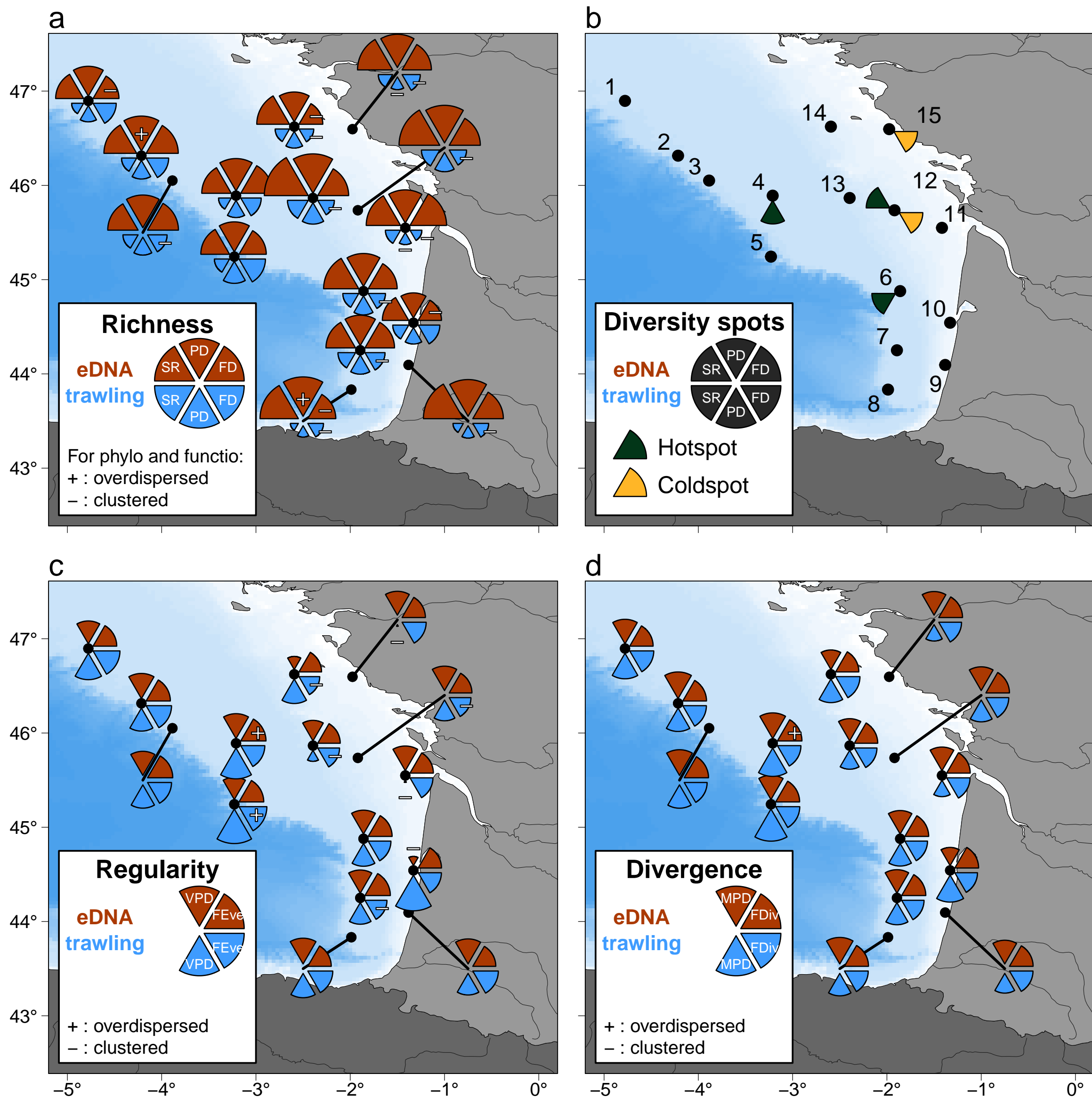

Figure 4: α diversity indices of (a) richness, (c) regularity and (d) divergence by site and by method for the three components of diversity (taxonomic, phylogenetic and functional). The radius of each circle part is proportional to the value of the index. For functional and phylogenetic diversity, indices significantly different from the null model (based on SES) are indicated with – and +. (b) Hotspots and coldspots of diversity richness: points identified as high/low clustering from the Getis-Ord statistics with $p < 0.05$.

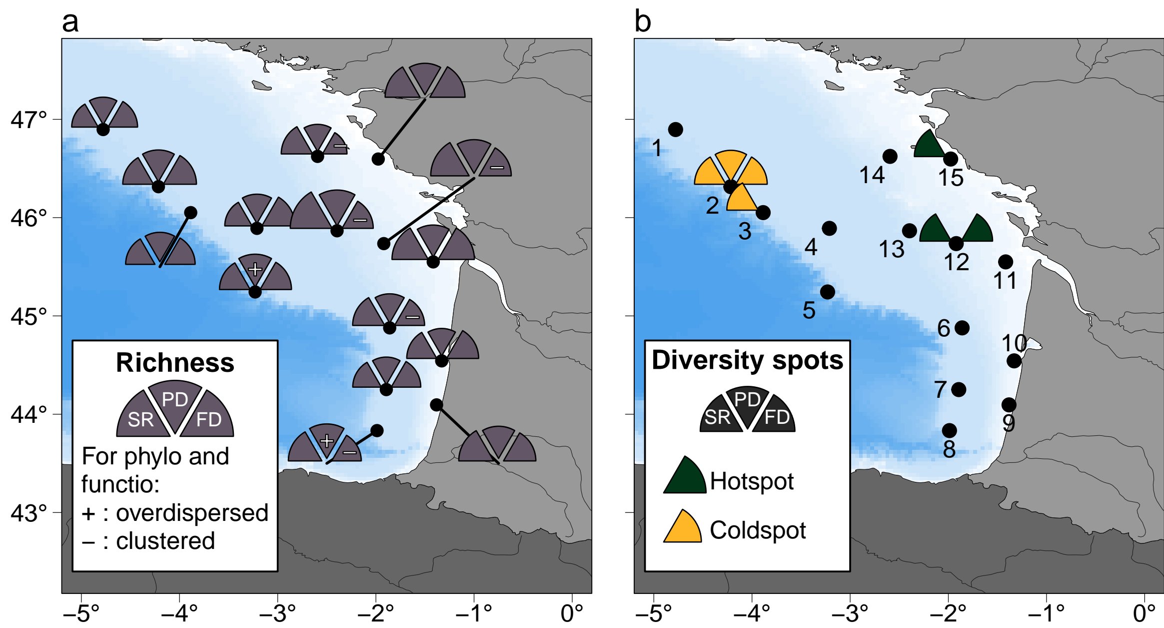

Figure 5: α diversity on **merged communities**, *i.e.* combining results from eDNA and trawling. (a) Indices of richness for the three components of diversity (taxonomic SR, phylogenetic PD and functional FD). The radius of each circle part is proportional to the value of the index. For functional and phylogenetic diversity, indices significantly different from the null model (based on SES) are indicated with − and +. (b) Hotspots and coldspots of diversity: points identified as high/low clustering from the Getis-Ord statistics based on any facet of diversity with $p < 0.05$.

Table 2: Values of species richness SR, phylogenetic diversity PD, phylogenetic signal of clustering (*D*-statistics) and functional diversity FD measured by eDNA and trawling in each site and in gamma diversity (*All*). For PD and FD, significant over-dispersed (+) and clustered (–) values compared to null model are indicated. For *D*-statistics, communities with significantly clustered taxa on phylogenetic trees are indicated with ∗. Significance threshold : 0.001, 0.01 and 0.05.

	SR		**PD**		***D*-statistics**		**FD**	
Site	eDNA	trawl	eDNA	trawl	eDNA	trawl	eDNA	trawl
1	35	15	4 490	2 440	0.88	1.06	5.33^{-}	4.77
2	41	19	$5\,240^{+}$	2 790	1.00	0.91	6.61	4.63
3	38	19	4 920	2 690	0.89	0.68	6.36	4.02^{-}
4	37	16	4 860	2 580	0.99	0.80	6.57	4.21
5	36	19	4 510	3 300	0.92	0.41^{**}	5.61	5.44
6	44	20	4 940	2 860	0.87	0.93	5.96	3.55^{--}
7	37	22	4 560	2 880	0.87	0.67	6.08	4.13^{-}
8	48	10	$5\,920^{+}$	1 710	0.88	0.55^{*}	5.75^{-}	3.23^{-}
9	50	13	5 520	1 860	0.92	0.96	6.29	3.26^{-}
10	33	20	3 770	2 490	0.95	0.51^{*}	4.80^{--}	4.46
11	43	19	4 990	$1\,810^{--}$	0.66^{*}	0.53^{*}	7.52	2.44^{---}
12	51	23	5 650	2 910	0.88	0.64^{*}	6.40	3.57^{--}
13	55	26	5 910	3 220	0.85	0.78	6.37	3.43^{---}
14	41	18	4 490	2 520	0.90	0.57^{*}	4.90^{---}	3.04^{--}
15	44	18	4 990	$1\,910^{-}$	0.85	0.76	6.03	3.75^{-}
All	92	70	$9\,180^{+++}$	7 060	1.10	0.84	8.79	9.36^{++}

5 and 8 had a significantly higher PD than expected under a null model ($SES_{PD} = 2.4$ and 2.2, $p = 0.015$ and 0.027) with no site having significantly lower PD than expected. Site 14 showed a significantly lower VPD ($SES = -1.96, p = 0.049$) and no other site having a significantly lower or higher VPD. No site led to significant SES_{MPD}, *i.e.* more or less phylogenetic divergence than expected by the number of taxa.

The spatial analysis on indices generated by both methods separately (Figure 4b) allowed identifying 4 sites having autocorrelated richness with only one common site between both methods (site 12). For trawling, we noticed two functional FD coldspots both located near to the coast (sites 12 and 15), and two hotspots associated with SR (site 6) and PD (4). Considering eDNA, only one site showed a SR hotspot (12). We identified significant hotspots of phylogenetic diversity for other facets: eDNA alone showed no phylogenetic significant hot- or coldspot with any of its facet whereas trawling shows coldspot for some coastal sites (12 and 15) and hotspot for some offshore sites (3 and 4; Supp. mat. S12). Considering functional diversity, we identified the hot- and coldspots of other facets: eDNA detects no spot of richness but sites 5 and 15 are respectively hotspot and coldspot of the two other facets (regularity and divergence). The autocorrelation is more pronounced in trawling with sites 6, 11, 12, 15 identified as coldspot of functional diversity for at least one facet and site 3

hotspot of functional divergence. The detailed map is in Supp. mat. S13.

We selected 4 particular sites to better illustrate the patterns of diversity (Figure 6). The focus on detail phylogenetic tree and functional space allowed to classify types of sites. Sites 2 and 15 displayed the same patterns for the three components. They were characterized by a relatively high species richness for both methods. Considering phylogenetic diversity, the detected taxa were dispersed on the phylogenetic tree for both methods. In terms of functional diversity, the eDNA functional space almost included the whole functional space of trawling, which was also the case for the majority of sites (except 5 and 10, see Supp. mat. S14). These sites were characterised by high richness for all components in eDNA (see Table 2). Moreover, site 8 showed a total inclusion of taxa detected by trawling in the taxa detected by eDNA (same for site 9; see Venn diagrams Supp. mat. S10). Finally site 5 was dominated by trawling in terms of functional space (the shark *Hexanchus griseus* only detected in this site and by trawling enlarged the space), but the relatively low D-statistics indicated a high level of phylogenetic clustering of species detected by trawling. Even with this large functional space, we measured a slightly lower FD with trawling (FD = 5.44) than with eDNA (5.61) as FD takes into account the functional groups inside the functional space (and not only the most extreme ones).

