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titre

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1 Structure and dynamics of ecosystems: how can species coexist in same environment?

Of all the questions raised when it comes to study Nature, the most common yet complex one is "how do organisms and environment interact with each other?" (Sutherland *et al.* 2013). In other words, what are the processes and rules that define structure and functioning of ecosystems? Taken as a whole, an ecosystem can be seen as a giant network: all individuals from every species are linked to one another through intra- and inter-specific relationships, that implies competition, parasitism, predation…; and each individual is linked to its physical environment, on which it depends for food prospection, shelter and/or favorable conditions for breeding. The main purpose of ecology is to study those links and ultimately, to be able to map the central relationships and flows that are keys to maintain stable ecosystems (Albouy *et al.* 2011). Community ecologists, regardless of the ecosystem they are studying, try to answer some fairly similar questions such as "how do species share environmental resources?" or "how can species relying on the same resource to thrive and survive can coexist?". Indeed, the mere observation that species can live and develop a population without encroaching each other suggests that, even if species compete to access the same resources, the use of resources is balanced and allows stable relationships between species to develop. Most of all, if species depend on the same resources to survive, how can diversity within an ecosystem last over time?

2 Concepts and definition for studying ecosystems' dynamic.

To answer those questions, the structure and dynamic of ecosystems need to be investigated and ecological concepts must be defined.

First, a "community" is made up of all living organisms (all species combined), which interact and occupy a specific habitat. Within this habitat, the concept of "ecological niche" reflects the fact that distinct populations use differently space and trophic resources to meet their needs. In 1917, Grinnell was the first to scientifically as "ecological niche" all the requirements that a species needs to thrive (Grinnell 1917). This concept covers both biotic (food abundance and availability, competition within and among species, predation-prey relationships …) and abiotic conditions (environmental factors such as temperature or pression, shelter availability …), and it shapes the areas suited for species according to their needs. This definition is refined by Hutchinson (1957): resources and their availability are the main drivers for the coexistence of species, since resources are essential for species to thrive and are therefore considered limiting factors. Furthermore, Hutchinson's definition distinguishes the concepts of (i)"fundamental niche", which is a potential niche for a given species that offers all the optimal conditions for that species to flourish and (ii) "realized niche", which corresponds to the actual resources used by

a species and which is often smaller than the fundamental niche, mainly because of competition between species. If resources are limited, competition between species that seek to simultaneously exploit the same resources may arise, either because they hunt the same prey or because they live in the same specific habitat and are therefore more likely to meet (Blondel & Bourlière 1979). When the resources are abundant enough, species may be able to share it without entering competition (Nagelkerke *et al.* 2018). According to competition theory, community structures are defined by the way species are able to share or not resources. Therefore, to study the structure and dynamics of community and to identify the main factors that enable species to coexist, it is essential to determine the degree by which species share resources, in other words, quantify the overlap between ecological niches (Geange *et al.* 2011).

3 Tools to study diversity in ecosystems and their limits

Niche overlap can be approached from the habitat (beta overlap) or food (alpha overlap) perspective (Mouillot *et al.* 2005). In both cases, a high degree of overlap means that the species are likely to compete for the same resources making their coexistence virtually impossible. Conversely, a low deree of overlap tends to suggest that species, even if they rely in part on the same resources, have a sufficiently wide range of accessible resources not to compete with each other (Mouillot *et al.* 2005). No overlap means that species occupy distinct niches, are likely to use very different resources and that no competition is expected (see 1. This approach has been widely developed over the last decades to study the distribution of abundance and the mechanisms favoring species coexistence, in particular to predict the impact of disturbances, such as the introduction of invasive species or climate change (Albouy *et al.* 2011; Geange *et al.* 2011; Martini *et al.* 2020).
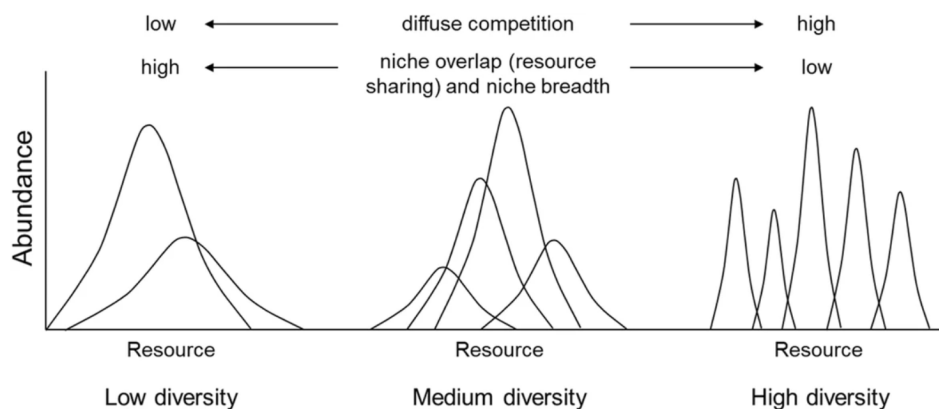

Figure 1: Caracteristics of niches along a resource gradient at different levels of species diversity, from Kim & Ohr (2020).

To quantify niche overlap, several indices have been developed since the 60's. Indices and threshold values are commonly used for studying specific, taxonomic or phylogenetic diversity.

However, used alone, a result of diversity estimation through any index is usually poor and inaccurate, because complex and rich systems can not be described only by the result of a computation (Mejri 2009). Indeed, four of the best-known niche overlap indices, which are based on the intensity of utilisation of a resource use by species, were compared by Linton *et al.* (1981) to assess the precision and accuracy: Morisita (1959) updated by Horn (1966), Schoener (1968) and Pianka (1973). Even if they lead to the same general conclusions, these four indices often give different results, because they use different computation parameters (Blondel & Bourlière 1979). Moreover, they are often highly sensitive to sample size, which adds uncertainty when it comes to interpreting their values (Linton *et al.* 1981). Finally, Grossman (2009) points out that threshold values for those indices can be considered as arbitrary and might differ from one ecosystem to another, leading to an impossibility of comparing them. For all these reasons, using those indices to estimate if species share or not the same resources, and if so, how much is shared, does not seem relevant (Mouillot *et al.* 2005). As such, they provide a qualitative assessment of the overlap rather than a quantitative one (Linton *et al.* 1981).

Therefore, to understand how the structure and the dynamics of an ecosystem are defined and how such complex relationships can last for several generations, numerical models are often used (see Ecopath models, `https://ecopath.org`). This approach requires a simplification of the ecosystem, because simulating very complex models make the outcome virtually impossible to compute (Albouy *et al.* 2011). Simplifying an ecosystem can be done in many ways: focusing on specific compartments of the ecosystem (*e.g*: pelagic or benthic fauna), grouping species based on their trophic level, or taxonomy or similaire behavior … Obviously, simplifying with any of these methods comes down to approximating the relationships and much of the complexity of an ecosystem, but if done properly, models are still able to produce reliable simulations of what is going on in real life (Albouy *et al.* 2011; Evans 2012; Piroddi *et al.* 2015). Yet, the main difficulty is to determine the criteria that are relevant to gather species and to simplify models. Whether they are too restrictive, or not enough, these criteria condition not only the accuracy of the model, but also its ability to be generalized (Moon *et al.* 2017; Pease *et al.* 2015; Pont *et al.* 2006). For instance, if a model uses a taxonomic grouping of species, it will only be suited to study other ecosystems that contain the ame set of species or taxonomic groups. Its transposition to other unrelated ecosystems will thus be limited, if not impossible (Moon *et al.* 2017). In the end, this modeling approach imposes a specific model for each ecosystem, which is highly time consuming and limits the possibilities of comparisons between ecosystems (Martini *et al.* 2020; Mcgill *et al.* 2006). Therefore, this approach remains very specific to a studied ecosystem and the species that compose it.

4 Emergence of a more global approach based on functional traits.

4.1 General overview

Community ecology aim to establish general rules explaining the functioning of communities. Species-centred approaches only provide information for a few specific systems but not general principles, that can be applied to a wide variety of communities or ecosystems (Albouy *et al.* 2011; Martini *et al.* 2020). Therefore, ecologists had to find a way to study ecosystems, to (i) give clues of how species interacts with each other and (ii) to assess how strongly species are related to their environment. Indeed, some scientists emphasized the urge to get rid of methods that were highly dependent of species, time or space, such as the ones described previously, and to use a more predictable and quantitative science that could play a major role in assessing global changes issues (Brind'Amour *et al.* 2011; Mcgill *et al.* 2006; Olden & Jackson 2002). To this extend, Mcgill *et al.* (2006) define a **trait** as a "well-defined, measurable property of organisms, usually measured at the individual level and used comparatively across species" and suggest that community ecology should try to understand how these traits interact with fundamental niches to define realized niches. The notion of "trait" has been widely used in the literature, but with slightly different meanings. For instance, Violle *et al.* (2007) defined a trait as "any morphological, physiological or phenological feature measurable at the individual level, from cell to whole organism". To ensure a consistent approach to community ecology studies, Martini *et al.* (2020) suggests that the definition of Violle *et al.* (2007) is precise enough, that it should serve as a reference and therefore should be used systematically. Yet, not all measurable traits provide the same information: for ecologists, traits that inform about (i) the interactions between species and the environment and (ii) the fitness of individuals are the most valuables (Kremer *et al.* 2017). These specific traits are defined as "functional traits" and can relate to behavior, life history, morphology or physiology, influencing the general performances of organisms Martini *et al.* (2020); Mcgill *et al.* (2006). They provide information on the main functions of organisms, such as acquisition of food or locomotion (Mejri 2009).

4.2 Improvement of the method over the years

The functional-traits approach was first developed in studies based on terrestrial plants. They showed that the morphology of species was correlated with their environment and that changes in their habitat could lead to changes of their morphology because this approach relies on the plasticity of traits (Boissezon 2014; Lavorel *et al.* 1997; Martini *et al.* 2020). Applied to aquatic animals, structure-function relationship has been well documented since the 1970s (Gosline 1971; Lagler *et al.* 1977; Webb 1984) and approaches based on morphological traits seemed suitable to compare species (Norton 1995) or to explore niches and compare communities (Winemiller 1991). For instance, Albouy *et al.* (2011) developed a model to determine the diet of any marine species based on morphological traits, and thus establish trophic guilds. Yet, the

model could not predict diet overlap nor resource partitionning among species, because of intrinsic variability in the diet of fish. Indeed, morphology alone is hardly a clue to determine diet, for generalist species are able to switch prey depending on which is more abundant, and they do not display specific morphological traits (Sibbing & Nagelkerke 2000). Moreoever, trophic level impacts how specialised a species can be in terms of diet: apex predators will often favor one feeding strategies among others, so they are very efficient for one strategy, and have limitating capacities in others. This principle can be summed up as a "trade-off strategy": greater abilities for one strategy lead to a decrease of abilities in other areas Norton (1995), because of morphological specificities (Nagelkerke *et al.* 2018).

While the flexibility and intrinsic variabiliy of species should not be ignored, they can be hard to predict (Diderich 2006; Martini *et al.* 2020). It is therefore essential to identify and select relevant traits, that can be used to explain most interactions between species and their environment. This is one of the main challenges of the functional traits approach, because the selected traits must be sufficiently variable beteen the levels being compared (species, populations, individuals …), and the observed variations must explain the actual differences in fitness or coexistence of species (Kremer *et al.* 2017).

Yet, the flexibility in traits is what makes this approach so useful, as it allows for the quantification of intraspecific variability (especially when the environmental conditions change Martini *et al.* (2020)) and interspecific variability that explains the interactions between species and their environment. In a nutshell, the traits to be used for functional trait approach must offer the best compromise between being (i) sufficiently informative with respect to the objectives, (ii) generic enough to be comparable across species — even if they are very different morphologically — and (iii) easily measurable to ensure repeatability between studies (Dumay *et al.* 2004; Kremer *et al.* 2017).

5   The advent of functional diversity

The functional approach is relatively recent. It developed in the 1980s with the collapse of populations, species extinctions and the biodiversity crisis (Wilson *et al.* 1988). The functions performed by species began to be studied in greater depth when ecologists noticed that if a species disappeared from an ecosystem, it did not necessarily mean that the whole ecosystem was disturbed or even collapsed (Mejri 2009). The question "Are all species essential for the proper functioning of ecosystems?" became central, as did the need to define the role of species within ecosystems. In other words, can we consider that species are "redundant" if they play the same role, fulfill the same function, in an ecosystem? To answer these questions, the functional trait approach seems relevant because it provides information on the roles of species in their environment, which is complementary to those provided by classical diversity indices, such as specific diversity, richness distribution or evenness (Marcon 2015; Mejri 2009).

