

# Rapport stage M2

Moi même

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## **Acknowledgements**

## **Présentation de la structure d'accueil**

# Literature review

## 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 pressure, 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 degree 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).

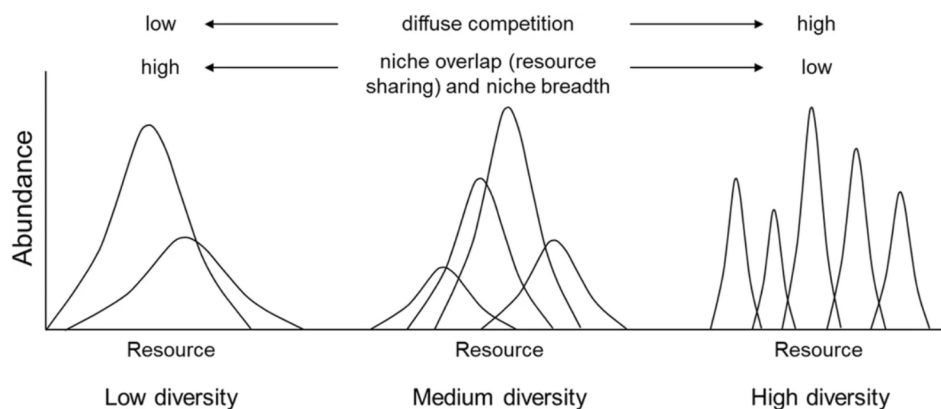


Figure 1: Characteristics of niches along a resource gradient at different levels of species diversity, from Kim & Ohr (2020).

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) developped 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 partitioning 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). *Moreover, 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 limiting 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).*

Conversely, when studying morphological trait associated with swimming performances, Webb (1984) noticed that most species were not specialized i.e not displaying any particular traits) and had fairly good performances in 3 of the main swimming methods (powerful short acceleration, cruise and maneuverability). Similarly, using only morphological traits to describe main functions such as food acquisition does not seem relevant. 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). The link between morphology and food acquisition is therefore not so robust.

While the flexibility and intrinsic variability 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 between 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 ecosystem 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.

## 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).

+ principe d'exclusion !!!

## Introduction

Deep-sea 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 epipelagic) zone, where the solar radiations are too low and precludes photosynthesis (Baker *et al.* 2020; Danovaro *et al.* 2017; Salazar *et al.* 2016) (see 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).

Despite these extremes 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

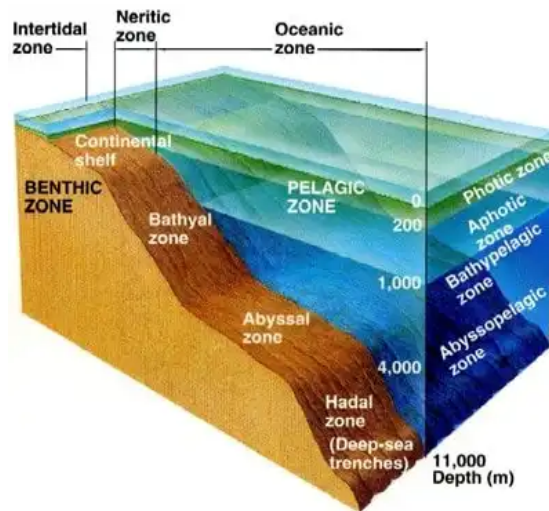


Figure 2: Sea layers along depth, from (fig 2018-06-17CDT19:13:06-05:00)

*et al.* 2016). Studies from Grassle & Maciulek (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 than 0.0001% of the area has been investigated so far and this whole 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 & Maciulek 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, 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 seachers to discover more about the depth of the oceans (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 chain (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). Because they are the main conduits transferring organic matter and sediments from rich and productive shallow shelf to the low-nutrients deep-sea, canyons constitutes peculiar habitats, with evidences of an important biomass and diversity of benthic organisms (Canals *et al.* 2006; Danovaro *et al.* 2009; De Leo

2012), but also of fishes assemblages (Sion *et al.* 2019; Stefanescu *et al.* 1994) around them. Indeed, canyons locally displays 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 favourable habitats for filters and suspension feeders (Fernandez-Arcaya *et al.* 2017; Sion *et al.* 2019), but also for low 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 those habitats (Aïssi *et al.* 2012). Specialized habitats, deep-sea canyons displays high level of endemism (Danovaro *et al.* 2009, 2017), are source of rich marine biodiversity and many services (Fernandez-Arcaya *et al.* 2017). Among those, canyons 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 those services, canyons enhance recruitment of commercialised 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, those 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 those 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 fishes play an important part of the biological pump (García-Seoane *et al.* 2021; Spitz *et al.* 2019). Meso- and bathypelagic fishes shows adaptations to their environment: 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, courtship behavior, with different patterns between males and females, and 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)

In terms of life history, Childress *et al.* (1980) and Salvanes & Kristoffersen (2009) observed some differences between meso- and bathypelagic fishes. The first are characterised by a relatively small size (2-15cm long), slow growth and have a rather long life span, with repeated reproduction and high reproductive rate. Conversely, bathypelagic fishes tend to have larger size, rapid growth but short lives and late reproduction, that seems to occur during the last year of their life. Yet, most of the life history traits of these fishes remains unknown and needs to be further investigated. 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).