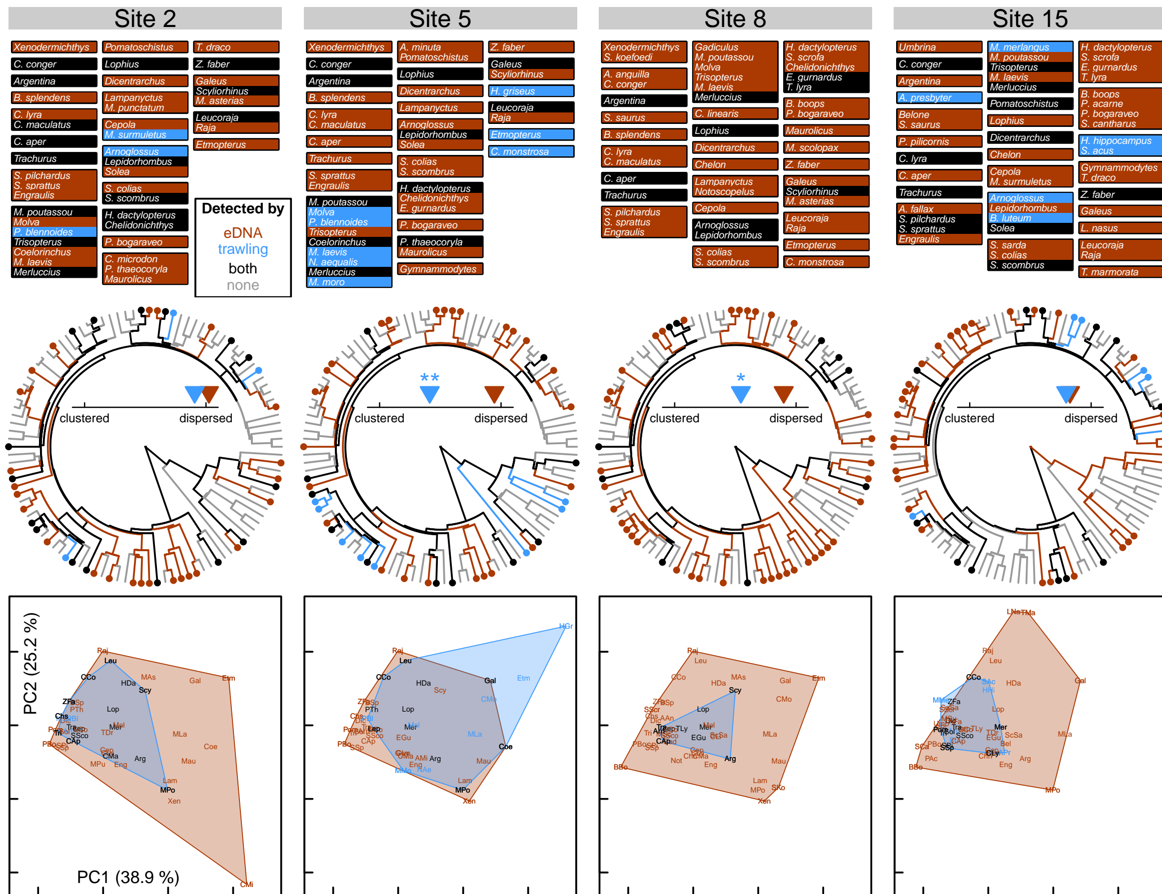

Figure 6: Taxonomic composition, phylogenetic tree and functional space of 4 given sites. The rule on phylogenetic tree corresponds to the D-statistics with significance test on dispersion of the detected taxa on the phylogenetic tree, with significance test (null hypothesis: taxa are randomly drawn on the tree).

3.3 β diversity

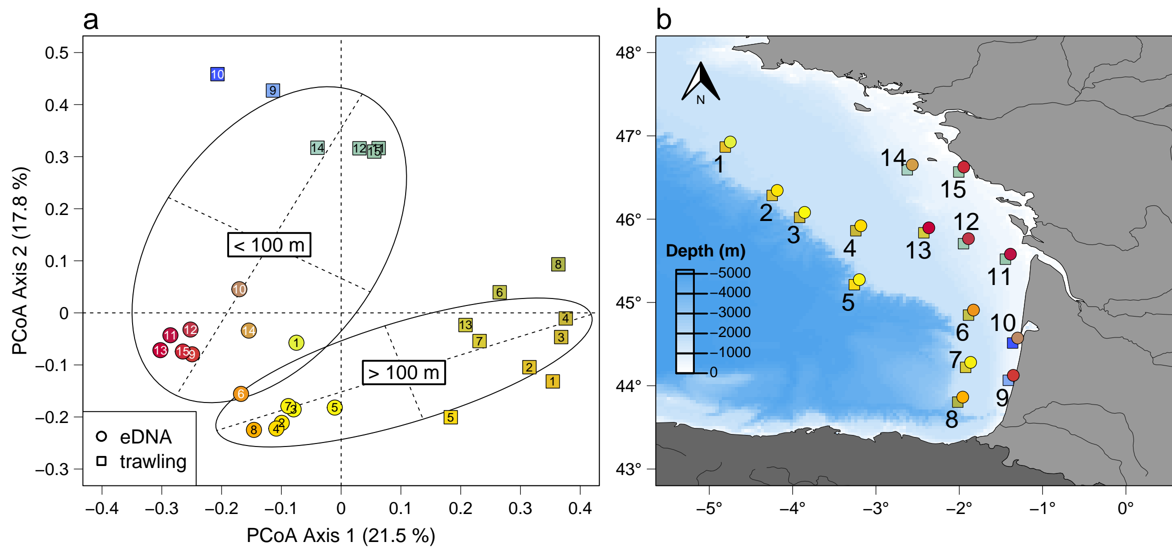

Figure 7: (a) Principal Coordinates Analysis (PCoA) of the species composition in eDNA filters (circles) and in trawling hauls (squares). Ellipses of dispersion of the points by depth criteria. (b) Geographical positions of the corresponding points. Colors of the points correspond to their position in the PCoA space, points with similar colors share a similar species composition.

Species composition between methods are discriminated in the PCoA space based on the Jaccard distance ; Figure 7a represents the first two axes and Supp. mat. S15 the third axis. eDNA and trawling points appeared to form disjoint sets on the PCoA plane but not on any axis taken separately. Points with deep or shallow bathymetry (above and below 100 m) formed almost disjoint ellipses of dispersion. The map Figure 7b shows the locations of the points with colors reflecting the position of communities in the PCoA space. With eDNA, there is a distinction between offshore sites (1 to 5 and 7 in yellow) and coastal sites (9 to 15 in orange-red). Sites 6 and 8 have intermediate colors. In trawling, the colors show a similar distinction with similar colors for sites 1 to 8 and 13 and for sites 9 to 12 and 14, 15. In trawling southern coastal sites 9 and 10 are distinguished from other coastal points which is not the case in eDNA. Site 13 is classified close to coastal sites in eDNA and offshore sites in trawling.

3.4 Abundance

We studied the distribution of the number of individuals N caught by trawling. We found that $\log N$ fitted well to an exponential distribution. For the number of reads R of each taxa in each site, we found that $\log R$ fitted well to a Weibull distribution. We transformed both of them to fit to a standard exponential distribution Supp. mat. S16. The correlation between transformed number of reads and transformed number of individuals was positive and significant ($p < 0.001$) but low ($r^2 = 0.15$; see Supp. mat. S17 scatter plot and regression

line). When restricted to a single common taxa (*e.g. Merluccius, Trachurus, Argentina*...), variable correlations were found. Among the 15 most frequent common taxa, 7 had a negative relationship between the transformed number of reads and the transformed number of individuals and 8 had a positive one. Almost none of the studied relationship was significant, but only a few points were considered here (< 15 sites) (see Supp. mat. S18).

4 Discussion

Several techniques exist to monitor marine diversity and in this study we compared the performance and selectivity of eDNA metabarcoding with classical bottom trawl surveys in the Bay of Biscay in terms of taxonomic, functional and phylogenetic diversity. We assessed their abilities to describe each fishes biodiversity components through their associated facets (richness, evenness and divergence). We also compared the variation in abundance between species and spatial patterns of diversity. We showed that eDNA was able to detect more taxonomic diversity than trawling with less sampling effort and that fish communities detected by eDNA can reliably reflect habitat differences. In terms of functional and phylogenetic diversity, performance of eDNA was better than trawling with eDNA being less selective than traditional survey and detecting taxa less clumped on phylogenetic trees at least for α diversity. For functional diversity however, trawling covered a broader space at the regional scale (γ diversity) than eDNA. We finally found positive associations between trawling abundance and eDNA number of reads, but this correlation remained too low to reliably use eDNA for quantitative surveys. These results suggested that trawling might be limited to correctly assess biodiversity and that eDNA metabarcoding can advantageously complete classical trawling surveys for fish biodiversity assessment.

4.1 More taxonomic diversity with eDNA

In this study we detected more taxa by eDNA. In each site, most taxa detected by trawling were also detected by eDNA and a majority of taxa were only detected by eDNA. This suggests that eDNA method is more sensitive than trawling, although eDNA sampling represents less effort than trawling as eDNA filtering only occurred at one point (only 60 L of water) whereas trawling haul covers $\sim$ 6 ha. This result is consistent with most studies concluding that eDNA metabarcoding can detect more taxa than classical methods (Aglieri et al., 2020; Polanco-Fernández et al., 2020), including trawling (Afzali et al., 2020; Fraija-Fernández et al., 2020; Liu et al., 2022) for comparable sampling effort. Aglieri et al. reported that eDNA can detect some species that can not be detected by visual census (*e.g.* pelagic and mobile fishes): In our case for example tunas (genus *Thunnus*) were never detected by trawling because they are pelagic fast fishes able to flee the trawler. eDNA is also able to detect rare and vulnerable species (Liu et al., 2022; Polanco-Fernández et al., 2020) and in our case eDNA highlighted the presence of some vulnerable species as the marbled electric ray (*Torpedo marmorata*), the shark spiny dogfish (*Squalus acanthias*), the ocean sunfish (*Mola mola*) that were not detected by trawling.

4.2 The importance of primers and reference database

eDNA metabarcoding is highly dependent on the reference database (Miya, 2022). In this study we used a custom database containing $\sim$ 11 000 species of $\sim$ 4 400 genus and $\sim$ 1 000 families: that must be compared to the more than 36 000 known species of fishes (Fricke et al., 2022). The 14 taxa detected by trawling and not by eDNA (see detail on community

matrix Supp. mat. S9) were either missing in the genetic reference database (5 of them: *Ammodytes marinus*, *Gaidropsarus macrophthalmus*, *Microchirus variegatus*, *Mora moro*, *Phycis blennoides* with the last 4 of them having no representative of the same genus). In this study we did not exclude from trawling the species missing from the database to account for eDNA weaknesses. An advantage of eDNA analyses is that we can store the unidentified sequencing output to later compare it to a more complete genetic reference database. The primer choice is also crucial for eDNA studies. Here we used the teleo primer (mitochondrial 12S region) which showed good performance in previous studies (Aglieri et al., 2020; Zhang et al., 2020), with good detection of Elasmobranchii. Polanco-Fernández, Richards, et al. suggest the use of two primers for better discrimination: teleo and MiFish-U since both primers have unequal performance for some clades depending on the variability of the targeted region of the genome. The use of both primers, although raising questions of data merging and cost, can improve the resolution of the assignations according to the authors of this study. Taxa detected by trawling and not by eDNA despite being present in the genetic reference database were rarely detected in our study (7 of the 9 remaining species were only detected in 1 site, 1 in 2 sites and 1 in 3 sites). Individuals caught by trawling and not by eDNA mostly came from coastal sites (we caught 92% of the individuals of those 9 species in sites 10 and 15). Collins et al., 2018 showed that DNA degrades 1.6 times faster in inshore regions than offshore regions. Our results are consistent with this phenomenon where DNA from detected species in those sites could have been degraded.