More importantly, functional traits and species role attribution are crucial in determining functional diversity, which is the primary factor explaining stability and productivity, and should therefore be preferred to specific or taxonomic diversity when studying community ecology (Dumay *et al.* 2004; Mejri 2009). In fact, the resilience and health of ecosystems depends much more on the range of functions and functional traits exhibited by species than on the number of species *per se* (i.e. species richness). Indeed, indices of specific abundance and diversity assume that all species are equivalent, and do not take into account the functions provided by these species (Mejri 2009). From this functional perspective, the richness of an ecosytem is determined by the extent of functional diversity provided by the species (Rocklin 2004).

To estimate functional diversity, species must first be classified into "functional groups", which reflects the similarities of species according to 3 criteria. Within a functional group, species must (i) share the same habitat and trophic level (Brind'Amour *et al.* 2016), (ii) play a similar role in the habitat, through the functions they provide (Dumay *et al.* 2004; Mejri 2009), and (iii) display similar responses to changing environmental pressures (Brind'Amour *et al.* 2016; Dumay *et al.* 2004; Mejri 2009).

To form these groups and to evaluate the response of species for each of these 3 items, morphological traits are often used, because they reflect the capacities as well as their modes of interaction with their environment. They can therefore be used as indicators of trophic networks or habitats (Brind'Amour *et al.* 2016). Indeed, according to the "niche filtering hypothesis", which considers habitat characteristics as filters, only species that with adapted traits can thrive in a specific set of environmental conditions (Brind'Amour *et al.* 2011; Zobel 1997). This assumption also means that species, if they share similar functional traits, must use the same resources, probably in the same way, and thus have overlapping niches. Conversely, if species have very different functional traits from each other, they probably use resources in very different ways, or even distinct resources. Quantifying the overlap between species is key to understand their coexistence or exclusion (Costa-Pereira *et al.* 2019).

5.1 Benefits of this approach

Species in a same functional group can be considered "functionally equivalent", with similar or interchangeable functions. The ecosystem in which they occur then has "functional redundancy", which reduces the risk of a functional loss in the event of ecosystem disturbance. Conversely, a species can also be the only representative of a functional group (qualified as a "monospecific group"). It is then considered "essential", because if it disappears, the functions it provides will also disappear, causing a major disturbance of the ecosystem and other essential functions (Mejri 2009).

For conservation issues and the prediction of climate change impacts on ecosystems and biodiversity, the functional approach and the study of niche overlap seem relevant, as these tools provide a quantitative estimate of the resilience and/or resistance to change of communities and ecosystems. At a specific level, knowing which species have the most specialised diet or

which are the species are essential, from a functional perspective, are really useful to target species that needs to be protected in conservation plans (Cooke *et al.* 2020; Mejri 2009; Norton 1995). In addition, those tools can also be used to predict changes in diet niche for species in competition, if one of the abundances is affected by fishing pressure (Diderich 2006) or if an invasive species colonizes the environment (Albouy *et al.* 2011; Geange *et al.* 2011; Nagelkerke *et al.* 2018). As these approaches are not based on species or taxonomy, they are better suited to the generalization and identification of the ecosystem services provided (Martini *et al.* 2020; Mcgill *et al.* 2006) and the relationships involved in stable coexistence of species (Albouy *et al.* 2011). They thus improve our ability to predict ecological dynamics and their fluctuations, in an environment facing strong anthropic influence (Kremer *et al.* 2017).

Introduction

The deep ocean is the largest marine habitat of Earth, and represents 95% of ocean's volume (Danovaro *et al.* 2017; Salazar *et al.* 2016; Webb *et al.* 2010). From a biology perspective, deep-sea encompasses everything beneath euphotic (or epipelagial) zone, where the solar radiations are too low and precludes photosynthesis (Baker *et al.* 2020; Danovaro *et al.* 2017; Salazar *et al.* 2016) (Figure 2). Between 200 to 1000m deep (mesopelagic zone), light fades and temperature decreases, because solar luminance is absorbed exponentially in upper sea layers (Reynolds & Lutz 2001). From 1000 to 4000m deep (bathypelagic zone), no sunlight remains and the habitat is pitch-black; salinity and temperature are stable (between -1.8 to 2°C), and pressure keeps on increasing by 1 atm every 10m (Danovaro *et al.* 2017).
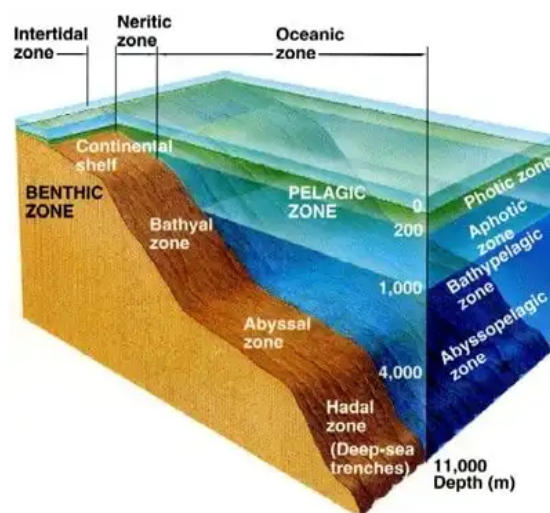

Figure 2: Sea layers along depth, from (fig 2018-06-17CDT19:13:06-05:00)

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Despite these extreme conditions, deep-sea is far from being lifeless. In fact, deep-sea is considered to be the largest biome of the Earth, and contains 70% of ocean's microbial cells

and 60% of its heterotrophic activity, playing a crucial role in biogeochemical cycles (Salazar *et al.* 2016). Studies from Grassle & Maciolek (1992); Parkes *et al.* (1994); Todo *et al.* (2005) shown that life could be found everywhere in the deep-sea, with remarkably high and stable diversity. Moreover, these very particular conditions have resulted in a high specialization of the inhabiting fauna, with species that are absent from shallower waters (García-Seoane *et al.* 2021). With first studies launched in the 60's, less that 0.0001% of the area has been investigated so far and this habitat remains understudied (Danovaro *et al.* 2017; Richards *et al.* 2019). Thus, deep-sea remains the most unknown biome of the planet with estimated 10 million species that are yet to discover (Danovaro *et al.* 2017; Grassle & Maciolek 1992). In particular, data are lacking to evaluate the impact of climate change on the biodiversity of the largest reservoir of biomass, mainly because exploring deep-sea is difficult and requires specific tools, such as rovers (Danovaro *et al.* 2008; Danovaro 2014). Firstly, deep-sea were regarded as a ore reservoir of its soil, where manganese and other metal deposits could be found and extracted, or even as a dumping site for nuclear wastes (Baker *et al.* 2020; Gillet 2013; Halfar & Fujita 2002). But since past decades, capacity of exploration of the deep-sea expanded spectacularly, allowing to discover more about the deep-sea ecosystems(Danovaro 2014).

In particular, continental margins, which separates continental shelf from abyssal plains are investigated, because their heterogeneous topography implies varied habitats and hydrodynamics, with impacts on the whole food webs (Danovaro *et al.* 2009; Fernandez-Arcaya *et al.* 2017). Along continental margins, deep-sea canyons, that incises the edges of continental shelf, appears to be "biodiversity hotspots" for pelagic life, in terms of diversity and abundance (Aïssi *et al.* 2012; Danovaro *et al.* 2009; Gillet 2013; Robertson *et al.* 2020). Caynons are also reported having a high level of endemism (Danovaro *et al.* 2009, 2017). Because they have a crucial role in transferring organic matter and sediments from rich and productive shallow shelf to the low-nutrients deep-sea, canyons constitute peculiar habitats, with evidences of an important biomass and diversity inside and around them (Canals *et al.* 2006; Danovaro *et al.* 2009; De Leo 2012; Sion *et al.* 2019; Stefanescu *et al.* 1994). Indeed, canyons have higher nutrients concentrations than in adjacent areas, due to down-welling currents creating a funnel-effect (Fernandez-Arcaya *et al.* 2017). Thus, primary production is enhanced, and makes canyons favorable habitats for filters and suspension feeders (Fernandez-Arcaya *et al.* 2017; Sion *et al.* 2019), but also for low to medium trophic levels organisms, such as euphausiids, shrimps, squids and meso- and bathypelagic fishes (Aïssi *et al.* 2012; Gaskett *et al.* 2001; Pusch *et al.* 2004). Abundance of nutrients and preys attracts top predators (cetacean, sharks, large pelagic), some of them being only encountered in these habitats (Aïssi *et al.* 2012). Finally, canyons provides many ecological services and play a role in sustaining deep-sea food webs through the transport of nutrients, providing habitat for nursery and refuges (Fernandez-Arcaya *et al.* 2017). Company *et al.* (2008) suggests that by these services, canyons enhance recruitment of commercialized species, and thus, may mitigate the effect of their overexploitation. Therefore, canyons can be described as "keystone structures", as an interface between productive continental shelf and deep-sea, with

evidence of their benefits and supports for fisheries (Company *et al.* 2012; Fernandez-Arcaya *et al.* 2017).

Meso- and bathypelagic fishes are found abundantly in every ocean, except Arctic, and are the dominant zooplankton consumers in most oceans, playing a key role in trophic networks (Davison *et al.* 2015; Salvanes & Kristoffersen 2009). Living between 200-1000m (mesopelagic) and over 1000m (bathypelagic) deep, these deep-sea fishes displays very high biomass, estimated to be around ten billion tonnes in total (García-Seoane *et al.* 2021; Gjoesaeter & Kawaguchi 1980; Richards *et al.* 2019). Though, abundance of these fishes varies along depth and daytime, because most of them perform vertical diel migration to feed on shallower depth during night, and abundance's estimation can be biased by sampling time (Catul *et al.* 2011; Gaskett *et al.* 2001; García-Seoane *et al.* 2021; Pusch *et al.* 2004; Salvanes & Kristoffersen 2009). Performing migrations, meso- and bathypelagic fishes ensure biogeochemical cycling through respiration and excretion but also when predated by carnivorous (García-Seoane *et al.* 2021; Spitz *et al.* 2019). Because of their ubiquity, their biomass and the high efficiency of energy transfer from phytoplankton (respiring 10% of the primary production), meso- and bathypelagic fish play an important part of the biological pump (García-Seoane *et al.* 2021; Spitz *et al.* 2019). Meso- and bathypelagic fish can show adaptations to their environment such as highly sensitive eyes, dark body and ventral light organs (photophores) to match their low-light habitat and reduced metabolic rates to lower oxygen consumption in poorly oxygenated waters (Salvanes & Kristoffersen 2009; Farré *et al.* 2016). Photophores have a role in camouflage, foraging, courtship behavior, with different patterns between males and females. They are also species specific which helps identification (Paitio *et al.* 2020; Salvanes & Kristoffersen 2009). Finally, depth and associated pressure play a role in the morphology of deep-sea fishes, which tend to have more elongated body with increasing depth, while manifesting an enlargement of the anterior body that increase gill surface and the ability to capture oxygen (Farré *et al.* 2016). Most of the life history traits of meso- and bathypelagic fish remains unknown and needs to be further investigated, with relatively poor and non consistent literature (Childress *et al.* 1980; Salvanes & Kristoffersen 2009). The mesopelagic communities are dominated by Myctophidae family, in terms of abundance, diversity and biomass, and represents at least 20% of the whole oceanic ichthyofauna (Catul *et al.* 2011; Kozlov 1995; Pusch *et al.* 2004).

Several studies focused on exploring deep-sea fish diversity near seamounts, mid-ocean ridges or in abyssal depths (Cook *et al.* 2013; Sutton *et al.* 2013), but very little is known about meso- and bathypelagic species inhabiting deep-sea canyons (Kenchington *et al.* 2020). Nevertheless, given the essential role of the oceanic pelagic fish community in food webs, linking the epipelagic organic matter to top predators, requires a better knowledge of species constituting this fundamental compartment (Davison *et al.* 2015; Gaskett *et al.* 2001). Furthermore, considering how important canyons are for fisheries and carbon sequestration, knowing more about the communities inhabiting them is crucial to ensure sustainability of ecosystems and provided services, through marine management and conservation (Fernandez-Arcaya *et al.* 2017; van den

Beld *et al.* 2017b).