4.3 eDNA detects spatial gradients in fish communities

Communities of fish detected by eDNA were not only richer but also spatially structured. Despite the observed persistence of eDNA in marine waters (10 to 50 h, Collins et al., 2018) predicting a transport along large ranges, most studies indicate a strong localisation in eDNA signal with a spatial range of detection limited from tens to hundreds of meters (Miya, 2022). In Rozanski et al., 2022 and Polanco-Fernández et al., 2020, the authors could indeed discriminate species composition between protected and unprotected areas and between different habitats respectively in a relatively small region. In this study we also found strong gradient in species composition with depth and proximity to the coast thanks to a β dissimilarity analysis (Figure 7). This discrimination was stronger than the one found in Fraija-Fernández et al., 2020 with eDNA in the same region but this study used abundance (estimated from eDNA reads) to assess the community composition, which we did not because we proved eDNA reads provide a too weak estimation of fishes effective abundance. Gradients in species composition in the Bay of Biscay are already documented: Persohn et al., 2009 (for demersal fishes) show for example preference of coastal habitat for *Trisopterus luscus* juveniles, *Merlangius merlangus*, and offshore habitat for *Micromesistius poutassou*, *Chelidonichtys cuculus* and *Lepidorhombus whiffiagonis*. For pelagic fishes, Doray et al., 2018 highlighted a preference of *Engraulis encrasicaulus* and *Sprattus sprattus* for coastal sites *Scomber scombrus* for offshore sites. These species being however very frequent, they were detected by both methods in all types of habitats in our study. Community discrimination was mostly based on rare taxa in our survey, *e.g. Notoscopelus, Myctophum*

punctatum, Lampanyctus, Beryx splendens, Xenodermichthys detected in offshore sites and *Argyrosomus regius, Umbrina, Alosa fallax, Boops boops* mainly detected in coastal sites. This is probably due to our incidence approach, not taking into account the abundance of frequent taxa, which were detected in almost all sites. This discrimination was strong in spite of our aggregation methods that might decrease variability between sites. Some merged species can have different known habitats, for example we merged *Solea senegalensis* and *S. solea* due to ambiguous identification, the first one is found more frequently in southern habitats (Froese & Pauly, 2022). Similarly *Pomatoschistus lozanoi* and *P. norvegicus* should be more localized in northern Bay of Biscay than *P. minutus*, the three are merged into one taxa in this study. More generally, detections with eDNA may be ambiguous due to sequencing errors or low variations of the targeted gene, eDNA provides then only eDNA genus. In this study we assumed that all representatives of the genus are equally likely to occur for comparison purposes, but one could advantageously benefit from the information about occurrence provided by trawling surveys to infer the detected taxa from the frequencies of catch.

4.4 eDNA outperforms trawling in phylogenetic diversity

Our result suggest that eDNA metabarcoding covers a broader part of the phylogenetic tree than trawling. Overall phylogenetic diversity (PD) was higher when considering taxa detected by eDNA and SES-analysis showed that these taxa were overdispersed on the phylogenetic tree whereas taxa caught by trawling were not. This result is in line with Rozanski et al., 2022 where eDNA communities were overdispersed or not significantly clustered in terms of phylogenetic diversity. Our results indicated that eDNA detected a community which is closer to the effective community present in the region (at the γ level) whereas trawling detected species that were as phylogenetically rich as randomly sampled species. In terms of α diversity, this result was confirmed by only 1 site having clustering phylogenetic signal in eDNA and 6 sites having significant clustering phylogenetic signal in trawling according to the D-statistics. This was similar to the result in Polanco-Fernández et al., 2020 where the authors found that eDNA detects spread taxa on the phylogenetic tree compared to visual census of fishes in coral reef and concluded that eDNA metabarcoding community are more representative of the actual diversity in the field based on the same statistics.

4.5 Differences in functional selectivity

In terms of functional diversity, there was also a clear signal in favor of eDNA metabarcoding. At the scale of one site, the functional space covered by taxa detected by eDNA was larger and richer than the one formed by trawling, which was almost always included in the first one. This was not only due to the higher species richness of eDNA communities, as SES had less negative values with eDNA (4) than with trawling (10). No community had a higher functional diversity than a random model, as in Rozanski et al., 2022, suggesting that fish communities showed functional redundancy or that detection methods were selective or both. The hypothesis of detection method selectivity is supported by Aglieri et

al., 2020 who strongly identified distinct functional spaces for eDNA, fisheries observations and visual/video census in Mediterranean coastal fish communities. Among those methods, the authors reported less functional distinctiveness between species than expected by a random draw of species, but distinctiveness found by eDNA fall within the confidence interval whereas the three other methods tested led to a significantly lower functional distance between species than expected by null model. This study is therefore in line with the explanation of differential selectivity with the measurement method, with eDNA being the less selective. This is consistent with the frequencies of functional traits found in this study: We found DNA of more pelagic and bathypelagic species and less demersal species than the ones collected by trawling. eDNA also detected more fusiform and less flat fishes than trawling. This is likely due to the trawling technique: bottom trawl targets more fishes living in or close to the sea bed, explaining why trawling captures more flat fishes (*e.g.* Pleuronectiformes) than eDNA as their habitat is often in the sea bed. Pelagic fishes like *Mola mola*, *Thunnus*, *Pagellus* were almost only detected by eDNA although known to be abundant in the Bay of Biscay. In this study we chose to represent each genus by only one species (with multiple random draws) consequently this approach might reduce the actual functional diversity as only one species was chosen whereas there could be several species of the same genus co-occuring simultaneously, however we used the same taxonomic aggregation for both trawling and eDNA sampling methods.

4.6 Spatial patterns of biodiversity

Besides communities comparison, biodiversity studies also aim at characterizing spatial patterns of diversity, *i.e.* places with low or high diversity. In this study we addressed this issue with a local autocorrelation analysis (Getis & Ord, 1992). eDNA provided little information about hotspots or coldspots of diversity, with only one site (12) showing a signal of high taxonomic richness correlated with neighbor sites. Trawling revealed more spatial patterns with less diversity in north coastal sites and more diversity in sites closer to the continental slope. One limitation of our approach is that this analysis was limited by the number of sites. Indeed, sites were compared with several distant neighbors for the analysis, which may even include coastal, middle shelf and upper slope stations. However the analysis led with combining results of both sampling methods (Figure 5) revealed interesting hotspots and coldspots detection. Both cold and hotspots were more consistent within components and revealed coastal hotspot and offshore coldspot of diversity in the northern BoB. This result has been already observed at least for demersal communities in the region (Eme et al., 2022) and can be explained by coastal habitat being more diverse due to the presence of physical gradients and the proximity to estuaries (Ray, 1991). In spite of the low number of points, we have here identified spatial patterns with a systematical method (Getis-Ord statistics) when combining two methods (eDNA and trawling). eDNA is therefore an advantageous complement to trawling surveys as any method taken independently can only detect weak signal of spatial pattern of diversity.

4.7 eDNA provides a poorly reliable estimation of fish abundance

Biodiversity analyses also rely on quantitative data *i.e.* estimation on fish abundance to determine if ecosystems are dominated by a few species or not or to estimate fish stocks. There is no scientific consensus on whether eDNA can reliably assess species relative abundance in ecosystems (Lamb et al., 2018). Our results clearly indicated a positive and significant correlation between the number of fishes individuals caught by trawling and the number of eDNA reads in the same place. However, this relationship was not strong enough and the distributions of both measure were not equivalent. We found that the logarithm of eDNA reads followed quite well a Weibull distribution whereas the log of the number of individuals was similar to an exponential distribution. This suggests that a transformation should be done on eDNA reads before any abundance-based measure using this proxy (*e.g.* Hill numbers of order $q > 0$) because these measures are sensitive to abundance distributions. We think that this correlation was not strong enough to reliably use eDNA reads in this study to assess abundance of fishes. We even found a negative relationship between eDNA reads and number of individuals when restricted to some fish species. A larger-scale study should be held to further investigate this relationship and find whether these weak results can be explained by experimental random fluctuations. Even if trawling is considered as a standard technique for fish stock assessment, in some cases it is subject to some bias (Benoít & Swain, 2003) and might reveal only an estimation of the actual abundance, possibly explaining the differences with eDNA. This is however consistent with the literature where weak relationship were found between eDNA and abundance estimations (Fraija-Fernández et al., 2020; Lamb et al., 2018).(Stoeckle et al., 2020) reported a good relationship between relative biomass and number of reads with a log-scale. Under controlled conditions (*i.e.* aquarium), stronger relationships were found (Karlsson et al., 2022) but they involved quantitative PCR (qPCR), a more reliable way to quantify the DNA concentration in the filters than the classic PCR approach performed in this study. In the natural environment, quantity of DNA can be subjected to fluctuations caused by many factors: currents (Andruszkiewicz et al., 2019), fish behaviour (Bylemans et al., 2017). Lamb et al., 2018 performed a meta-analysis of several studies investigating a link between the number of eDNA reads and the abundance of taxa and concluded to a significant but weak correlation between both, suggesting quantitative analysis only based on eDNA must be taken carefully. For the next research, we therefore suggest to sample more points and to use qPCR to calibrate the samples with the total quantity of DNA. The ability of eDNA to reliably reflect relative or absolute fish or abundance is highly dependant on several biases such as eDNA capture technique, extraction method, choice of primer as noted in Rourke et al., 2021. The authors also pointed out the fact that the quantity of DNA released by individuals is driven by the species and the fishes life stage (spawning, migration, presence of juveniles tend to increase the amount of released DNA). This review concluded that eDNA is likely to be used as supplementary tool for abundance surveys.

5 Conclusion

Marine biodiversity studies for fish stock assessment or conservation purposes require reliable information about species distribution and abundance. eDNA metabarcoding is a rising method for multiple ecological and biological purposes. In marine ecology, several projects have tried to compare it to classical trawling surveys but only taxonomic diversity have been studied. In this work we added phylogenetic and functional diversity to the comparison to perform a spatial analysis on the three diversity indices and fish communities. The originality in this project relies on a more holistic approach to estimate the biodiversity including several components and facets of diversity, when comparing two methods of sampling in a scientific survey carried on at a regional scale. It relies on data from a single campaign in Bay of Biscay in 2019. eDNA metabarcoding targeted a common gene to fishes in the mitochondrial 12S region and was sampled on 15 sites in parallel with bottom trawl. Our analysis was based on taxonomic identification, but also included the phylogenetic and functional diversity components based on phylogenetic trees and functional traits respectively, associated with 106 identified taxa in the region.

We found that eDNA had a higher sensitivity than trawling in terms of taxonomic and phylogenetic diversity at any scale. Functional diversity was locally higher with eDNA but when considering all sites, we observed a slightly higher functional diversity with trawling. We identified clades or functional traits more targeted by eDNA than by trawling that allowed us to conclude on the selectivity of each method. We were able to discriminate communities by region or by depth with eDNA measurements as well as with trawling data. In terms of spatial diversity patterns, methods taken independently provided weak estimates of diversity hotspots and coldspots whereas combining both methods allowed detecting consistent diversity cold and hot spots in spite of the low number of sampling sites. Finally a quantitative analysis revealed insufficient evidence of the consistence between trawling estimates of abundance and number of eDNA reads. We suggest for future studies to integrate more eDNA sampling to the oceanographic campaign and to use a quantitative PCR technique to assess the total quantity of eDNA in each sample.

Our results showed that eDNA can be used to reflect incidence of fishes and to calculate the three components of diversity (taxonomic, phylogenetic and functional). We believe that eDNA measurements can successfully supplement trawling campaign with many advantages: It is more cost-effective, less invasive and requires less taxonomic expertise. As trawling measurements are still considered more reliable to assess abundance of some fish species, we suggest to use both of them in the future monitoring campaigns to benefit from their complementary advantages. Selectivity of one method taken alone is likely to lead to erroneous view of the ecosystem, which is an issue in the context of rapid loss of biodiversity, increasing demand for conservation and sustainable resources management.

List of terms

BoB Bay of Biscay.

EVHOE *Évaluation halieutique Ouest de l'Europe*, the measuring campaign of fish abundance in Atlantic, see page 11.

FD Functional diversity, value of the 0-order functional Hill number, represents the number of equivalent functional entities, see page 8.

FDiv Functional divergence, mean distance of taxa from the center of gravity in a functional space, see page 16.

FEve Functional evenness, length of the minimum spanning tree linking all species in a functional space, see page 16.

FRic Functional richness, volume of the convex hull in a functional space, see page 16.

Jac, Jne, Jtu Jaccard's dissimilarity index and its two additive components: nestedness and turnover, see page 17.

MPD Mean pairwise phylogenetic distance between species in a community, a measure of the phylogenetic evenness, see page 15.

PCoA Principal coordinates analysis, a statistical method to display points in a space based on a distance measure.

PD Phylogenetic diversity, value of the 0-order phylogenetic Hill number, represents the sum of all branch lengths in the phylogenetic tree, see page 15.

SES Standardised effect size, see page 16.

SR Species richness, number of different taxa, see page 8.

VPD Variance of pairwise phylogenetic distance between species in a community, a measure of the phylogenetic divergence, see page 15.

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Supplementary material

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Supp. mat. S1: eDNA extraction, amplification and sequencing protocol.