Located in the temperate North-east Atlantic Ocean, the Bay of Biscay's continental shelf is highly productive, with nearly 700 fish species and 35% of the world total marine mammals identified in this region (Borja *et al.* 2019). This productivity relies on heavy rivers discharge and strong influence of eastward winds, tides and eddies (Borja *et al.* 2019; Akpınar *et al.* 2020). Thus, plankton, benthic and pelagic communities have been widely studied for several decades, with some fish communities being annualy monitored (Borja *et al.* 2019; Doray *et al.* 2018). Conversely, there is little knowledge on canyon, abyssal and bathyal communities in this area (Borja *et al.* 2019). The continental slope of the Bay of Biscay divides in two the of France's Atlantic EEZ (Exclusive Economic Zone) and is incised by about 135 canyons (Bourillet *et al.* 2006; Spitz *et al.* 2019; van den Beld *et al.* 2017a) (Figure 3). If proven to be rich in cold-water coral reefs, the largest part or the area remains poorly explored, especially deep-pelagic communities (García-Seoane *et al.* 2021; van den Beld *et al.* 2017b; Webb *et al.* 2010). In consequence, the similarity or differences within species inhabiting these ecosystems are unknown (Kenchington *et al.* 2020).
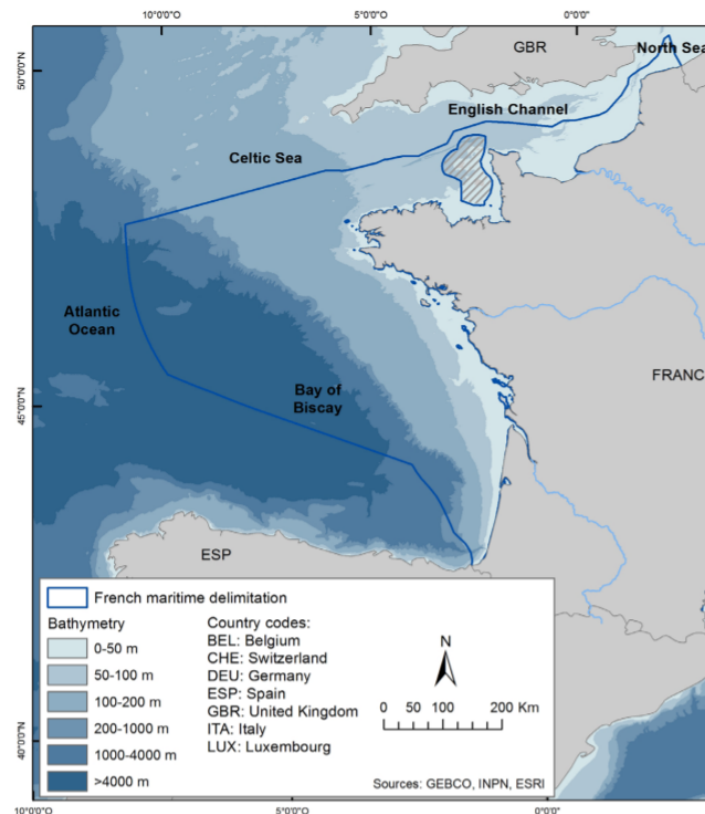

Figure 3: Location of the studied area, from (Béarez *et al.* 2017).

One way to characterize an ecosystem is to look at the factors that control biodiversity patterns and to identify the key functions provided by this ecosystem (Aneesh Kumar *et al.* 2017; Brind'Amour *et al.* 2011; Farré *et al.* 2016). Functional diversity, which is the value and range

of functional traits displayed by the organisms of a given ecosystem, can inform on ecosystems functioning and about their resilience facing a change in the environment (Dumay *et al.* 2004; Martini *et al.* 2020). Moreover, the use of functional traits to characterize functional niches of species highlights some competition or adaptation processes within a communtinity of an ecosystem (Aneesh Kumar *et al.* 2017). Indeed, comparison of functional niches is an effective way of assessing ecological similarity of species, based on the way they share, or not, certain morphological, behavioral or physiological characteristics (Aneesh Kumar *et al.* 2017; Farré *et al.* 2016; Winemiller 1991).

This approach seems particularly well suited to study fish communities, because morphological traits are considered being good indicators of ecological habits of species, indicating how species use available resources (Farré *et al.* 2016; Winemiller 1991). Successfully applied for freshwater ecosystems and marine coastal environments, this approach has not been much used on deep-sea communities where functional traits shaping ecological niches remains mostly unknown (Aneesh Kumar *et al.* 2017; Farré *et al.* 2016). Conditions become more extreme and the food availability decreases with depth, so deep-sea are often thought to be poor in terms of functional diversity (Aneesh Kumar *et al.* 2017; Mason *et al.* 2008; Novotny 2018). This would mean that most (if not all) deep-sea species are generalists, and suggests that competition is highly probable to access the little food available .

Because species displaying the same functional niche can be considered as part of the same functional group, our hypothesis is that species occupying similar functional niches insure redundant function within an ecosystem and be in competition, whereas species displaying very different functional niches would be segregated. Hence, the aim of this work is to assess functional diversity of deep-sea canyons fish of the Bay of Biscay, which, for the moment, is barely known (Kenchington *et al.* 2020). Using functional traits to assess functional niches of species, our main objectives are (i) to characterize functional diversity of most-abundant canyon species, (ii) to measure the range and degree of overlap of functional niches and (iii) to identify the traits that structure the most these communities.

Materials & Methods

1 Sampling and specimens

Fishes were collected during Ifremer's EVHOE (EValuation Halieutique de l'Ouest Européen) research cruises, surveying the Bay of Biscay every fall onboard the *R/V Thalassa*. **Préciser les années** Several hauls are regularly performed at night to investigate pelagic deep fauna. Each station is precisely defined with its GPS coordinates and located above canyons, at the edge of the continental shelf. Pelagic trawling is performed at night, between 700 and 2000 meters, because those fishes perform diel vertical migrations and tend to come closer to the surface at nighttime. To this end, a 25 meters-wide opening trawl is used, with a mesh size decreas-

ing from 76mm to 48mm at the end of the trawl. The trawl-haul duration was 1 hour at 4 kn. Once the trawl is pulled back onboard, fishes are sorted, identified up to the species level, and frozen at -20°C. Eleven of the most abundant species in the Bay of Biscay (all teleosts) have been selected for this study. Four of them belong to the Myctophid family (lanternfish), which is the most abundant and widespread family across all oceans (de Busserolles *et al.* 2014) and could represent up to 65% of the pelagic deep-sea biomass (Poulsen *et al.* 2013): *Lampanyctus crocodilus*, *Myctophum punctatum*, *Notoscopelus kroeyeri* and *Ceratoscopelus maderensis*. The second most represented family is the Platytroctidae with two species: *Searsia koefoedi* & *Normichthys operosus*. This family seems to be found in all oceans but not in the Mediterranean Sea (Orrell & Hartel 2016). Finally, five families are represented by one species each: *Xenodermichthys copei* (Alepocephalidae); *Arctozenus risso* (Paralepididae), *Argyropelecus olfersii* (Sternoptychidae - Hatchetfishes), *Serrivomer beanii* (Serrivomeridae) and *Stomias boa* (Stomiidae) which are common species, found abundantly in every ocean (Carvalho & Almeida 1988; Froese & Pauly 2019; Geidner 2008; Germain *et al.* 2019). See A.1 for a phylogenetic tree of these species.

2 Morphological measurements and functional traits

In the laboratory, the fish were thawed and 24 morphological variables were measured, using an electronic caliper with a precision of 0.01mm. Some of these measurements had previously been recorded by students from La Rochelle University during practical classes in 2018 ($n = 99$), 2019 ($n = 45$), 2020 ($n = 9$) and the rest during this study ($n = 212$). For the sake of statistical robustness and representativity, at least 25 individuals were measured for each species (Table 1).

Table 1: Number of individuals measured for each species (n_1: previous studies, n_2: this study, n_{Tot} : $n_1 + n_2$), with their mean standard size and range values in millimeters.

Species	n_1	n_2	n_{Tot}	Mean length (mm)	Size range (mm)
Lampanyctus crocodilus	39		39	107.60	73.3 - 146.5
Xenodermichthys copei	38		38	109.68	82.3 - 132
Normichthys operosus		38	38	104.69	75.64 - 131.62
Argyropelecus olfersii	37		37	56.55	32.16 - 89.07
Notoscopelus kroyeri	6	30	36	76.30	52.63 - 130.84
Searsia koefoedi	5	31	36	119.94	84.8 - 142.75
Arctozenus risso	20	10	30	158.36	117.6 - 181.31
Serrivomer beanii		30	30	546.17	373 - 879
Ceratoscopelus maderensis		30	30	62.72	53.29 - 78.95
Stomias boa		26	26	239.00	144 - 311
Myctophum punctatum	8	17	25	65.48	52.53 - 80.14

21 functional traits were calculated for each individual from the morphological measurements. They inform on 3 main functions: food acquisition, locomotion and habitat (see Table 2).

Table 2: Description and formulas of the functionals traits computed from morphological measurements, following (Albouy *et al.* 2011; Aneesh Kumar *et al.* 2017; Boyle & Horn 2006; Brind'Amour *et al.* 2016; Diderich 2006; Dumay *et al.* 2004; Habib *et al.* 2019; Ibañez *et al.* 2007; Sibbing & Nagelkerke 2000; Webb 1984; Winemiller 1991). Abbreviations used in formulas are provided by raw measurements and detailed in appendices A.2, A.3 & A.4. `oga`, `git`, `pc`, `pht` are categorial variables directly provided by raw measurements with the first two scores detailed respectively in appendices A.5 & A.6.

Function	Functional trait	Description	Formula
Feeding	Oral gape axis	Feeding position and depth in the water column	oga
	Eye size	Detection of preys and visual acuity for predators	ed/hd
	Orbital length	Preys size and behavior (buried, camouflaged)	ed/sl
	Oral gape surface	Type and size of preys	mw*md / bw*bd
	Oral gape shape	Strategy to capture prey	md/mw
	Oral gape position	Fedding position in the water column	mo/hd
	Lower jaw length	Compromise between power and opening speed of the mouth	ljl/sl
	Gill raker type	Filtration capacities of fish	git
	Gill outflow	Succion capacities of fish	ow
	Head length	Maximum prey size	hl/sl
	Pyloric caeca	Presence/Absence of pyloric caeca	pc
	Anus position	Digestive tract length	pal/sl
Locomotion	Body depth	Swimming capacities of fish linked to their food prospection behavior	bd/sl
	Pectoral fin position	Maneuvrability of fish	pfi/pfb
	Pectoral fin insertion	Maneuvrability of fish	ppl/sl
	Transversal shape	Position in the water column and hydrodynamism	bd/bw
	Caudal throttle width	Swimming strategy (cruiser/sprinter) and endurance	cpd
	Dorsal fin insertion	Swimming type and behavior	pdl/sl
Habitat	Eye position	Position in the water column (pelagic/sedentary)	eh/hd
	Presence photophores	Presence/Absence of photophores (chercher à quoi ça sert)	pht
	Operculum volume	Filtering capacity and oxygen captation	od/ow

3 Data analysis

All data analyses were performed using R version 4.0.3 (R Core Team 2021).

Commentaire : je vois que tu utilises \texttsc{} quand tu parles de tes mesures et des traits. Attention, je crois que le Times New Roman ne dispose pas de cette police spéciale qui fait des "Petites majuscules". Du coup, la commande n'a aucun effet. J'ai donc remplacé par \texttt partout où je l'ai trouvé ! D'ailleurs, utilises aussi plutôt ça plutôt que l'italique pour les noms de logiciels, de packages, etc.

3.1 Data pre-processing

Because measurements came from several observers, raw data had to be checked for outliers. To do so, all values (except the standard length `sl`) were standardized by `sl` and the interquartile range (IQR) method of outlier detection was applied to remove outliers. According to this method, for each measurement and species, outliers are defined as every value outside this interval:

$$[Q1 - 1.5 \times IQR, Q3 + 1.5 \times IQR]$$

with $Q1$ and $Q3$ being respectively the first and third quartile, and $IQR = Q3 - Q1$.

Missing values initially present in the dataset ($n = 52$) and induced by the outlier removal function ($n = 307$), were then imputed using the k-Nearest Neighbor (kNN) algorithm. Suppose that the individual i has a missing value X_i for the variable X. The algorithm identifies the k nearest neighbors of i based on all available variables (*i.e.* all variables but X). The values of X observed in the k nearest neighbors of i are then used to infer X_i using Euclidean distances between i and its k nearest neighbors. The computations were performed by the `step_knnimpute()` function from the `tidymodels` R package (Kuhn & Wickham 2020), with a number of nearest neighbors of $k = \sqrt{N}$, with N being the number of individuals for each species. The accuracy of the imputation was then checked with a linear regression of each variable with respect to `sl`. From this cleaned dataset, the functional traits were computed using formulas in Table 2.

3.2 Factorial Analysis of Mixed Data (FAMD)

To assess the similarities or differences of traits in species, a Factor Analysis of Mixed Data (FAMD) was performed using the `FactoMineR` package. This type of multivariate analysis is suited for datasets containing a mix of qualitative and quantitative variables. It performs a Principal Component Analysis (PCA) on quantitative variables and a Multiple Correspondence Analysis (MCA) on qualitative variables. The results of an FAMD are interpreted in the same way as those of a PCA: both methods are used to assess (i) similarities and differences among individuals and (ii) to check for associations between variables. Because *Serrivomer beanii* does not have pectoral nor pelvic fins, and because this analysis can not handle missing values,

zero values were attributed for `PFB`, `PFI`, `PPL` and `PVL`. Because of this specific particularity, complementarty analysis was run. First, the same FAMD analysis was run without *S. beanii*, to assess the discrimination between all remaining species. Then, the analysis was run with all species (including *S. beanii*) but without the traits missing for *S. beanii* (*i.e.* `PFB`, `PFI`, `PPL` and `PVL`), to verify that the observed differences were not exclusively dependants on these traits. The categorical variables were managed as follow: scores were used for both oral gape axis and gill raker type (see Figures A.6 and A.5), whereas pyloric caeca and photophores were binary defined (0 = absent, 1 = present). For each principal component (PC), all traits that have a contribution greater than or equal to a threshold t are considered relevant (with $t = 100/$number of variables). Here, 21 functional traits were computed, meaning that $t \approx 4.8$. On the resulting FAMD graph, we added inertia ellipses representing the functional niche of each species. These ellipses assume a multinormal distribution of the functional traits.

4   Functional niche analysis

The coordinates of individuals projected on the FAMD axes were used to compute (i) the surface of the functional niche of each species, and the overlap of niches for all possible pairs of species. This analysis was only run on the first two factorial axes (PCs), because they are the ones carrying most of the information about the community's structure. The method used here is similar to isotopic niche analysis, which is much more documented. We used the `SIBER` package (Stable Isotope Bayesian Ellispes in R) and adapted it to our purpose (Jackson *et al.* 2011). For each species the ellipse surface was computed, and the overlap of ellipses between all pairs of species was assessed with the `maxLikeOverlap()` function. Absolute niche surfaces were then standardized by the smallest niche, to facilitate the comparison of relative differences in niche sizes. The relative overlap was assessed as the ratio of the overlap value to the size of the niche, for each species of each pair. Finally, the total overlap for a pair of species was determined by dividing the overlap value by the sum of the area of the niches of the two species. In order to assess the sensitivity of the method to insufficient sample size, niche surfaces were also computed for various sample sizes (n) following a bootstrap procedure. To this end, between 100 to 10 000 individuals from our dataset were sampled at random, and area of all niche's was recalculated 10 000 times.

Functional niches were further investigated using the `funrar` R package, to compute functional rarity (Matthias Grenié *et al.* 2017). Based on indices characterizing the rarity of functions within a system (Violle *et al.* 2017), the aim is to assess the local functional diversity of the traits in our dataset. First a distance matrix is computed using Gower's distance as it can deal with both quantitatives and qualitatives variables (Brind'Amour *et al.* 2016; Matthias Grenié *et al.* 2017). Then, the `distinctiveness_global()` function is applied to measure how functionnally rare a species is, compared to other species of the community. Distinctiveness results range from 0 (no distinctiveness) to 1, when a species is, locally and/or functionnally, different from the

others (Matthias Grenié *et al.* 2017).

5   Kernel density estimation

When two or more niches overlap, it is interesting to detail which traits are most similar between species. To this end, we used a parametric kernel density function (Mouillot *et al.* 2005) , which has been used in a similar context by Aneesh Kumar *et al.* (2017). Along a trait axis, the function returns the overlap value between N overlapping species, ranging from 0 (no overlap) to 1 (N species have identical, fully overlapping densities).

Results

1   Factorial Analysis of Mixed Data

The first 5 FAMD components explained 80% of the total variation (Table 3). The first principal component (PC1) (30.5% of explained variance) is strongly correlated with shape of the body and of the head with traits such as *body depth* (a = 11.7), *lower jaw length* (a=11.5), *oral gape axis* (a=11.1), orbital length (a = 8.35) and head length (a = 8.21), thus, mostly to feeding and locomotion (Table 3). Along this horizontal axis, all traits have increasing values toward the right, mouth orientation shifting upward (see A.7 for details). Three groups of fish can be distinguished 4. For low PC1 values, species have a low transversal shape (meaning that both bd and bw have similar values, consistent with an elongated body), short lower jaw, small oral gape surface and a terminal oral axis, such as *A. risso*, *S. boa* and *S. beanii*. On the right of this axis, species display high body depth values suggesting a laterally compressed form and a superior-oriented oral axis, such as *A. olfersii*.

The second axis (21.6% of explained variance) is correlated to feeding behavior, through food prospection with *pectoral fin insertion* (a = 11.4), *eye size* (a = 9), *pectoral fin position* (a = 7.1) and food acquisition through *gill raker type* (a = 17.8) and *oral gape axis* (a = 12,3) (Table 3). This vertical axis separates the three species on the left, *A. risso* and *S. boa* display higher values of pectoral fin insertion, meaning that the fin is inserted further on the body than *S. boa*, while the fin position on the body depth is lower. As *S. beanii* does not have pectoral fin, same analysis has been run without traits referring to pectoral or pelvic fins to look and confirmed the discrimination between these species were highly dependant if these traits. Same results than Figure 4 were obtained.

The third axis (explaining 12.2% of total variance) mainly carries traits linked to the foraging and swimming behavior, with strong influence of *anus position* (a = 23.8), *gill raker type* (a = 19.2), *dorsal fin insertion* (a = 15.5) and *pectoral fin position* (a = 14.2) (Table 3). On the left of this horizontal axis, species are characterized by a rather high pectoral fin insertion and close-to-head dorsal fin insertion and anus position (Figures 5 and A.8). Finally, the fourth

axis (explaining 7.9% of variance) is mainly related to feeding and habitat traits, with *pyloric caeca* (a = 31.6), *operculum volume* (a = 17) and *presence of photophores* (a = 10.9) (Table 3). Because *X. copei* is the only species having pyloric caeca, this variable clearly separates that species from the other, on the PC4 axis. The remaining PC scores (20% of variance) are mainly linked to food acquisition. Overall, FAMD analysis detects similarities between species niches', with ellipses overlapping. Conversely, some species are well segregated along these first four axis, suggesting the existence of several functional groups within studied community.

Because PC1 and PC2 have most of the weight in the functional analysis, it suggests that the traits they carry are the most relevant to segregate species. In particular, *lower jaw length*, *body depth*, *pectoral fin insertion* and *eye size* are the quantitative traits that are the most distinct among species and helps to distinguish them. As for qualitative variables, it seems that *oral gape axis* and *gill raker type* are the one which separates the most species. This makes sense considering they have the most modalities, allowing a more precise description than binaries *presence of photophores* and *pyloric caeca* scores.

Table 3: Correlation between 5 first PC's and functional traits. In bold, correlations higher than threshold (4.8).

Function	Trait	PC1 (30.5%)	PC2 (21.6%)	PC3 (12.2%)	PC4 (7.9%)	PC5 (7.8%)
	Oral gape axis	**11.07**	**12.28**	3.32	3.27	**7.13**
	Eye size	1.29	**9.01**	3.52	4.08	1.40
	Orbital length	**8.35**	2.38	0.00	2.24	4.54
	Oral gape surface	**7.78**	3.06	2.93	0.10	2.78
	Oral gape shape	0.18	3.10	0.05	**9.49**	**10.41**
	Oral gape position	0.42	1.21	1.99	**9.16**	3.94
Feeding	Lower jaw length	**11.52**	0.00	0.04	1.97	2.44
	Gill raker type	4.38	**17.80**	**19.23**	0.32	3.42
	Gill outflow	**5.47**	0.82	0.02	2.22	**22.48**
	Head length	**8.21**	3.10	2.50	0.78	4.50
	Pyloric caeca	0.23	0.48	0.04	**31.62**	**5.81**
	Anus position	0.00	**5.28**	**23.81**	0.07	0.77
	Body depth	**11.68**	0.93	1.41	0.64	1.92
	Pectoral fin position	1.72	**7.15**	**14.22**	0.37	0.32
Locomotion	Pectoral fin insertion	**4.95**	**11.39**	0.05	0.12	0.74
	Transversal shape	**5.96**	4.33	5.45	1.70	2.10
	Caudal throttle width	3.72	**5.01**	0.28	1.60	**16.30**
	Dorsal fin insertion	2.58	4.78	**15.52**	0.00	1.33
	Eye position	0.19	**5.41**	0.78	2.34	1.40
Habitat	Presence photophores	**7.79**	2.45	3.23	**10.89**	0.59
	Operculum volume	2.52	0.03	1.61	**17.02**	**5.68**

2 Functional niche surface and overlap

Overall, several species' ellipses overlaps on these first four principal components (Figures 4 and 5). For these species, the aim is now to measure the intensity of these overlaps. On the first and second principal components, all 4 Myctophidae and 2 Platytroctidae species, plus *X.*
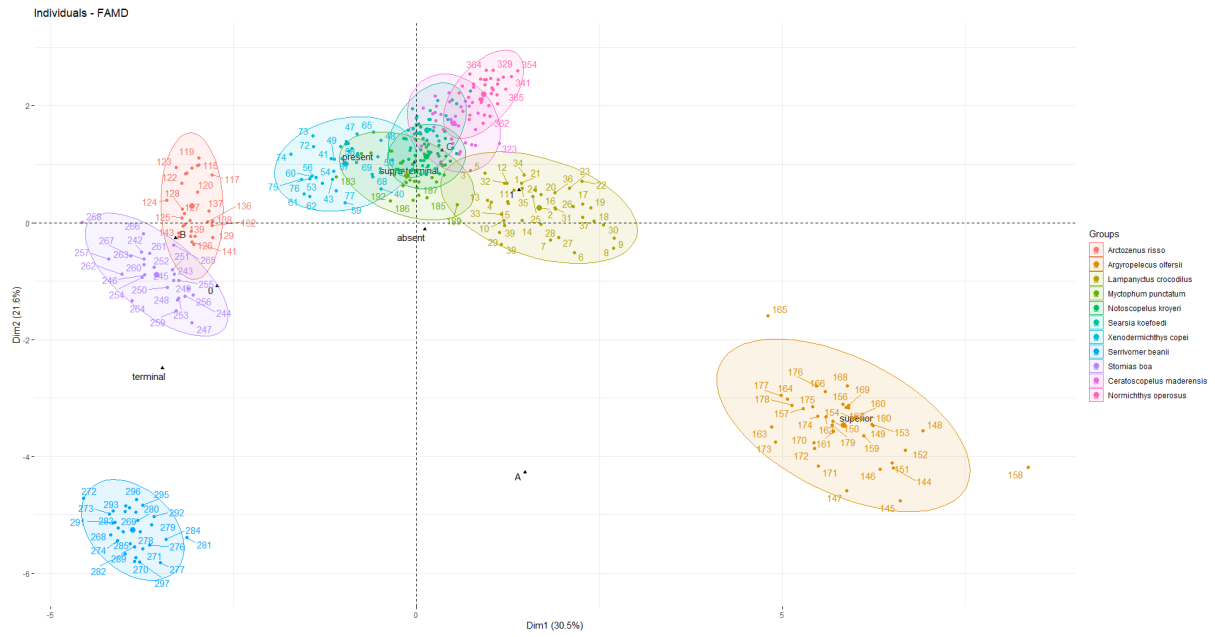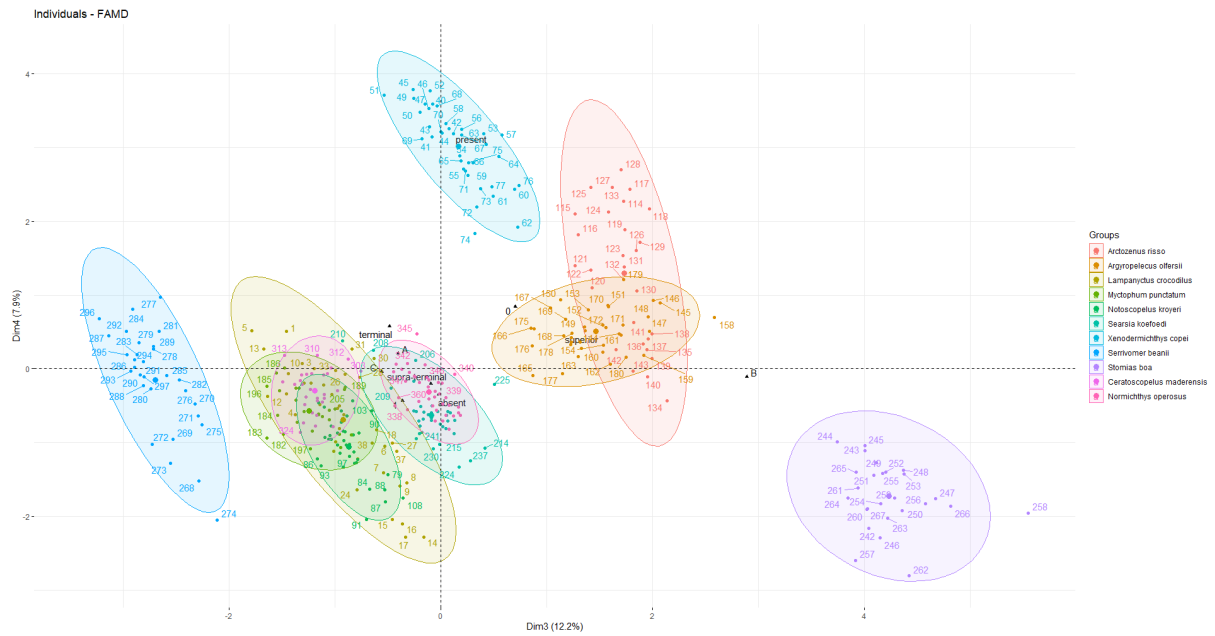
Figure 4: FAMD results for PC 1 and 2.