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 company following the protocol proposed in Polanco-Fernández et al., 2020. 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. The amplification mixture contained 1 U of AmpliTaq Gold DNA Polymerase (Applied Biosystems, Foster City, CA), 10 mM Tris–HCl, 50 mM KCl, 50 mM $MgCl_2$, 0.2 mM each dNTP, 0.2 µM of each primer, 4 µM human blocking primer and 0.2 µg μL^{-1} 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., 2014; 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.

Supp. mat. S2: Sequences treatment protocol and assignation protocol, taken from Polanco-Fernández, Richards, 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 the reads were assigned to each sample (ngsfilter program). 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 genetic reference database used in this study. 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 also applied a filter to remove rare detection (*i.e.* taxa identified in only 1 filter, in only 1 replicate of the PCR and with a number of reads smaller than 10% quantile of all reads) considering that these detections were probably associated to PCR or sequencing errors. Two genuses were removed with this filter (*Pegusa* and *Callionymus*). 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.

Supp. mat. S3: Aggregated taxa.

Taxa detected	Merged into
A., A. fallax	*Alosa fallax*
Anguilla	*Anguilla anguilla*
A., A. silus, A. sphyranea	*Argentina*
A., A. imperialis, A. laterna	*Arnoglossus*
B., B. capriscus	*Balistes capriscus*
B. B. belone	*Belone*
B., B. splendens	*Beryx splendens*
B. B. boops	*Boops boops*
C., C. aper	*Capros aper*
C., C macrophthalma	*Cepola*
C., C. cuculus, C. obscurus	*Chelidonichthys*
C., C. ramada	*Chelon*
C., C. caelorhincus	*Coelorinchus*
C., C. conger	*Conger conger*
C., C. linearis	*Crystallogobius linearis*
D., D. labrax, D. punctatus	*Dicentrarchus*
E., E. encrasicolus	*Engraulis*
E., E. spinax	*Etmopterus*
E., E. gurnardus	*Eutrigla gurnardus*
G., G. argenteus	*Gadiculus*
G., G. melastomus	*Galeus*
G., G. semisquamatus	*Gymnammodytes*
H., H. dactylopterus	*Helicolenus dactylopterus*
L., L. boscii, L. whiffiagonis	*Lepidorhombus*
L., L. circularis, L. fullonica, L. naevus	*Leucoraja*
L., L. budegassa, L. piscatorius	*Lophius*
M., M. muelleri	*Maurolicus*
M., M. merluccius	*Merluccius*
M., M. poutassou	*Micromesistius poutassou*
M., M. mola	*Mola mola*

Taxa detected	Merged into
M., M. molva, M. macrophtalma	*Molva*
M., M. surmuletus	*Mullus surmuletus*
N., N. elongatus, N. kroyeri	*Notoscopelus*
P., P. acarne, P. bogaraveo, P. erythrinus	*Pagellus*
P. P. lascaris	*Pegusa*
P., P. fluviatilis	*Perca*
P., P. blennoides	*Phycis*
P., P. lozanoi, P. minutus, P. norvegicus	*Pomatoschistus*
R., R. brachyura, R. clavata, R. microocellata, R. montagui, R. undulata	*Raja*
S. S. sarda	*Sarda sarda*
S., S. pilchardus	*Sardina pilchardus*
S., S. colias	*Scomber colias*
S., S. canicula, S. stellaris	*Scyliorhinus*
S., S. koefoedi	*Searsia koefoedi*
S. S. senegalensis, S. solea	*Solea*
S., S. cantharus	*Spondyliosoma cantharus*
S., S. boa	*Stomias*
T., T. thynnus	*Thunnus*
T., T. draco	*Trachinus draco*
T., T. mediterraneus, T. picturatus, T. trachurus	*Trachurus*
T., T. esmarkii, T. minutus	*Trisopterus*
U., U. canariensis	*Umbrina*
X., X. copei	*Xenodermichthys*
Z., Z. faber	*Zeus faber*

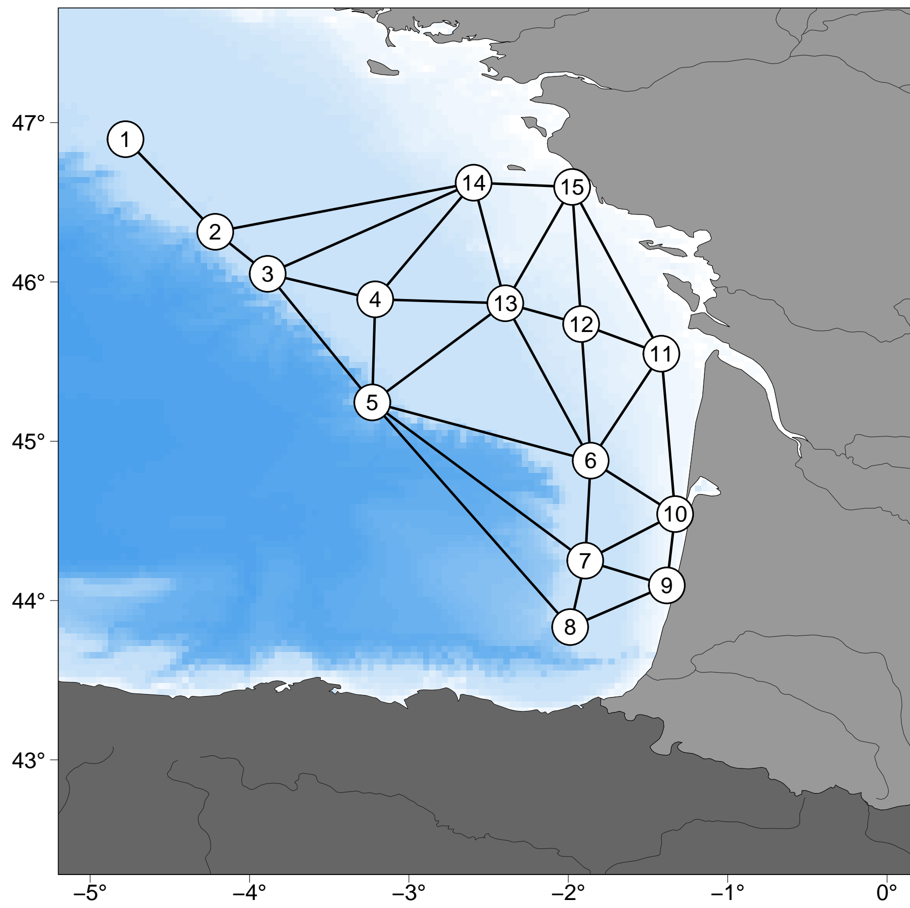
Supp. mat. S4: Traits table. Repro = reproduction mode (D: dioecism, A: protandry, G: protogyny, H: hermaphroditism), Fert = fertilization mode (E: external, I: internal, B: brood pouch), parental care (Y: yes, N: no).

	Max length (cm)	Average depth (m)	Depth range (m)	Trophic level	Environment	Body shape	Repro	Fert	Parental care
Alosa fallax	60	205	390	4	pelagic	fusiform	D	E	N
Ammodytes marinus	25	80	140	3,3	demersal	elongated	D	E	N
Anguilla anguilla	122	350	700	3,6	demersal	eel-like	D	E	N
Aphanopus carbo	151	1250	2100	4,5	bathypelagic	eel-like	D	E	N
Aphia minuta	7,9	48,5	97	3,1	pelagic	elongated	D	E	
Argentina silus	70	790	1300	3,3	bathypelagic	elongated	D	E	N
Argentina sphyraena	35	375	650	3,5	bathydemersal	elongated	D	E	N
Argyrosomus regius	230	157,5	285	4,3	demersal	fusiform	D	E	
Arnoglossus imperialis	25	185	330	3,8	demersal	flat	D	E	N
Arnoglossus laterna	25	105	190	3,6	demersal	flat	D	E	N
Arnoglossus rueppelii	15	491	812	4	demersal	flat	D	E	N
Arnoglossus thori	18	157,5	285	3,3	demersal	flat	D	E	N
Atherina presbyter	20	10	20	3,7	pelagic	elongated	D	E	N
Balistes capriscus	60	50	100	4,1	reef-associated	short/deep	D	E	Y
Belone belone	104	10	20	4,2	pelagic	elongated	D	E	N
Belone svetovidovi	41,8	10	20	4	pelagic	elongated	D	E	N
Beryx splendens	70	662,5	1275	4,3	demersal	fusiform	D	E	
Boops boops	40	175	350	2,8	demersal	fusiform	G	E	N
Borostomias antarcticus	30	1465	2330	3,6	bathydemersal	elongated	D	E	
Buglossidium luteum	16,4	227,5	445	3,3	demersal	flat	D	E	N
Callionymus lyra	30,5	217,5	425	3,3	demersal	elongated	D	E	N
Callionymus maculatus	16,5	347,5	605	3,3	demersal	elongated	D	E	N
Capros aper	30	370	660	3,1	demersal	short/deep	D	E	N
Cepola macrophthalma	80	207,5	385	3,1	demersal	elongated	D	E	N
Ceratoscopelus maderensis	8,1	765,5	1429	3,3	bathypelagic	elongated	D	E	
Chelidonichthys cuculus	70	207,5	385	3,8	demersal	fusiform	D	E	N
Chelidonichthys lastoviza	40	80	140	3,5	demersal	fusiform	D	E	N
Chelidonichthys lucerna	75,1	169	298	4	demersal	elongated	D	E	N
Chelidonichthys obscurus	50,5	95	150	3,7	demersal	fusiform	D	E	N
Chelon auratus	59	15	10	2,8	pelagic	fusiform	D	E	N
Chelon labrosus	75	7,5	15	2,6	demersal	elongated	D	E	N
Chelon ramada	70	15	10	2,3	pelagic	fusiform	D	E	N
Chimaera monstrosa	150	720	1360	3,5	bathydemersal	elongated	D	I	N
Coelorinchus caelorhincus	48	787,5	1395	3,5	demersal	elongated			
Coelorinchus caudani	36	1090	640	3,5	bathydemersal	elongated			
Coelorinchus labiatus	50	1340	1760	4	bathydemersal	elongated			
Conger conger	300	585,5	1171	4,3	demersal	eel-like	D	E	
Crystallogobius linearis	4,7	200,5	399	3,4	demersal	elongated	D	E	Y
Cyclothone microdon	7,6	2750,5	5101	3	bathypelagic	elongated	A		
Dasyatis pastinaca	69,5	102,5	195	4,1	demersal	ray-like	D	I	Y
Dasyatis tortonesei	80	150	100	4	demersal	ray-like	D	I	
Dicentrarchus labrax	103	55	90	3,5	demersal	fusiform	D	E	N
Dicentrarchus punctatus	70	55	90	3,9	pelagic	fusiform	D	E	N
Dicologlossa cuneata	30	235	450	3,3	demersal	short/deep	D	E	N
Dipturus intermedius	230	750,5	1499	4,1	demersal	ray-like	D	I	N
Echiichthys vipera	15	75	150	4,4	demersal	elongated	D	E	N
Enchelyopus cimbrius	41	335	630	3,5	demersal	elongated	D	E	N
Engraulis encrasicolus	20	200	400	3,1	pelagic	elongated	D	E	N
Etmopterus princeps	94	1256,5	1913	4,2	bathydemersal	elongated	D	I	
Etmopterus pusillus	50	560	1120	4,2	bathydemersal	elongated	D	I	Y
Etmopterus spinax	60	1280	2420	4,1	bathydemersal	elongated	D	I	Y
Eutrigla gurnardus	60	175	330	3,9	demersal	elongated	D	E	N
Gadiculus argenteus	15,3	550	900	3,6	pelagic	fusiform	D	E	N
Gadiculus thori	15	550	900	3,5	pelagic	fusiform	D	E	N
Gaidropsarus macrophthalmus	25	340	380	3,5	demersal	elongated	D	E	N
Galeus atlanticus	45	540	200	4	bathydemersal	elongated	D	I	
Galeus melastomus	75	964	1818	4,2	demersal	elongated	D	I	N

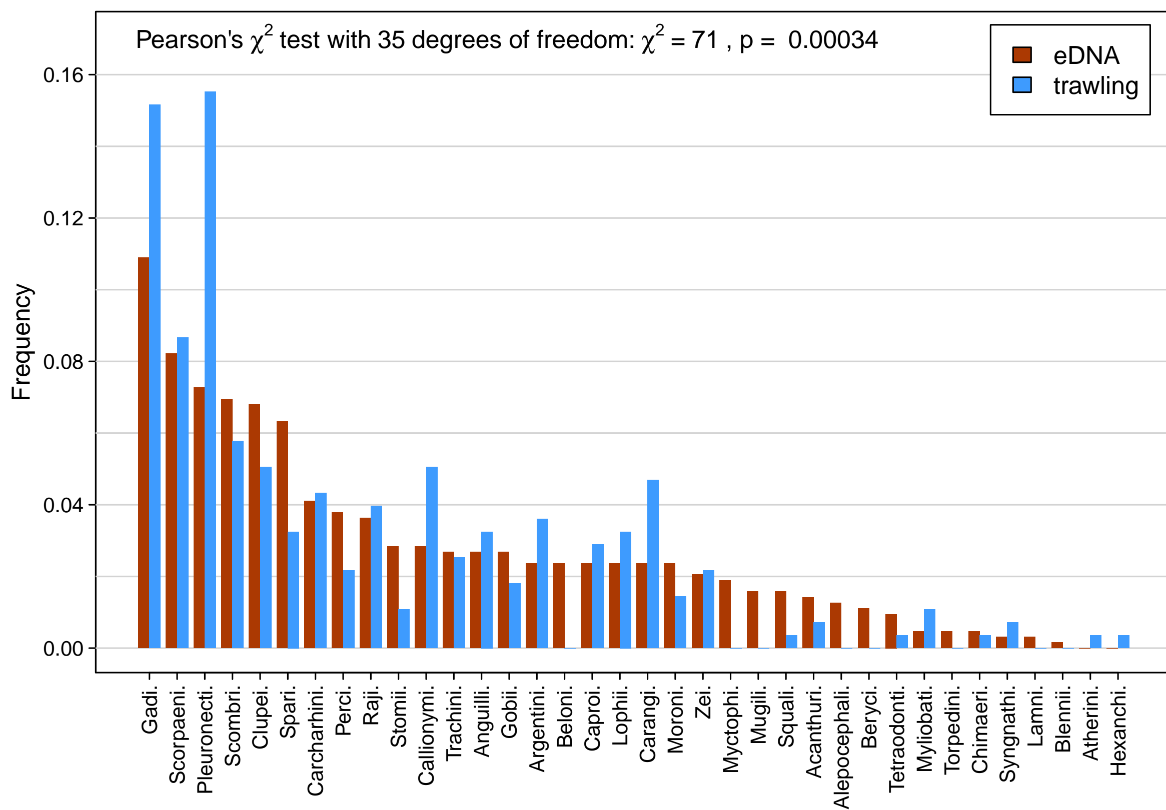
	Max length (cm)	Average depth (m)	Depth range (m)	Trophic level	Environment	Body shape	Repro	Fert	Parental care
Galeus murinus	63	837,5	725	4	bathydemersal	elongated	D	I	
Gymnammodytes cicerelus	17	60	120	3,4	demersal	eel-like	D	E	N
Gymnammodytes semisquamatus	30	65	110	2,7	demersal	elongated	D	E	
Helicolenus dactylopterus	50	575	1050	3,5	bathydemersal	fusiform	D	I	N
Hexanchus griseus	482	1250,5	2499	4,5	bathydemersal	elongated	D	I	Y
Hippocampus hippocampus	15	15	30	3,2	demersal	other	D	B	Y
Lamna nasus	350	680	1360	4,6	pelagic	fusiform	D	I	
Lampanyctus crocodilus	30	600	1200	3,2	bathypelagic	elongated	D	E	N
Lampanyctus festivus	13,8	546	1012	3,2	bathypelagic	elongated			
Lampanyctus intricarius	20	395	710	3,4	bathypelagic	elongated			
Lampanyctus macdonaldi	16	762	1404	3,1	bathypelagic	elongated			
Lampanyctus photonotus	8,5	570	1060	3,2	bathypelagic	elongated			
Lampanyctus pusillus	4,3	445	810	3,4	bathypelagic	elongated			
Lepidorhombus boscii	40	403,5	793	3,7	demersal	flat	D	E	N
Lepidorhombus whiffiagonis	60	400	600	4,3	bathydemersal	flat	D	E	N
Lepidotrigla dieuzeidei	20	328	536	3,7	demersal	fusiform	D	E	N
Lesueurigobius friesii	13	70	120	3,4	demersal	fusiform	D	E	
Leucoraja circularis	120	405	790	3,5	demersal	ray-like	D	I	N
Leucoraja fullonica	120	315	570	3,5	bathydemersal	ray-like	D	I	N
Leucoraja naevus	81	456	888	4,2	demersal	ray-like	D	I	N
Lithognathus mormyrus	55	75	150	3,4	demersal	fusiform	A	E	N
Lophius budegassa	100	541,5	943	4,4	bathydemersal	short/deep	D	E	N
Lophius piscatorius	200	510	980	4,5	bathydemersal	short/deep	D	E	N
Macroramphosus scolopax	20	312,5	575	3,5	demersal	short/deep	D	E	N
Malacocephalus laevis	60	600	800	3,8	bathydemersal	elongated			
Maurolicus amethystinopunctatus	5	765	670	3,1	pelagic	fusiform			
Maurolicus muelleri	8	897,5	1253	3	bathypelagic	elongated	D		
Melanostigma atlanticum	15	1126,5	1453	3	bathypelagic	elongated	D	E	N
Merlangius merlangus	91,5	105	190	4,4	demersal	fusiform	D	E	N
Merluccius merluccius	140	552,5	1045	4,4	demersal	elongated	D	E	N
Merluccius senegalensis	81	407,5	785	4,5	demersal	elongated	D	E	N
Microchirus variegatus	35	210	380	3,3	demersal	flat	D	E	N
Micromesistius poutassou	55,5	1575	2850	4,1	bathypelagic	elongated	D	E	N
Microstomus kitt	65	105	190	3,2	demersal	short/deep	D	E	N
Mola mola	333	255	450	3,3	pelagic	short/deep	D	E	N
Molva dypterygia	155	575	850	4,5	demersal	elongated	D	E	N
Molva macrophthalma	108	515	970	4,5	demersal	elongated	D	E	N
Molva molva	200	550	900	4,4	demersal	elongated	D	E	N
Mora moro	80	1475	2050	3,8	bathypelagic	fusiform	D	E	N
Mullus surmuletus	40	207	404	3,5	demersal	fusiform	D	E	
Mustelus asterias	140	175	350	3,6	demersal	elongated	D	I	
Myctophum punctatum	11	500	1000	3,4	bathypelagic	fusiform	D	E	
Myliobatis aquila	183	150,5	299	3,6	demersal	ray-like	D	I	
Nezumia aequalis	36	1260	2120	3,3	demersal	elongated	D	E	N
Notoscopelus bolini	10,2	650	1300	3,1	pelagic	fusiform			
Notoscopelus caudispinosus	14	180	360	3,2	bathypelagic	fusiform			
Notoscopelus kroeyeri	14,3	500	1000	3,2	pelagic	fusiform			
Pagellus acarne	36	270	460	3,8	demersal	fusiform	A	E	N
Pagellus bogaraveo	70	425	550	4,2	demersal	fusiform	A	E	N
Pagellus erythrinus	60	160	280	3,5	demersal	fusiform	G	E	N
Parablennius pilicornis	12,7	12,5	25	3,2	demersal	fusiform	D	E	
Pegusa lascaris	40	177,5	345	3,3	demersal	short/deep	D	E	N
Phycis blennoides	110	605	1190	3,7	demersal	fusiform	D	E	N
Polymetme thaeocoryla	21,6	806	1187	3,6	demersal	fusiform			
Pomatoschistus lozanoi	8	75	10	3,1	demersal	fusiform	D	E	
Pomatoschistus marmoratus	8	45	50	3,4	demersal	fusiform	D	E	
Pomatoschistus microps	9	6	12	3,3	demersal	elongated	D	E	

	Max length (cm)	Average depth (m)	Depth range (m)	Trophic level	Environment	Body shape	Repro	Fert	Parental care
Pomatoschistus minutus	11	102	196	3,2	demersal	elongated	D	E	Y
Pomatoschistus norvegicus	8	171,5	307	3,3	demersal	fusiform	D	E	
Pomatoschistus pictus	6	28	54	3,1	demersal	fusiform	D	E	
Prionace glauca	400	500,5	999	4,4	pelagic	fusiform	D	I	
Raja asterias	75	172,5	341	3,8	demersal	ray-like	D	I	N
Raja brachyura	120	195	370	3,8	demersal	ray-like	D	I	N
Raja clavata	105	512,5	1015	3,8	demersal	ray-like	D	I	N
Raja microocellata	87	60	80	3,9	demersal	ray-like	D	I	N
Raja miraletus	63	239,5	445	3,7	demersal	other	D	I	N
Raja montagui	83,5	269	522	3,9	demersal	ray-like	D	I	N
Raja undulata	100	125	150	3,5	demersal	ray-like	D	I	N
Rhynchoconger flavus	150	104,5	157	4,2	demersal	eel-like	D	E	
Sarda sarda	91,4	140	120	4,5	pelagic	fusiform	D	E	N
Sardina pilchardus	27,5	55	90	3,1	pelagic	fusiform	D	E	N
Sarpa salpa	51	37,5	65	2	demersal	fusiform	A	E	N
Scomber colias	55	500	1000	3,9	pelagic	fusiform	D	E	N
Scomber scombrus	60	500	1000	3,6	pelagic	fusiform	D	E	N
Scomberesox saurus	50	15	30	3,9	pelagic	elongated	D	E	
Scophthalmus maximus	100	45	50	4,4	demersal	short/deep	D	E	
Scophthalmus rhombus	75	27,5	45	4,4	demersal	short/deep	D	E	N
Scorpaena scrofa	50	260	480	4,3	demersal	fusiform	D	E	N
Scyliorhinus canicula	100	395	770	3,8	demersal	elongated	D	I	N
Scyliorhinus stellaris	170	200,5	399	4	reef-associated	elongated	D	I	N
Searsia koefoedi	15	975	1050	3,4	bathypelagic	elongated			
Serranus cabrilla	40	252,5	495	3,4	demersal	fusiform	H	E	
Solea senegalensis	60	38,5	53	3,3	demersal	short/deep	D	E	N
Solea solea	70	75	150	3,2	demersal	flat	D	E	N
Spondyliosoma cantharus	60	152,5	295	3,3	demersal	fusiform	G	E	
Sprattus sprattus	16	80	140	3	pelagic	fusiform	D	E	N
Squalus acanthias	160	730	1460	4,4	demersal	elongated	D	I	Y
Syngnathus acus	50	55	110	3,3	demersal	eel-like	D	B	Y
Thunnus alalunga	140	300	600	4,3	pelagic	fusiform	D	E	N
Thunnus albacares	239	125,5	249	4,4	pelagic	fusiform	D	E	N
Thunnus obesus	250	750	1500	4,5	pelagic	fusiform	D	E	N
Thunnus thynnus	458	492,5	985	4,5	pelagic	fusiform	D	E	N
Torpedo marmorata	100	186	368	4,5	reef-associated	ray-like	D	I	
Trachinus draco	53	75,5	149	4,2	demersal	elongated	D	E	N
Trachurus mediterraneus	60	250	500	3,8	pelagic	fusiform	D	E	N
Trachurus picturatus	60	337,5	65	3,3	demersal	fusiform	D	E	N
Trachurus trachurus	70	525	1050	3,7	pelagic	fusiform	D	E	N
Trachyscorpia cristulata	50	615	970	4,2	demersal	fusiform	D	E	N
Trigla lyra	60	425	550	3,7	bathydemersal	fusiform	D	E	N
Trisopterus esmarkii	35	175	250	3,2	demersal	fusiform	D	E	N
Trisopterus luscus	46	65	70	3,7	demersal	fusiform	D	E	N
Trisopterus minutus	40	220,5	439	3,7	demersal	fusiform	D	E	N
Umbrina cirrosa	73	50	100	3,4	demersal	fusiform	D	E	N
Umbrina ronchus	100	110	180	3,4	demersal	fusiform	D	E	N
Xenodermichthys copei	31	1375	2550	3,2	bathypelagic	elongated	D	E	
Zeus faber	90	202,5	395	4,5	demersal	short/deep	D	E	N