Figure 5: FAMD results for PC 3 and 4.

copei are more or less overlapping, not displaying much differences along PC1 nor PC2 (Figure 4). *A. risso* and *S. boa* seems to slightly overlap each other niches, which are mainly separated along PC2 (Figure 4). *S. beanii* and *A. olfersii* are the only two species not showing any overlap. *A. risso* and *A. olfersii* are showing some overlap (Figure 5). On the same figure, the same species (except *X. copei*) than Figure 4 overlaps. Especially, *N. operosus* and *S. koefoedi* have very similar looking niches, which seems virtually fully overlapping. *L. crocodilus*, which have the widest niche among these species, overlaps *C. maderensis*, *M. punctatum* and *N. kroyeri*'s niches.

The niche surface estimation showed that *N. kroyeri* had the narrowest niche among the studied community, followed by *N. operosus* and *S. koeofedi* (Table 4). Then, *C. maderensis*, *A. risso*, *S. beanii* and *M. punctatum*, *S. boa* and *X. copei* all have niches almost two to three times wider than *N. kroyeri*'s. Finally, comparing to *N. kroyeri*'s niche, *L. crocodilus*'s is four time wider, while *A. olfersii*'s is more than seven time wider. In fact, all Myctophidae (except *L. crocodilus*) and Platytroctidae have rather small niches and are the one overlapping in Figure 4.

Bootsrapped niche surface estimation did not show any difference in the surface of estimated niche through sample size *n*. Hence, surface of niches seems to be more influenced by the trait variability of the sampled individuals rather than the number of inviduals itself. Yet, estimated niche surface value are tightly converging for $n = 30$.

Table 4: Standardized surface of functional niches.

Species	Area
Argyropelecus olfersii	7.4
Lampanyctus crocodilus	4.00
Xenodermichthys copei	2.60
Stomias boa	2.5
Myctophum punctatum	2.1
Serrivomer beanii	1.9
Arctozenus risso	1.8
Ceratoscopelus maderensis	1.7
Searsia koefoedi	1.3
Normichthys operosus	1.2
Notoscopelus kroyeri	1.00

Niche overlap analysis confirms that 9 species show overlapping niches with at least one other species (Figure 4) and that smallest niches overlaps each other the most (Table 5). The maximum overlap is found between *M. punctatum* and *N. kroyeri*, as almost 69% of the latter's niche is covered by the first. In total, these two species share nearly 22% of their niches. Same observation is made between *S. koefoedi* whose niche is 65% covered by *C. maderensis*. These two species have the highest total overlap value, with 28% of their niches overlapping. Finally, *N. kroyeri* and *N. operosus* show minimum total overlap value of 2.1%. This is due to some individuals of the latter in *N. kroyeri*'s ellipse (see Figure 4). Overall, both *N. kroyeri* show overlap with six other species, while *C. maderensis*, *S. koefoedi* and *M. punctatum* are overlapping five

other species. Finally, *L. crocodilus*, *X. copei* and *N. operosus* are involved in overlap with three other species, and *A. risso* and *S. boa* are only ovrelapping each other (Table 5).

Table 5: Species' ellipses overlap. All the others comparisons that are not present in this table did not present any overlap.

Species1	Species2	Total overlap (%)	Overlap of Species 2 over Species 1 (%)	Overlap of Species 1 over Species 2 (%)
Searsia koefoedi	Ceratoscopelus maderensis	28.20	65.40	49.60
Notoscopelus kroyeri	Searsia koefoedi	28.10	65.40	49.20
Myctophum punctatum	Notoscopelus kroyeri	22.00	32.30	68.70
Myctophum punctatum	Xenodermichthys copei	20.20	44.90	36.60
Ceratoscopelus maderensis	Normichthys operosus	19.00	31.80	47.10
Notoscopelus kroyeri	Ceratoscopelus maderensis	15.10	41.60	23.70
Myctophum punctatum	Searsia koefoedi	12.50	20.30	32.40
Searsia koefoedi	Normichthys operosus	7.90	15.00	16.90
Notoscopelus kroyeri	Xenodermichthys copei	6.40	22.90	8.80
Searsia koefoedi	Xenodermichthys copei	5.90	17.50	8.90
Lampanyctus crocodilus	Myctophum punctatum	4.20	6.50	12.20
Arctozenus risso	Stomias boa	3.90	9.40	6.60
Myctophum punctatum	Ceratoscopelus maderensis	3.20	5.80	7.00
Lampanyctus crocodilus	Ceratoscopelus maderensis	1.70	2.50	5.70
Lampanyctus crocodilus	Notoscopelus kroyeri	1.00	1.20	4.80
Notoscopelus kroyeri	Normichthys operosus	0.20	0.50	0.40

Niches distinctiveness informs on functional diversity of species within a community, increasing values meaning that

from Myctophidae and Playtroctidae families are all equally functionnally distinct from one another (see Table 6). Even if the values are rather close, *S. koefoedi* and *M. punctatum* seems to be the most alike species. Conversely, *A. olfersii*, *S. beanii* and *S. boa* tend to have more distinct niches, which are consistent with previous results (Figure 4). Here, species with the most atypical morphological feature are the more distinct in terms of niche.

Table 6: Niche dissimilarity of studied species

Species	Distinctiveness value
Argyropelecus olfersii	0.54
Serrivomer beanii	0.51
Stomias boa	0.46
Arctozenus risso	0.40
Lampanyctus crocodilus	0.37
Xenodermichthys copei	0.37
Ceratoscopelus maderensis	0.31
Normichthys operosus	0.31
Notoscopelus kroyeri	0.30
Searsia koefoedi	0.29
Myctophum punctatum	0.29

3 Kernel density estimation

Kernel density estimation helps to understand which are the traits that have the same distributions for species. Looking at these distributions for overlapping species gives informations on traits, and thus functions, similarities among species. The estimation of kernel density overlaps for

functional traits of the 7 overlapping species and shows that these species are all overlapping for 7 of the 17 computed traits (Figure 6; Table 7). The overlap is maximum for the position of the oral gape (trait n°5) with an overlap value of 0.34. This means that, along this functional trait, these 6 species share nearly 34% of their density. For this trait, most of the distributions are centered around a range of values of [0.5-0.8], yet *L. crocodilus* display a pretty wide distribution, despite being the most sampled species (see Table 1). This same observation can be done for this particular species for traits n°11 (body depth) and n°13 (pectoral fin insertion). Species also share nearly 25% and 29% of their density when looking at body depth (trait n°11) and eye position (trait n°17), respectively. Finally, lower jaw length (trait n°6) and pectoral fin position (trait n°12) values also seem to be common to those species, with 16% and 19% of density shared, respectively. To a lesser extent, species share nearly 12% of the eye size values (trait n°2). On most plots of Figure 6, *N. kroyeri* (green) and *M. punctatum* (blue) have very similar distributions. When looking at these two species only, analysis show that they are overlapping for every 17 traits, with particularly high values for eye size ($o = 0.915$), operculum volume ($o = 0.901$), gill outflow ($o = 0.882$), pectoral fin insertion ($o = 0.828$) and caudal throttle width ($o = 0.782$), with the mean overlap of the 17 traits being $\bar{o} = 0.561$.

Table 7: Kernel density overlap values for the 17 computed traits for the seven overlapping species. Values in bold are significant ($p < 0.01$) and shown in Figure 6.

Trait code	Functional trait	Total overlap (o)
1	Eye size	0.00
2	Orbital length	**0.12**
3	Oral gape surface	0.00
4	Oral gape shape	0.00
5	Oral gape position	**0.34**
6	Lower jaw length	**0.16**
7	Gill outflow	0.00
8	Operculum volume	0.00
9	Head length	0.00
10	Anus position	0.00
11	Body depth	**0.25**
12	Pectoral fin position	**0.20**
13	Pectoral fin insertion	**0.01**
14	Transversal shape	0.00
15	Caudal throttle width	0.00
16	Dorsal fin insertion	0.00
17	Eye position	**0.29**

Discussion

The results of our study provide evidence for differentiation of functional niches of deep-sea fishes inhabiting canyons of the Bay of Biscay. Specifically, differences among species were
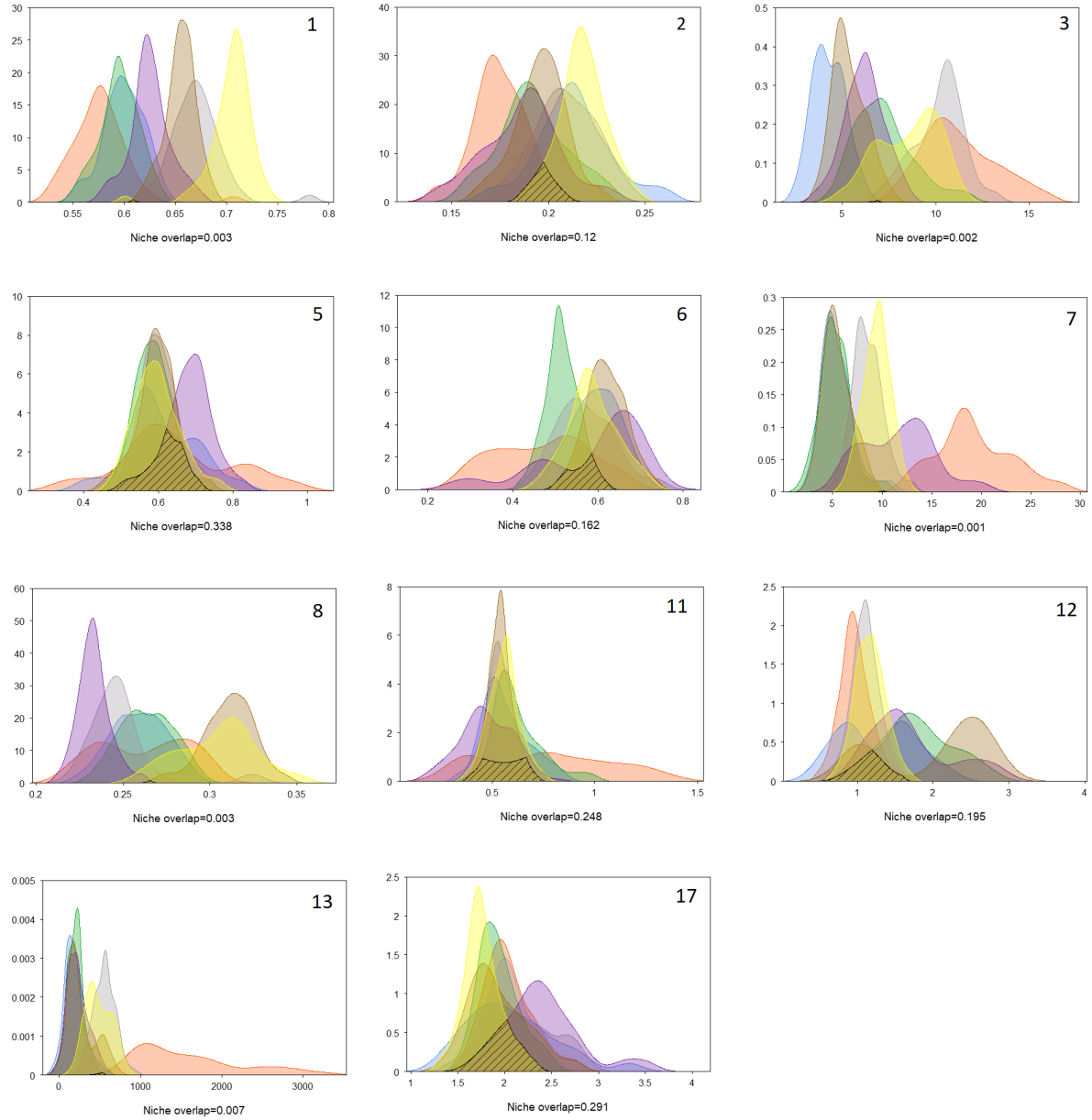
Figure 6: Kernel density overlap for 11 functional traits and the overlaping species. Colors correspond to following species: orange - *L. crocodilus*; brown - *C. maderensis*; yellow - *N. operosus*; purple - *X. copei*; green - *N. kroyeri*; blue - *M. punctatum*; grey - *S. koefoedi*. Overlap is represented by shaded lines. Here, are displayed every traits that showed non-null overlap.