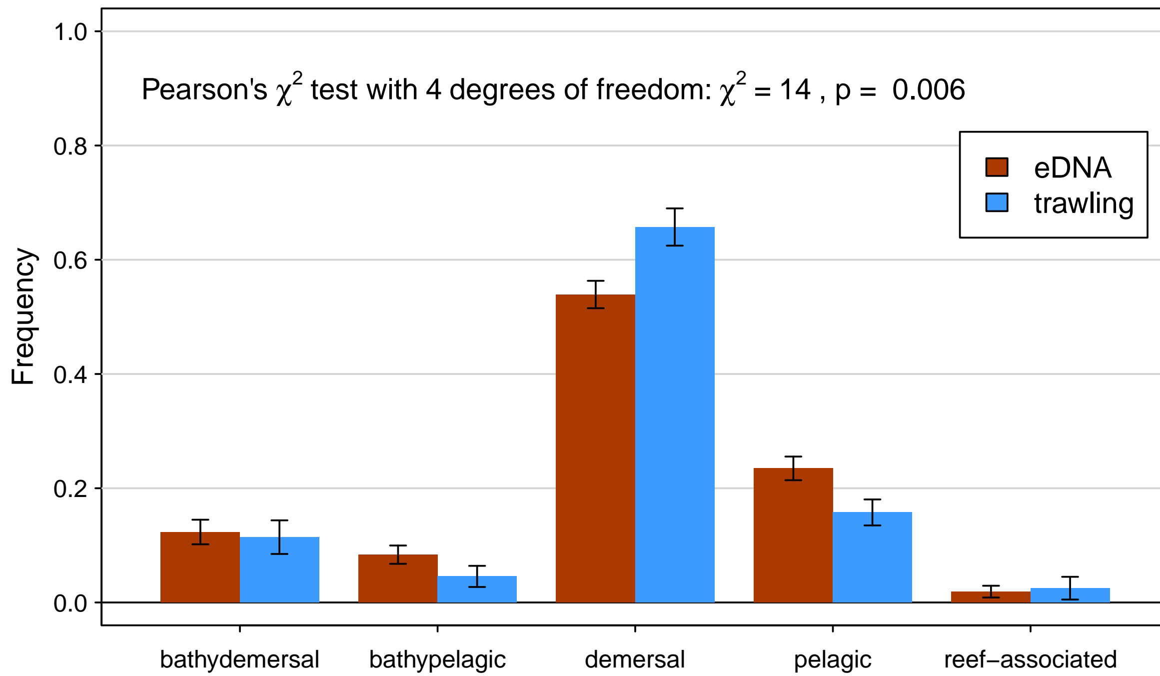
Supp. mat. S5: Connectivity graph of the neighbourhood used for the Getis-Ord analysis.

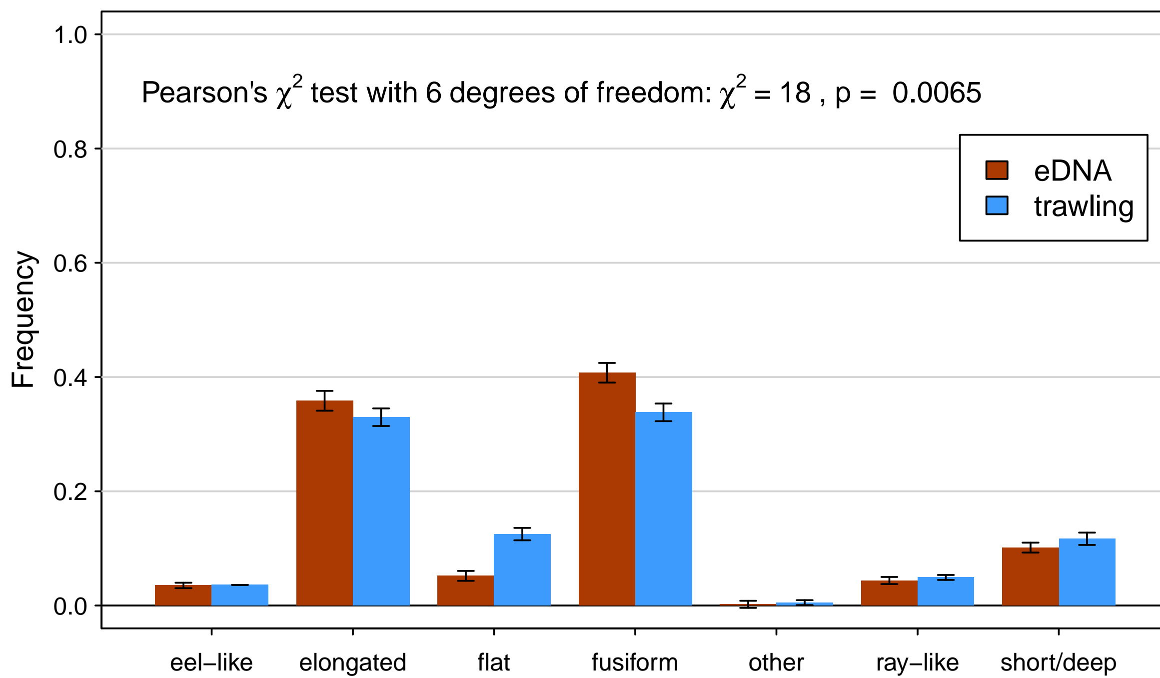


Supp. mat. S6: Detection frequencies of the fishes by order and by method. One occurrence corresponds to one taxa of each order detected in one site.

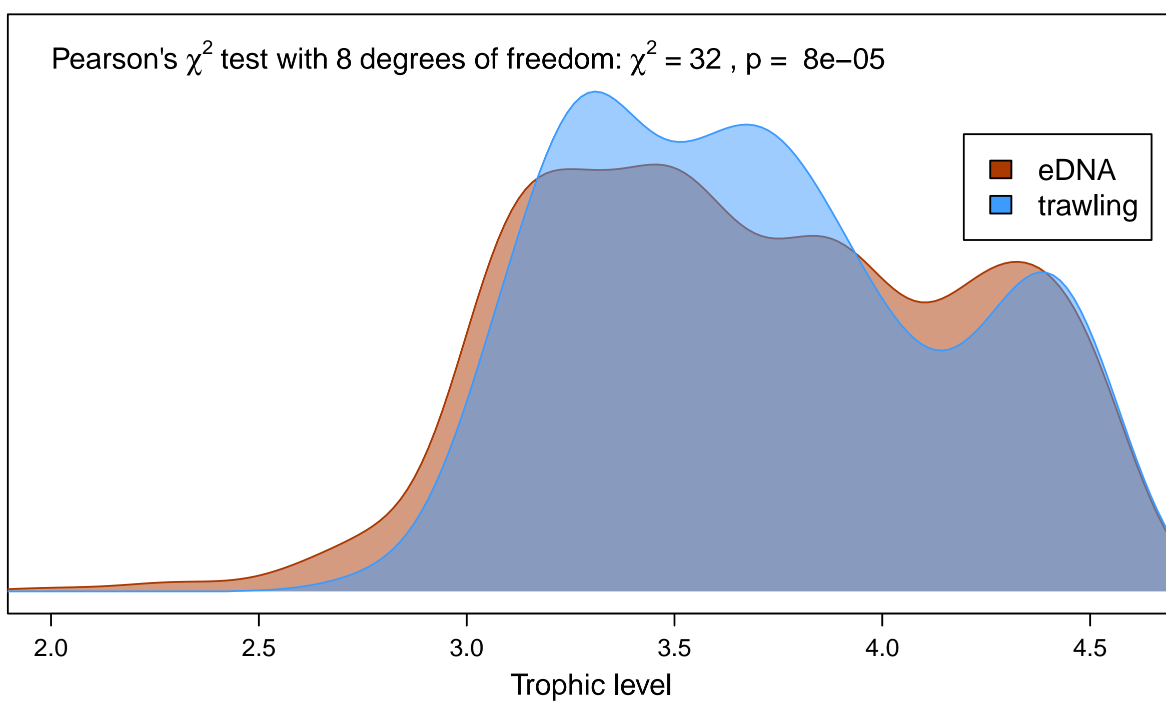


Supp. mat. S7: Environment and body-shape of fishes caught by eDNA and trawling. Error bars indicate the standard deviation due to the taxa detected at genus level for which an uncertainty on the traits can exist.