best described by traits refering to body and head morphology and by food-related traits, which also give informations on their habitat (Schoenfuss & Blob 2007). Estimating functional niche with ellipses revealed distincts functional groups. Most of the detected overlap is found between Myctophidae, Platytroctidae and Alepocephalidae (intra- and inter-families). However, segregation could also be highlighted inside these families, mainly based on diet differenciation. Similarly, species with the most atypical morphology (*i.e A. risso*, *A. olfersii*, *S. beanii* and *S. boa*) showed null/low overlap, thus segregation. These results reveals that the most common species of deep-sea communities of the Bay of Biscay show functional diversity and even specialization. This supports the hypothesis of a high partitioning of resources in these ecosystems and promotes coexistence of species, which might be essentially driven by food resources, but also swimming abilities (Aneesh Kumar *et al.* 2017; Preciado *et al.* 2017).

RAJOUTER PARTIE SUR l'EXPLICATION DES AXES ?

PC4 –> linked to prey selection

In this study, environmental (biotic or abiotic) parameters were not taken into account. Though, within an ecosystem, species are not only interacting with each other, but also with their environment. Whether it shapes the habitat or define availability of resource breadth, environment is influencing realized niche (Costa-Pereira *et al.* 2019; Ibañez *et al.* 2007; Kremer *et al.* 2017). Adding these parameters in future studies could potentially change the results, as well as investigate site influence. Because traits are morphological responses to environmental constraints, their interpretation could vary from one context to another, making it hard to extract the main drivers of trait variation. (Kremer *et al.* 2017). Comparing communities living in different sites is relevant to link some functional traits with habitat particularities, and thus assess how environment influence functional niches (Mejri 2009). With climate change, studying this relationship is even more important to predict how disturbances of the habitat will affect fishes communities (Brind'Amour *et al.* 2011). Moreover, including local environmental conditions could explain the part of trait variability due to pressures from ecological divergence (da Silva *et al.* 2019).

Similarly, potential seasonal effect on functional traits was not assessed. Because plankton diversity and abundance is varying with seasons, species that directly relies on this resource as their main food resource might express seasonal patterns in their food-related traits (Kremer *et al.* 2017). Furthermore, no sex or maturity distinction was made when measuring individuals, and this source of variability was not investigated in our analysis. For fishes, both variables could influence morphologic features: sexual dimorphism being mostly related to standard length and fins position and maturity to prey selection (Geidner 2008; Nagelkerke *et al.* 2018). These biaises emphasize the crucial importance of traits selection, because selectionning lots of traits that are highly dependant of these two variables might lead to very different results of niche partitionning (da Silva *et al.* 2019; Dumay *et al.* 2004; Nagelkerke *et al.* 2018).

Previous studies showed that functional niche overlap and species abundances were linked (Aneesh Kumar *et al.* 2017; Mason *et al.* 2008). More precisely, the most abundant species

of an ecosystem tend to be functionnally separated from the others (Farré *et al.* 2016). For Bay of Biscay's canyons specifically, no studies assessing the species diversity and abundance were found. Looking at literature from other studies meso- and bathypelagic communities give divergent results. For García-Seoane *et al.* (2021) and Kenchington *et al.* (2020), deep-sea pelagic fish assemblages are dominated by Gonostomatidae (family not studied here), Eduardo *et al.* (2020) considers Sternoptychidae (family of *A. olfersii*) as one of the most conspicuous components of the mesopelagic ichthyofauna and (Sutton & Sigurdsson 2008) refers to *S. boa* and *S. beanii* as the most abundant species. Therefore, explicit work of diversity and abundance of fishes inhabiting Bay of Biscay canyons might be needed to have more precise functional niche overlap estimations.

Here, using morphological measurements alone highlighted clear differences among species, with segregation along functional traits. Yet, using only morphological traits to describe mains functions has some limits (da Silva *et al.* 2019). Indeed, Grossman (2009) showed that species with strong morphological divergences sometimes use the same resources in a similar way, whereas morphologically close species can have very different diets. In order to overcome the limits imposed by their morphology and/or habitat for the acquisition of food, organisms can indeed modulate their behavior and show great adaptability (Blondel & Bourlière 1979; Grossman 2009). In fact, if morphology sets limits to resource use, species usually display some plasticity to adapt to prey availability and environmental conditions (Ibañez *et al.* 2007; Sibbing & Nagelkerke 2000). Completing present results with other analysis could increase robustness and confirm firsts conclusions. For example, assessing trophic levels will inform on the accuracy of what we think is species functional specialization. To do so, Preciado *et al.* (2017) suggests that both stable isotope analysis and stomach content analysis give complementary, or even opposites informations. Considering few informations known about present studied species, additional analysis might also help drawing conclusions from functional analysis. Especially, examining stomach content can be useful when not enough functional traits were computed, or if the latters can not explain much of the variability found between species (Albouy *et al.* 2011). This will also informs on how, for deep-sea communities species, functional traits change regarding trohic level or diet, and thus, help interpretation of functional diversity assessment.

First, *A. olfersii* have the most distinct yet biggest niche of all studied species (see Table 6 and Table 4), with very differenciated morphological and habitat-related traits (see Figure 4). *A. olfersii* showed an atypical laterally compressed body, long lower jaw, superior-oriented gape-axis and absent/rudimentary gill rakers (see A.5). All these elements are consistent with *A. olfersii* being a predator, mainly feeding on teleostei juveniles, euphausiids and gelatinous organisms (Eduardo *et al.* 2020). These morphological features suggests that this species catch its preys from underneath, with what might be a succion mecanism. On the opposite side of the morphologic spectrum are found the elongated, short-head fishes, with (supra-) terminal oriented mouth. Because running the same analysis without pectoral fin related traits did not lead to *S.*

beanii overlapping neither *A. risso* or *S. boa*' ellipse, the differences observed between these three species on Figure 4 mainly relies on gill rakers type (absent for *S. beanii*, low-developped for *A. risso* and *S. boa*) and eye size, which are bigger for the two latest. These characteristics suggests that *A. risso* and *S. boa* have similar functional traits, in terms of morphology and habitat, which explains niches overlap on Figure 4.

All three species being primarily piscivorous top predators with sharp teeth, *S. beanii* has been reported having a generalist diet, feeding on wide range of preys (cephalopods, teleosts, crustaceans …) (Geidner 2008). Ultimately, this varied diet require less time and energy prospecting for food (Geidner 2008). This is consistent with *S. beanii*'s which seems to have a different swimming strategy than *A. risso* and *S. boa* (see PC3 on Figure 5). Conversely, the latter has a rather selective diet which is dependant of their hunting strategie (Sutton & Hopkins 1996). Because Stomiids uses lures to attract preys, they are dependants on preys appeal for lures to feed and target rather big ones, which narrows the range of potential preys (Geidner 2008; Germain *et al.* 2019). Yet, *S. boa* seems to have a rather spreaded niche surface (see 4), which might be explained by the fact it mainly feeds on Myctophidae, which is the most diversed family of the meso- bathypelagic ecosystems (García-Seoane *et al.* 2021; Sutton & Hopkins 1996).

Being opposed in Figure 4, *A.risso* and *A. olfersii* nonetheless seem to share some of their locomotion strategies, with their niche partly overlapping (see Figure 5). For the moment, being the only known species of its genus, very little is known about *A. risso* and recent studies highlights confusions between this particular species and what might be a new species, based on morphological differences (Ho & Duhamel 2019). Though lack of literature limits their intrepretation, our results suggests that both *A. olfersii* and *A.risso* might feed on same preys. If the first tend to have a wider spreaded global niche (see Table 4), the latter seems to have a wider range of potential preys (see Figure 5). Moreover, *A. olfersii* is the only species that has a stretched niche along PC3, while all other species displayed on Figure 5 tend to have it stretched along PC4 . This might indicate a narrower range of prey diversity, which could be linked to the differences in feeding behavior showed on PC1 (see Figure 4) . Finally, it is interesting to notice that despite close phylogenic history between *S. boa* and *A. olfersii*, both belonging to Stomiiformes order (see Figure A.1), no similarities in niche's occupation were found. This suggest that, when looking at how species share resources, functional traits overrides the effects of phylogeny (Kremer *et al.* 2017).

Overall, all four species located in the periphery of Figure 4 have the most extremes morphology of all eleven studied species and live in deeper waters (Froese & Pauly 2019). Differenciated from the resting seven species along head anatomy (PC1) and food-acquisition related features (PC2), these species all are mesopelagic top predators, confirming the observed relation between oral anatomy and trophic level (Colborne *et al.* 2013; Wainwright & Richard 1995). Consistent with Farré *et al.* (2016) observations, redundancy seems to decrease with depth, as these four deep-living species show null/low redundancy and have the four most distinct niches (see Table 6). Therefore, these four species occupies different niches and are not likely to be competing

(Mouillot *et al.* 2005).

On the other hand, high overlap is found in Myctophidae, Platytroctidae and in between these two families (see Figures 4 and 5). Indeed, the six species can hardly separated based on the morphology of their body and head (PC1), their feeding strategies (PC2), their diet (PC3) and prey selection (PC4), suggesting similar use of resources. Morphologically, these species are all characterised by a rather large and elongated body, supra-terminal oral orientation, well-developped gill rakers and the presence of photophores (except *N. operosus*). Both families have relatively big eyes, which are highly specialised for dim-light environments and detecting/localizing sources of light (de Busserolles *et al.* 2014; Novotny 2018). Platytroctidae also display a luminous organ, called shoulder organ, that produces light through bioluminescent fluid that appears to disorient predators (Novotny 2018).

Mainly living at around 1000m deep (Froese & Pauly 2019), Myctophidae perform diel vertical migration to feed on wide variety of shallower-water zooplankton preys, which Platyctroctidae do not (Sutton 2013). Furthermore, Myctophidae are reported to be opportunistic predators, feeding on euphausiids, copepods, ostracods, fish eggs and larvae, depending on the available food and the habitat Catul *et al.* (2011); Kozlov (1995). Yet, Platytroctidae seems to have a more specialized diet, not being truly a generalist Novotny (2018). This may explain the segregation observed between the two families, with Myctophids' niches all overlapping one another, while both species of Platytroctidae overlaps each other too (see PC3 on Figure 5).

When looking at niches surfaces, *L. crocodilus* indeed displays the widest niche among these two families, four time the size of the smallest one (see Table 4). Eventually, this wider niche lead to overlap with functionally close species, such as *M. punctatum*, *C. maderensis* and *N. kroyeri* (Table 5). The latter conversely display the smallest niche, overlapped by all species of Myctophidae and Platyctroctidae (Table 5). Because all six species have rather similar niches, size of niche might therefore inform on the way species partition resources (see Table 6). One hypothesis might be that species with wider niche have higher flexibility in resource utilisation and can thus feed on more diversed preys. For example, *L. crocodilus* wide feeding-niche can be explained by seasonal variations of prefered preys Fanelli *et al.* (2014). Conversely, species that have small niches might no switch prefered preys through time, because it is equally abundant all year or because they are not morphologically equiped to feed on other preys (Mejri 2009). An other hypothesis is the competition theory in which communities' structures are constraints by competition relationships, which make sense here regarding the similarity in niches of these species (Geange *et al.* 2011). Under this hypothese, the size of the niche is directly influenced by the availability of preys, which depends on what the other species of the community predate and how resources are shared.

In our case, *N. kroyeri* and *M. punctatum* have highly similar niches, the latter overlapping nearly 69% of the first (Table 5). Because *M. punctatum*'s niche is twice bigger , this might suggest that while both species are competing for the same resource, *N. kroyeri* is limited in its resource use by *M. punctatum* (see Table 4). For these two species, phylogenic closeness might

explain the likeness of niches, as it is linked to functional-trait diversity (Tucker *et al.* 2018). Indeed, traits density estimation showed very similar results for both species, which are 56% overlapping on the 17 functional-traits studied (see Figure 6). Overlap is the highest for traits that are linked to feeding and/or hunting strategies, suggesting that while the two species use the same resource, they also do it in the same way. Hence, *N. kroyeri* and *M. punctatum* could theoretically compete, especially if the preys they feed on were to be less abudant.

Finally, *X. copei*, which is not Myctophidae nor Platyctroctidae but Alepocephalidae, is partly overlapping three of the latters niches, with resemblance in morphology and feeding strategy (see Figure 4 & Table 5). Yet, *X. copei* has the third widest realized niche of all studied species, mostly elongated, indicating a rather high morphological variability (see Table 4 & PC1 on Figure 4). Thus, no overlapping is found when looking at prey selection (see Figure 5). This species being the only one here to have pyloric caeca, it position along PC4 might be influenced by that specific feature, which plays a role in digestion for fishes. An other explanation might be the high variability of prey they feed on, depending on the habitat they are living in. Mauchline & Gordon (1983) indeed showed that, for this species, diet varied along life stage, with juveniles feeding exclusively on copepods and ostracods, while adults showed a much more diversed diet, including euphausiids and other fish from deeper waters.

Looking at overlap for each traits helps us to understand in which ways *X. copei* resemble to Myctophidae and Platyctroctidae. *X. copei* showed similar trait-density variation with most species of these two families, being the closest with *M. punctatum* (see Table 5). In particular, these two species are similar regarding at morphological features, such as body depth (o = 0.702), pectoral fin position (o = 0.719) and insertion (o = 0.85). For this latter trait (n°13 on Figure 6), high resemblance is found between *X. copei* and Myctophidae (except *L. croco*), while the two Platyctroctidae species look similar to one another. Finally, considering all these traits together suggest that despite high morphological and locomotion similarities, *X. copei* is unlikely to compete with neither Myctophidae or Platyctroctidae, because they are targeting different preys. Again, no obvious effect of phylogeny is found here, Alepocephalidae being evolutionnary close to Platyctroctidae (see Figure A.1), null/low overlap is found (see Table 5).

Conclusion

Because studies of functional diversity in submarine canyons communities are scarce, comparisons with other systems are limited. This work provides a first overview of how deep-sea fishes functional niches are structured in the canyons of the Bay of Biscay. We found that deep-sea fishes displayed significant functional diversity, which is consistent with Aneesh Kumar *et al.* (2017) and Carrington *et al.* (2021). Some of these species being functionally specialized, they are therefore not competing, conversely to what might be expected in such a nutrient-poor environment. These results are in agreement with Preciado *et al.* (2017), who showed that

these communities do not seem to display high dietary overlap, indicating a high degree of resources partitioning. Finally, overlap even seems to decrease with depth, because specialization is stronger (Carrassón & Cartes 2002; Farré *et al.* 2016).

Furthermore, having better knowledge of these communities is crucial to evaluate their vulnerability facing disturbance of ecosystem. Carrington *et al.* (2021) highlighted that, if diversity in deep-sea ecosystems is not to be questionned, very little is known about the way species inhabiting these systems might respond to pressures shifting. Because diversity range within an ecosystem is a good indicator of its health, measuring functional diversity might help quantify the effect of environmental disturbance Carrington *et al.* (2021); Villéger (2017). Despite being, currently, rather spared by anthropic influence, deep-sea ecosytems are nonetheless facing several threats. With the improvement of technology, deep-sea exploitation, and especially fishing, is increasing (Carrington *et al.* 2021). Yet, because of their slow life histories and the complexity of their diversity, deep-sea communities might be more sensitive to biodiversity loss than shallow-water communities (Carrington *et al.* 2021; Danovaro *et al.* 2017). An other concerning issue that deep-sea communities is facing is ocean pollution. In particular, submarine canyons being conduits linking shallow to deeper waters, they are particularly exposed to pollution coming from continental shelf. In particular, studies have shown high density of marine litter in Bay of Biscay's canyons (van den Beld *et al.* 2017a). Being mainly microplastic, this pollution affects all water column, from pelagic to deep-sea species (Pereira *et al.* 2020). Metalic and organic pollutants contamination has also been reported for deep-sea communities (Spitz *et al.* 2019).

Finally, climate change could be the most influent yet harder to quantify threat of all for these communities. Inhabiting deep-sea environments for million of years, meso- and baythpelagic species had to adapt to previous changes, but none was as fast and intense as the current one (Catul *et al.* 2011). In particular, by 2100, ocean warming is projected to induce an 1°C increase in deep-waters, reducing oxygen concentrations and acidifying water (Danovaro *et al.* 2017). These changes are foreseen to be even more important in shallower waters, on which deep-sea communities feed on, with already happening changes (Danovaro *et al.* 2017). Ultimately, this will affect capacity of these community to recover from other disturbance, with potential detrimental impacts on their metabolism, growth rate and reproduction success. Because of their essential role, ensuring energy transfer from shallow to deep-waters, health of meso- and bathypelagic communities is key determining the whole trophic chain (Davison *et al.* 2015; Gaskett *et al.* 2001). If deep-sea fishes abundance were to decrease, the established relations between competing species will change, with repercussion on higher trophic levels. Aïssi *et al.* (2012) and Kenchington *et al.* (2020) emphasized the importance of canyons deep-sea communities as major food supply supporting whale, large pelagic predators and also marine birds.

To mitigate global change effects on deep-sea communities, and thus others compartments, an effective management of these resources have to be decided. To do so, a much complete un-

derstanding of functional diversity and composition of these communities is required, and could help predict impact and responses to global change and exploitation (Carrington *et al.* 2021; Dumay *et al.* 2004; Kremer *et al.* 2017). Special effort should be made to expand knowledge on biology, life history and trophic relations of deep-sea communities, which is essential to adress the additive effects of human pressures and global change (Danovaro *et al.* 2017).

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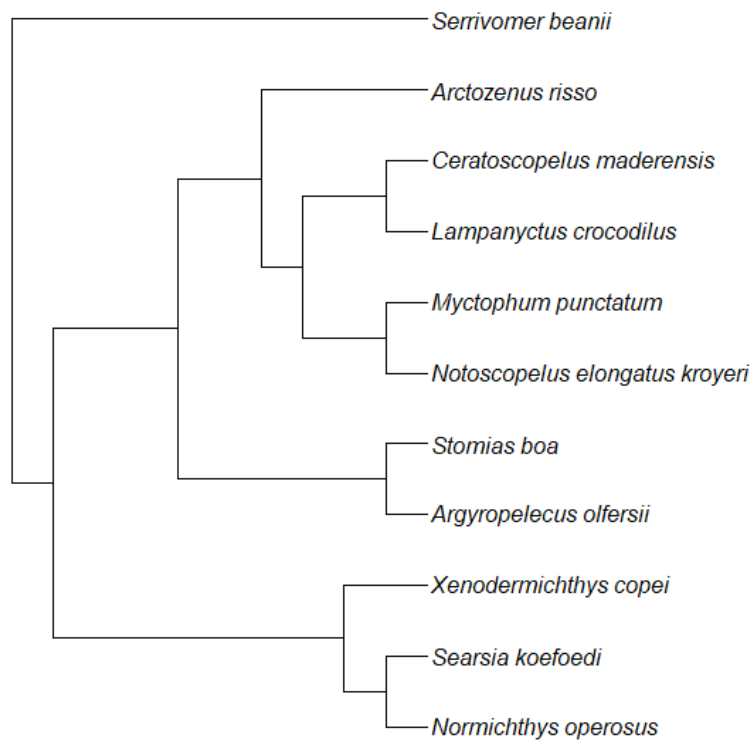
Appendice