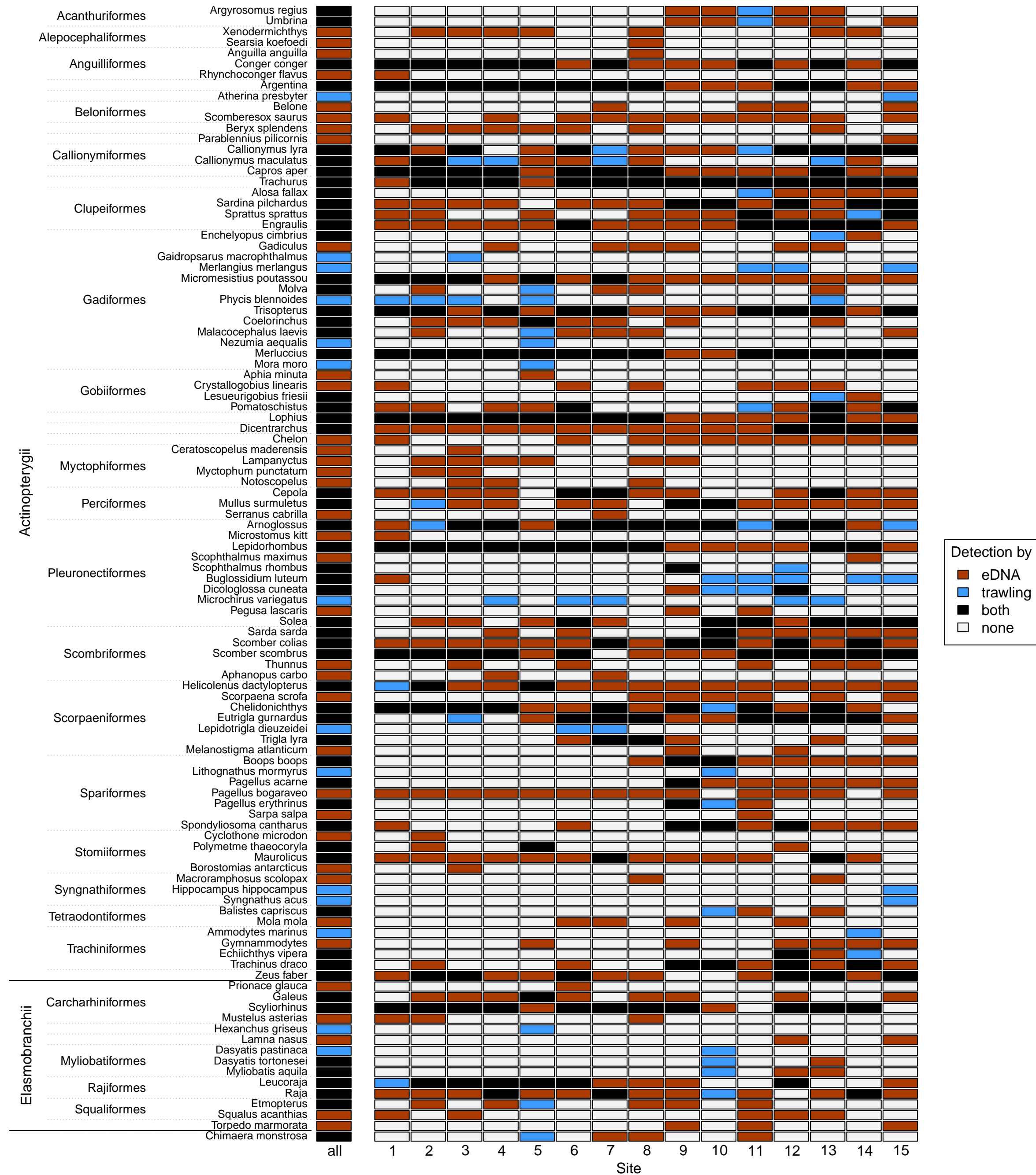




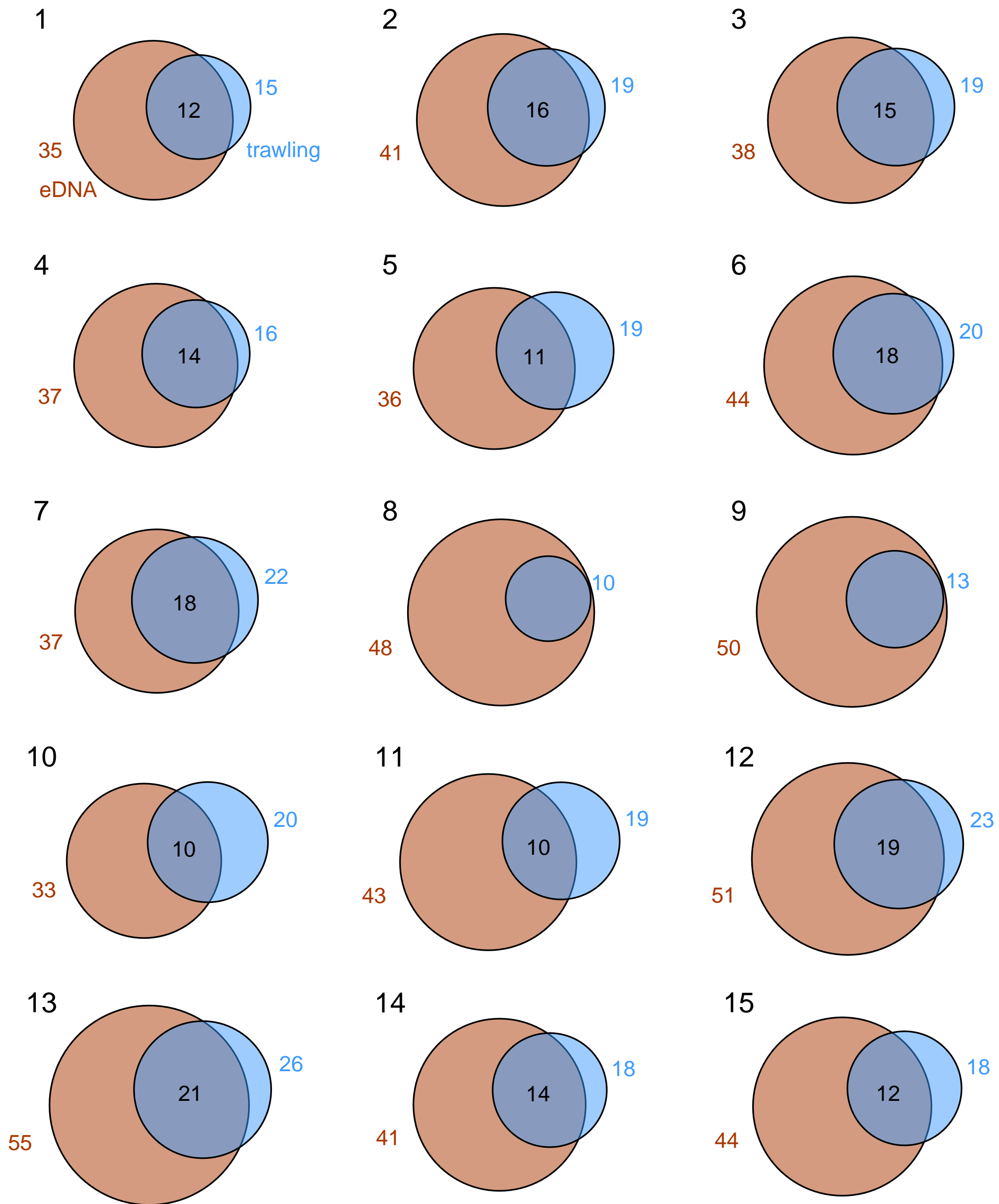
Supp. mat. S8: Density plot of trophic level of fishes caught by eDNA and trawling.



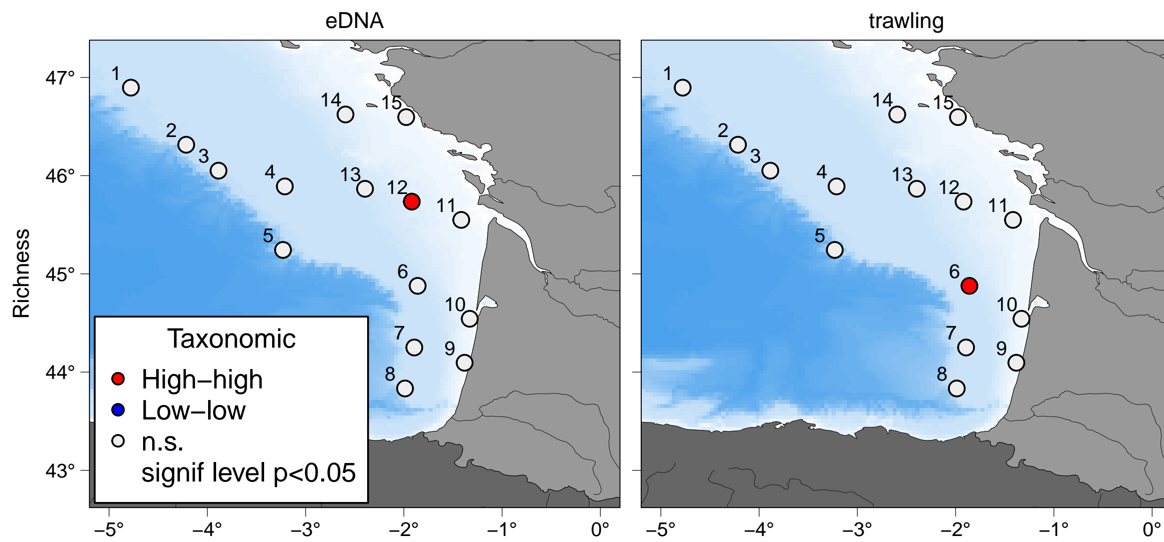
Supp. mat. S9: Community matrix of the detected taxa by site. Taxa are indicated with their class and order.



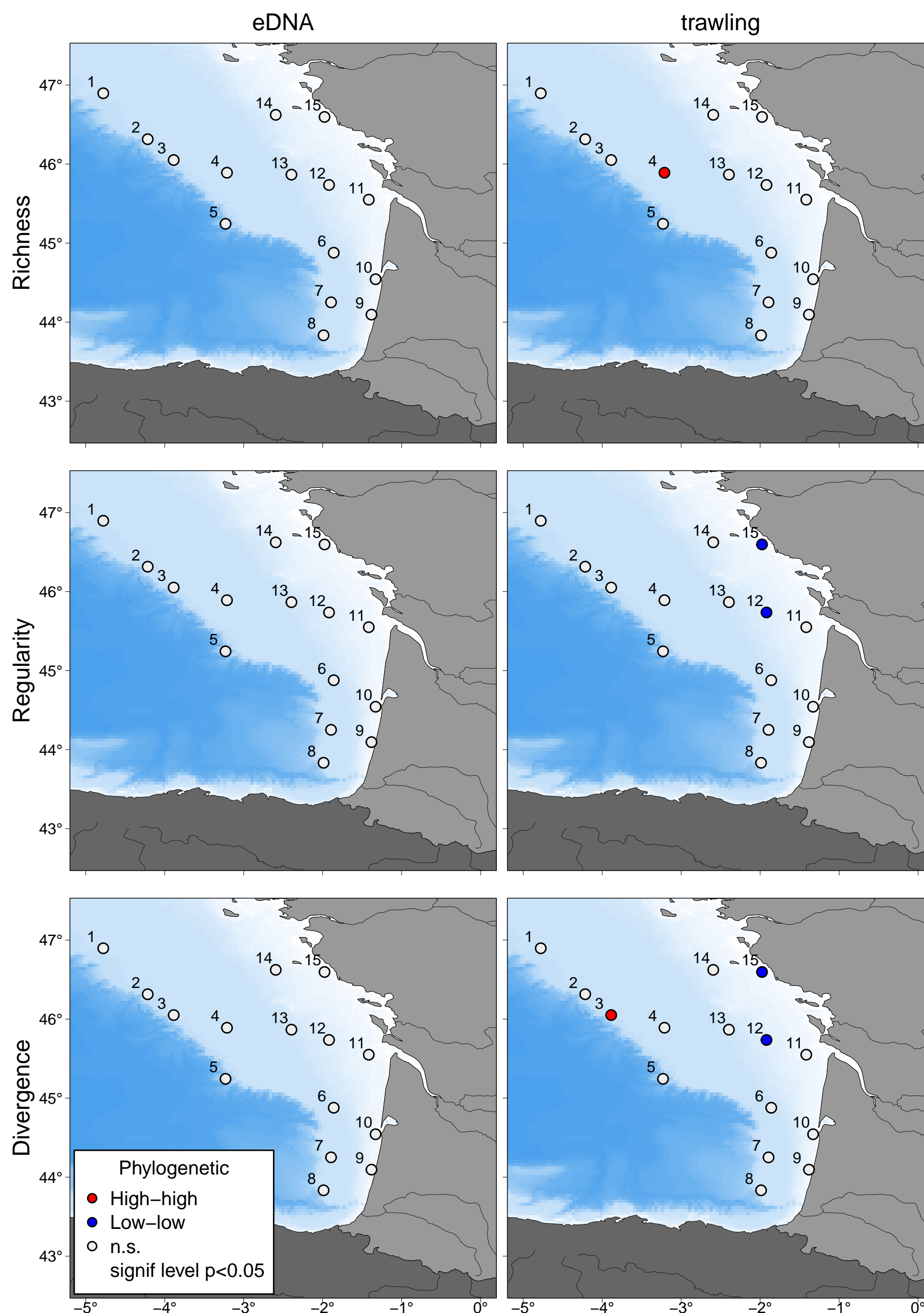
Supp. mat. S10: Venn diagrams of detected taxa, by site between eDNA and trawling with number of taxa.



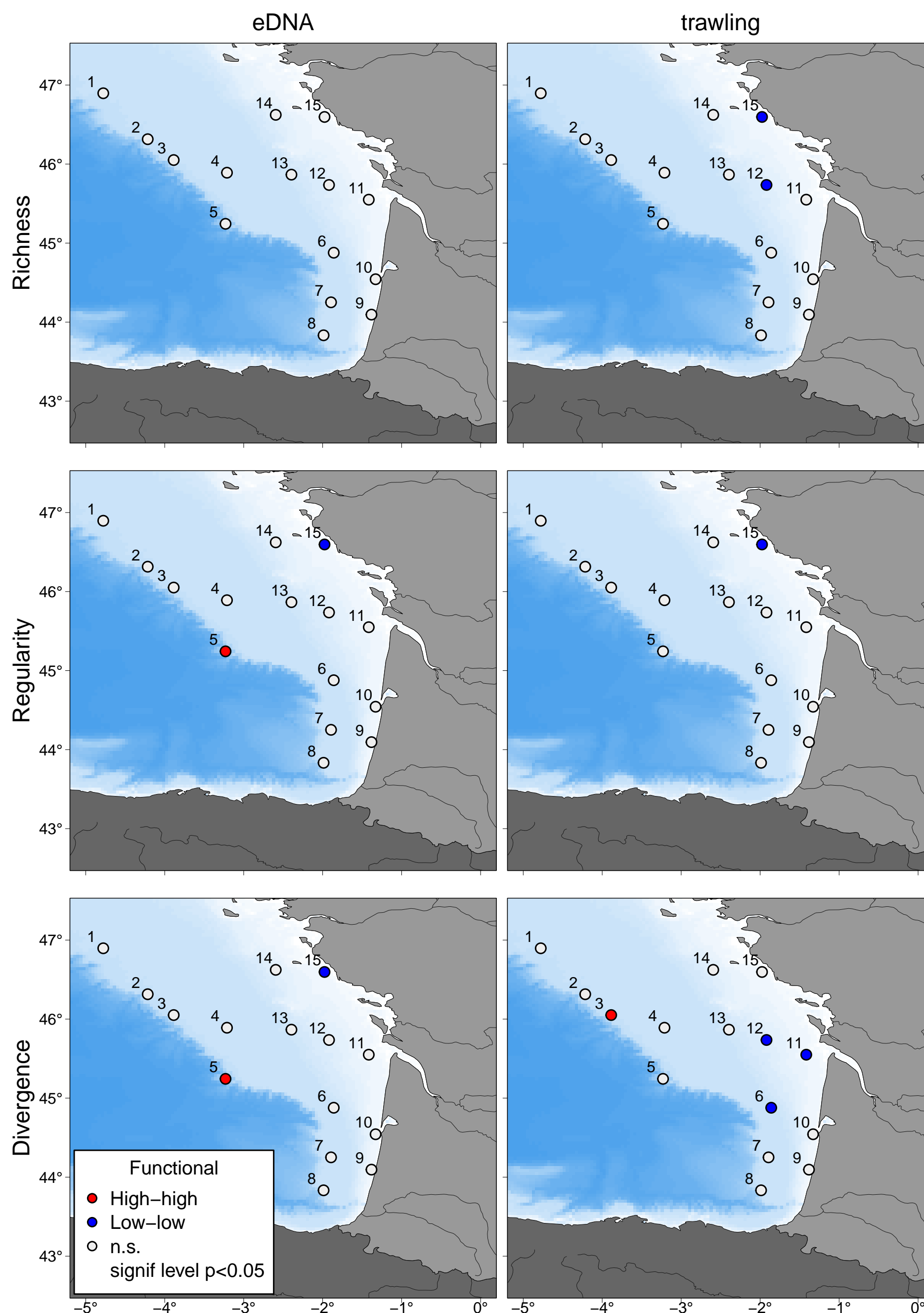
Supp. mat. S11: Significantly ($p < 0.05$) correlated values of **taxonomic** richness by method of detection, with the Getis-Ord statistics.