Figure A.1: Phylogenic tree of studied species, using R *rotl* package (OpenTreeOfLife *et al.* 2019) .
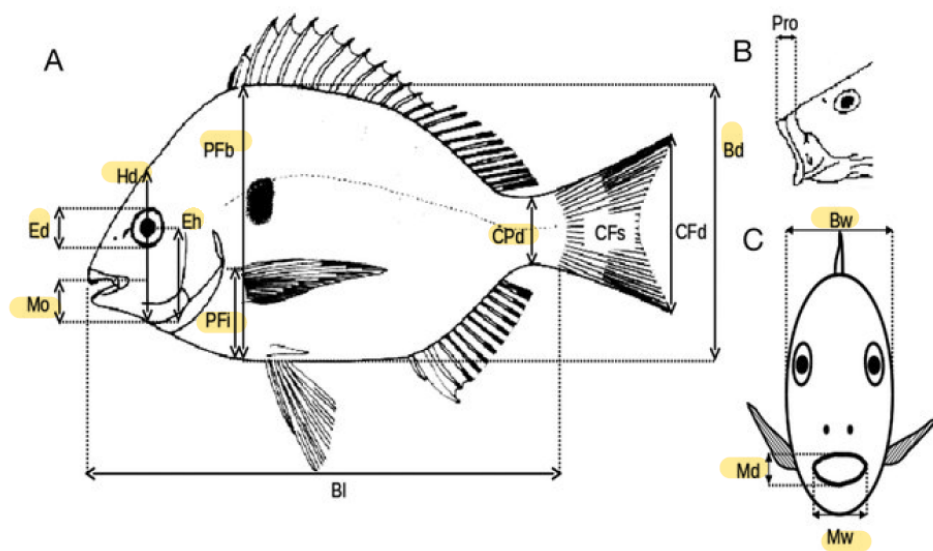
Figure A.2: Morphological measurements, from Albouy *et al.* (2011). `bd`, body depth; `bw`, body width;`cpd`, caudal peduncle minimal depth; `ed`, eye diameter; `eh`, distance between the bottom of the head and the eye center along the head depth axis; `hd`, head depth along the vertical axis of the eye; `md`, mouth depth; `mo`, distance between the tip of the upper jaw and bottom of the head; `mw`, mouth width; `pfb`, body depth at the level of the pectoral insertion; `pfi`, distance between the insertion of pectoral fin and the bottom of the body.
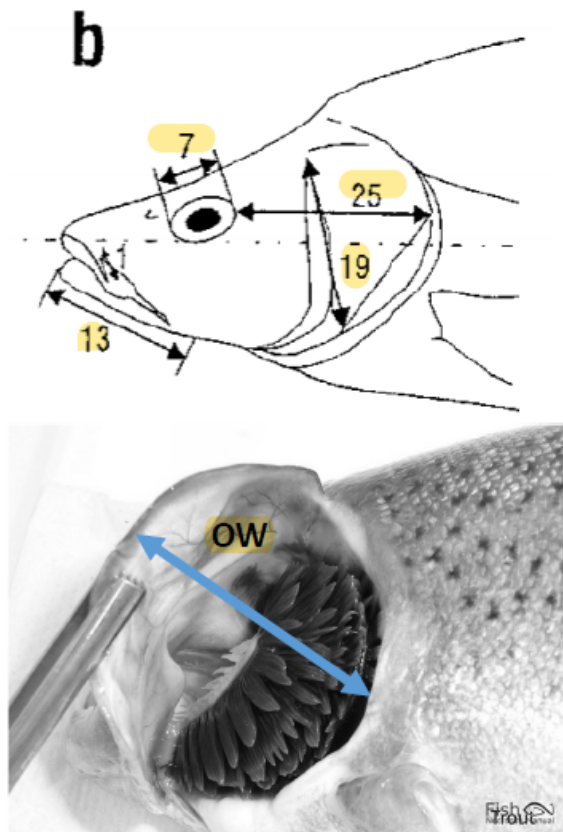
Figure A.3: Morphological measurements of the head, from Diderich (2006), following Sibbing & Nagelkerke (2000). 7 being `ed`, eye diameter; 13 `ljl`, distance between the tip and the insertion point of lower jaw; 19 `od`, depth of the operculum from point of insertion to bottom; 25 `pol`, shortest distance between the eye and the end of the head; `ow`, operculum maximum width.
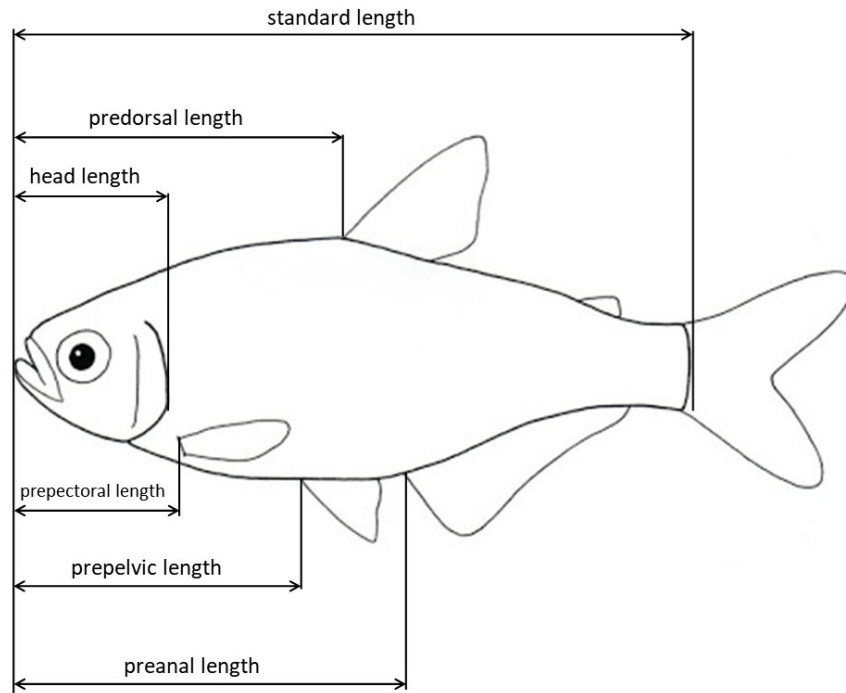
Figure A.4: Morphological measurements of the head and fins, adapted from Keat-Chuan Ng *et al.* (2017); Habib *et al.* (2019). `hl`, head length, from the nose to the closest-to-caudal-fin point of the operculum; `pal`, distance bewteen the tip of the nose and the insertion of anal fin; `pdl`, distance bewteen the tip of the nose and the insertion of dorsal fin, `ppl`, distance bewteen the tip of the nose and the insertion of pectoral fin; `pvl`, distance bewteen the tip of the nose and the insertion of pelvic fin; `sl`, standard length.
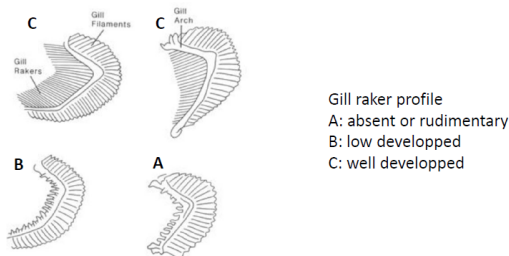
Figure A.5: Scores of gill rakers types `git`, based on their length.
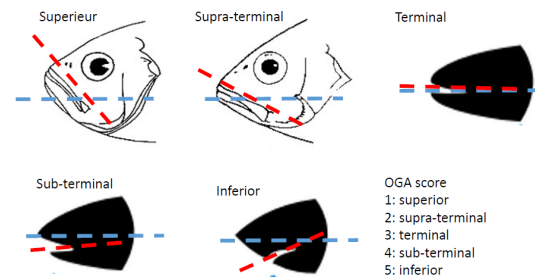

Figure A.6: Scores of oral gape axis `oga`, based on the angle between mouth orientation (red) and a fictive mid-depth lateral lign (blue).
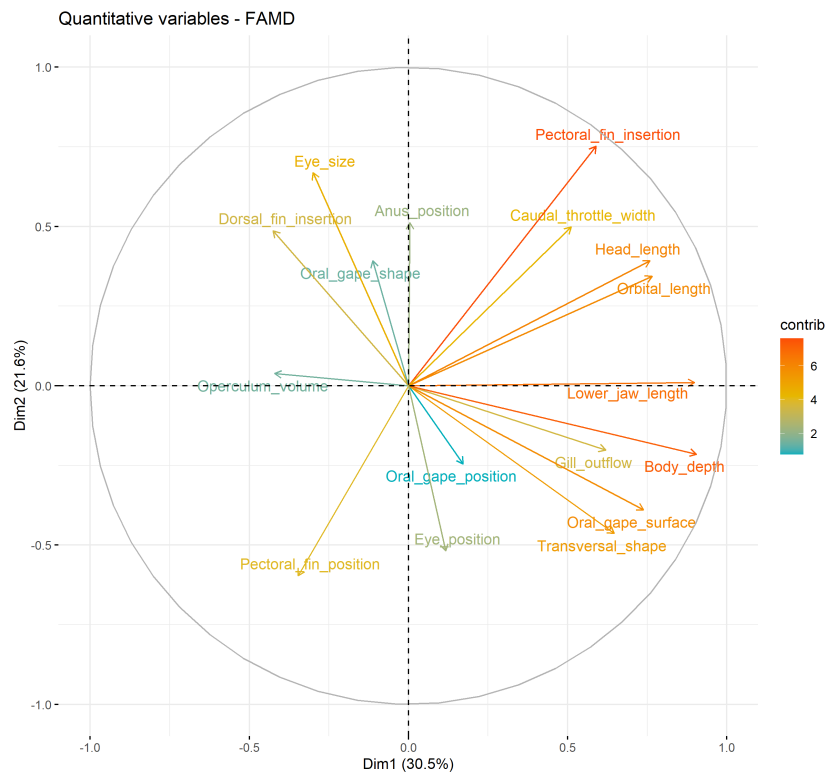
Figure A.7: Correlation circle of axis 1 and 2. The "contrib" variable refers to the representativity of the variable on the axis. The higher the value is, the more the corresponding variable contributes to the axis.
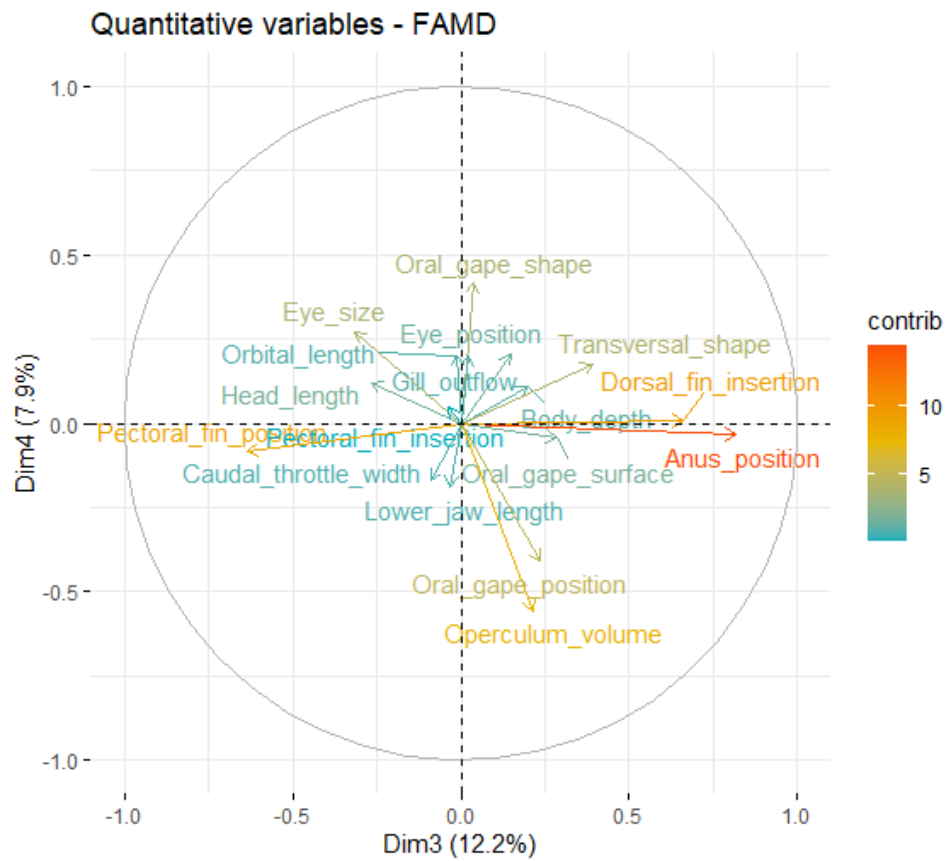
Figure A.8: Correlation circle of axis 3 and 4. The "contrib" variable refers to the representativity of the variable on the axis. The higher the value is, the more the corresponding variable contributes to the axis.

Abstract

The deep ocean is the largest biome of the Earth, yet, these extrem ecosystems remain mostly unknown, with only 0.001% of it having been investigated. At the interface between nutrients-rich continental waters to impoverished deep-sea waters, are found submarine canyons. Being highly heterogeneous, these habitats appears to be "biodiversity hotspots" and support many ecological services. Species and communities living in such habitat are understudied and very little is known on resource partitioning supporting co-existence of species and functioning of deep sea ecosystems. In this study, our objectives was to characterise functional diversity through morphology, of 11 common species of Bay of Biscay's canyons, and to measure the degree of overlap bewteen functional niches. Our results revealed significant differences in functional niches between species and in functional traits for species with relatively close niches. Ecological data being scarce on studied species, this work confirms that functional analyses is adapted to deep-sea fishes and that it give informations on the main functions performed by species. Finally, our results supports the hypothesis of high functional diversity in deep-sea ecosystems, promoting co-existence of species du to high resource partitioning. The present work is a first attempt to compare the morpho-functional characteristics and niche partitioning in the deep-sea fish assemblages from the canyons of Bay of Biscay.

Key words: Functional diversity, niche overlap, functional traits, resource partitioning, deep-sea fishes, Bay of Biscay, canyons.

Résumé

Les eaux profondes constituent le plus grand biome de la Terre, pourtant, ces écosystèmes extrêmes restent pour la plupart inconnus, seuls 0,001% d'entre eux ayant été étudiés. À l'interface entre les eaux continentales riches en nutriments et les eaux profondes appauvries, on trouve les canyons sous-marins. Très hétérogènes, ces habitats apparaissent comme des "points chauds de la biodiversité" et assurent de nombreux services écologiques. Les espèces et les communautés vivant dans ces habitats sont peu étudiées et l'on sait très peu de choses sur le partage des ressources favorisant la coexistence des espèces et le fonctionnement des écosystèmes d'eaux profondes. Dans cette étude, nos objectifs étaient de caractériser la diversité fonctionnelle, à travers la morphologie, de 11 espèces communes des canyons du Golfe de Gascogne, et de mesurer le degré de chevauchement entre les niches fonctionnelles. Nos résultats ont révélé des différences significatives dans les niches fonctionnelles entre les espèces et dans les traits fonctionnels pour les espèces ayant des niches relativement proches. Les données écologiques étant rares sur les espèces étudiées, ce travail confirme que l'analyse fonctionnelle est adaptée aux poissons d'eaux profondes et qu'elle donne des informations sur les principales fonctions remplies par les espèces. Enfin, nos résultats soutiennent l'hypothèse d'une grande diversité fonctionnelle dans les écosystèmes d'eaux profondes, favorisant la coexistence des espèces grâce à un partage élevé des ressources. Le présent travail est le premier se proposant de comparer les caractéristiques morpho-fonctionnelles et le partage de niche des assemblages de poissons des canyons du Golfe de Gascogne.

Mots clés : Diversité fonctionnelle, chevauchement de niche, traits fonctionnels, partitionnement des ressources, poissons d'eau profonde, Golfe de Gascogne, canyons.