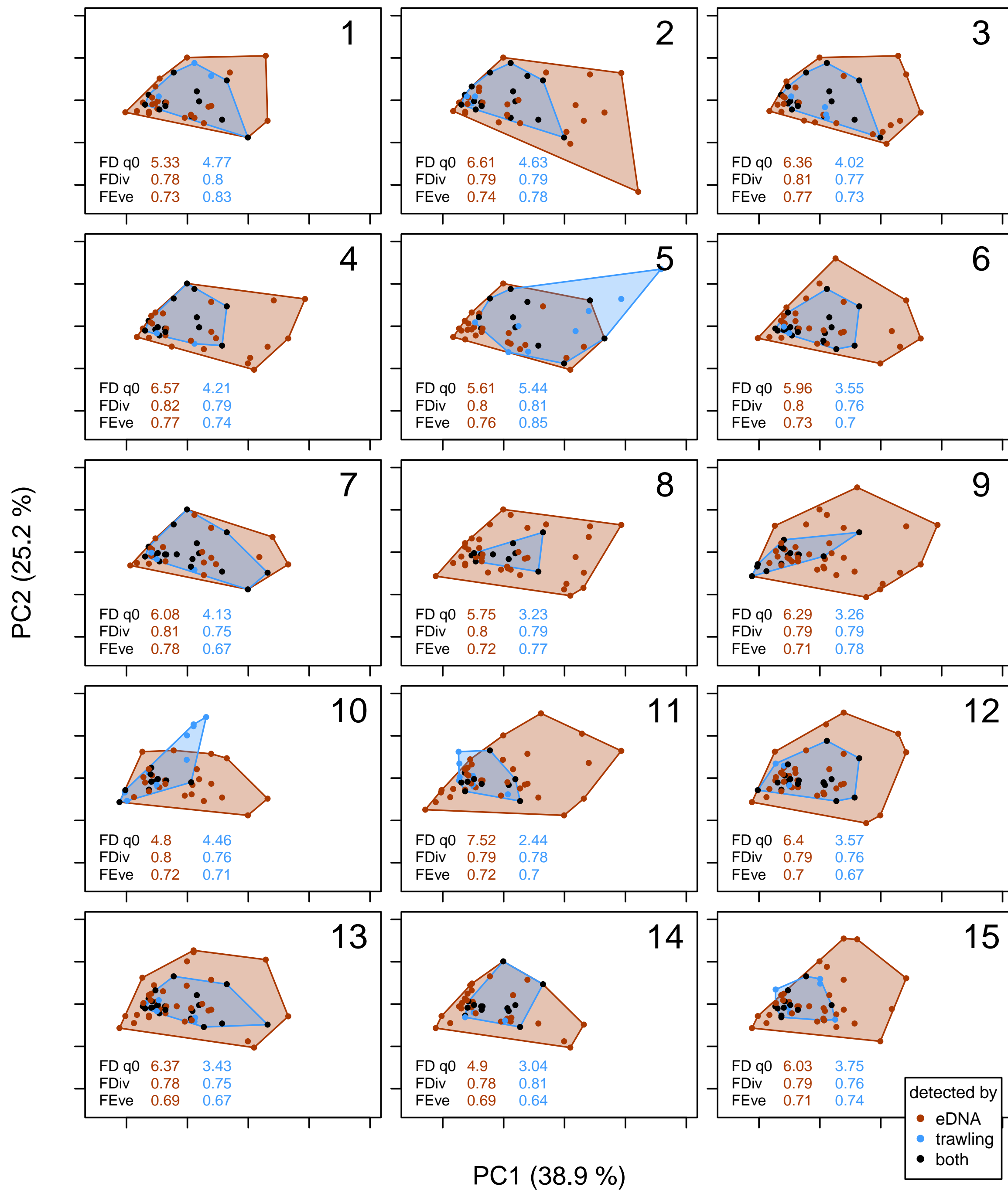
Supp. mat. S12: Significantly ($p < 0.05$) correlated values of **phylogenetic** indices of diversity by method of detection, with the Getis-Ord statistics.



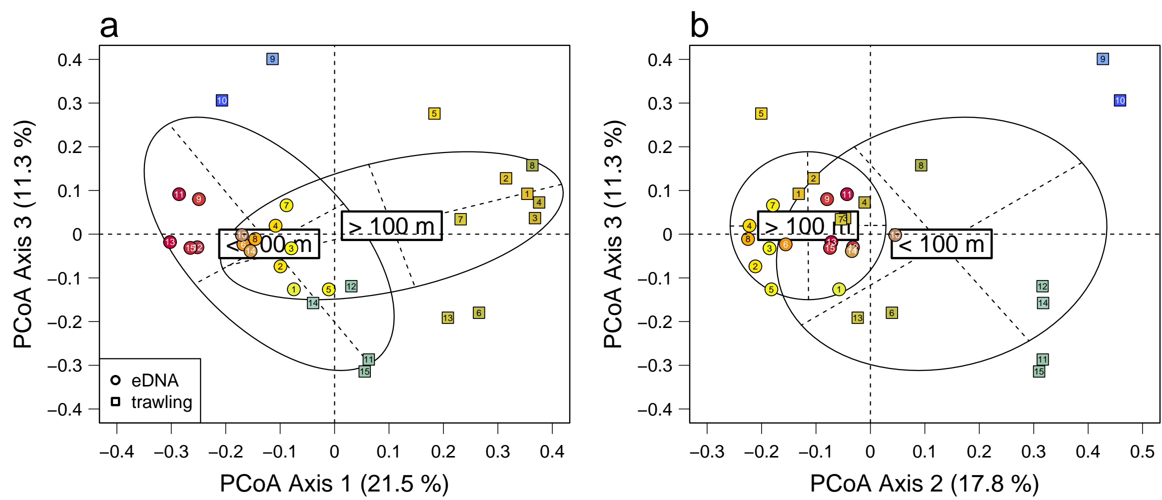
Supp. mat. S13: Significantly ($p < 0.05$) correlated values of **functional** indices of diversity by method of detection, with the Getis-Ord statistics.



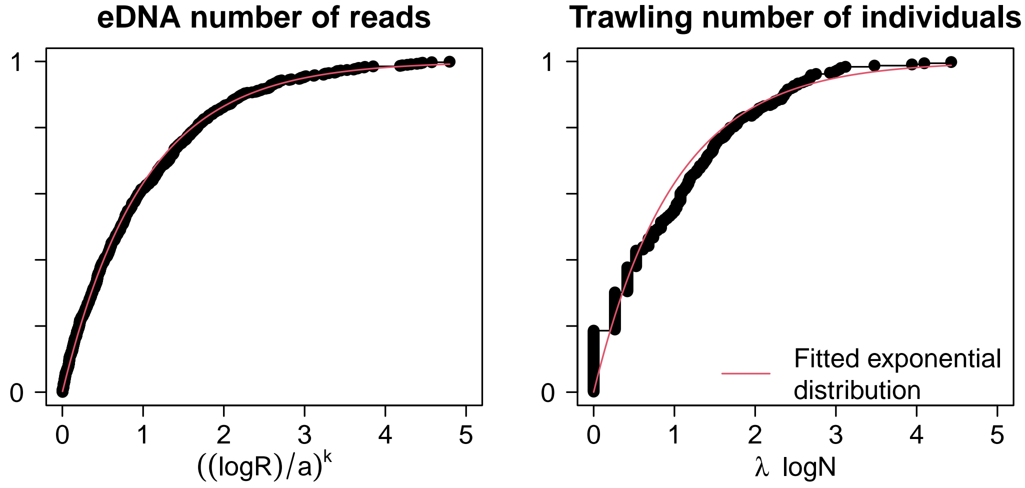
Supp. mat. S14: Functional space (first two axes of PCoA) by site by detection method (eDNA and trawling) and associated functional measures of richness (FD), evenness (FEve) and divergence (FDiv).



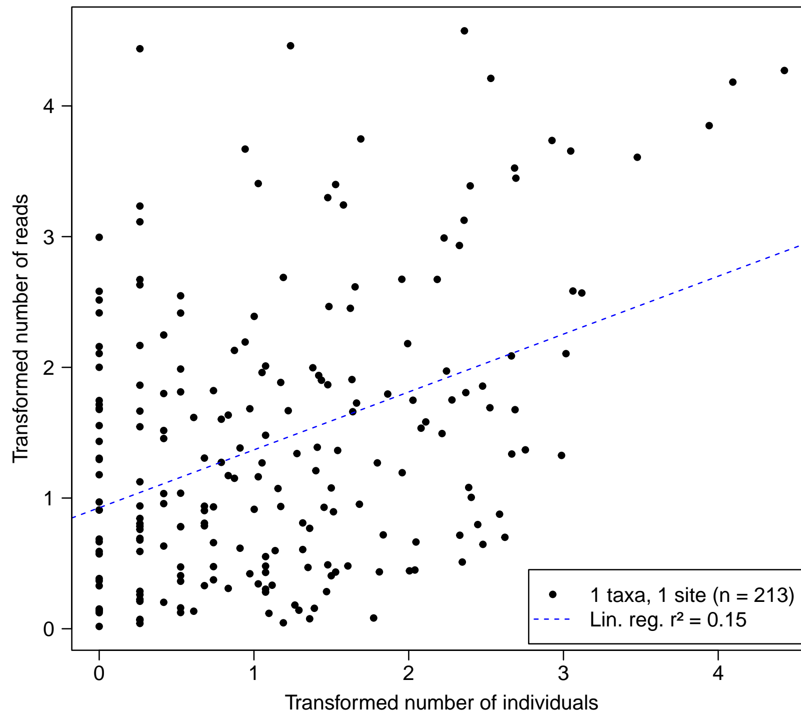
Supp. mat. S15: PCoA axes 1, 2 and 3 (50% of inertia) of species composition in trawling and eDNA sampling points, with ellipses of dispersion by depth criteria. (a) Axis 1 and 3 (b) Axis 2 and 3. Colors are the same as in Figure 7.



Supp. mat. S16: Cumulative density functions of the number of eDNA reads and the number of individuals after transformation to fit an standard exponential distribution. Parameters: $a = 9.32$, $k = 4.38$, $\lambda = 0.380$.



Supp. mat. S17: Transformed number of eDNA reads compared to transformed number of individuals caught by trawling and linear regression (intercept 0.93, slope 0.439, $p < 10^{-8}$). Each point corresponds to a site and a fish.



Supp. mat. S18: Transformed number of eDNA reads compared to transformed number of individuals caught by trawling for the 15 more frequent taxa in site where they are both detected and associated linear regressions.
s: slope, ** ($0.001 < p < 0.01$), * ($0.01 < p < 0.05$) and ns ($p > 0.05$) indicate the significance of the linear model. *M. poutassou* is *Micromesistius poutassou.*