If 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), very little is known about meso- and bathypelagic species inhabiting deep-sea canyons (Kenchington *et al.* 2020). Not only does this lack of information precludes comparisons between canyons, hence limiting the chances to highlight endemism, but it also restrains reliability of ecosystemics and biogeochemistry models (Davison *et al.* 2015; Kenchington *et al.* 2020). Indeed, given the essential role of these pelagic fishes in food webs, linking the epipelagic organic matter they feed on to the deep-sea, and in biogeochemical cycling, better knowledge of species constituting this fundamental compartment is crucial (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).

Studied here, the continental margin of the Bay of Biscay covers nearly half 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) (see Figure 3). If proven to be rich in cold-water coral reefs, the largest part of 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 virtually unknown (Kenchington *et al.* 2020).

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, give informations about how ecosystems are functioning and about their resilience facing a change in the environment (Dumay *et al.* 2004; Martini *et al.* 2020). Moreover, using functional traits to characterize functional niches of species provides informations of the relationships between species within an ecosystem, in terms of competition or adaptation (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 resources and the role they play in the ecosystem (Aneesh Kumar *et al.*

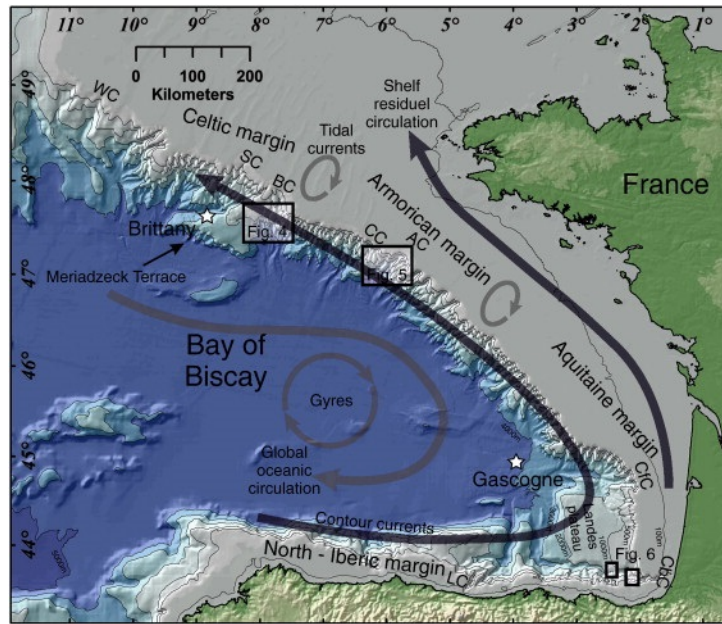


Figure 3: Location of the studied area, from (Mulder *et al.* 2012)

2017; Farré *et al.* 2016; Winemiller 1991). For fishes, this approach seems well suited, because morphological traits are considered being good indicators of ecological habits of species, indicating the way 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 and ecological factors that shapes ecological niches remains mostly unknown Aneesh Kumar *et al.* (2017); Farré *et al.* (2016). Because the conditions become more extreme and the food availability decreases with depth, deep-sea are often thought to be poor in terms of functional diversity, suggesting that competition is highly probable to access the little food available (Aneesh Kumar *et al.* 2017). Yet, Preciado *et al.* (2017) showed that these communities do not seem to display high dietary overlap, indicating a high degree of resources partitioning. Moreover, along depth, dietary overlap even seems to decrease because specialization is stronger (Carrassón & Cartes 2002).

Hence, the aim of this work is to assess functional diversity of deep-sea canyons fishes of the Bay of Biscay, which, for the moment, is barely known (Kenchington *et al.* 2020). Using functional traits to characterize functional niches of species, our main goals are (i) to characterise functional diversity of most-abundant canyon species, (ii) to measure the range and degree of overlap of functional niches and (iii) to explore the methods and parameters (number of individuals to measure, species, site) for this type of study. 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.

# 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*. 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 continental shelf. Pelagic trawling is performed during night, between 700 and 2000 meters, because those fishes perform diel vertical migrations and tends to come closer to the surface at nighttime. To this end, 25 meters-wide opening trawl is used, with as mesh size decreasing 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 species, and frozen at -20°C. Eleven of the most abundant species in the Bay of Biscay have been selected for this study. All teleost, 4 of them belong to the Myctophid family (lanternfish), which is the most abundant and widely spread 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 Platytrocididae with 2 species: *Searsia koefoedi* & *Normichthys operosus*. This family seems to be found in all oceans but not in Mediterranean Sea (Orrell & Hartel 2016). Finally, 5 families are represented by one species each: *Xenodermichthys copei* (Alepocephalidae); *Arctozenus risso* (Paralepididae), *Argyropelecus olfersii* (Sternoptychidae), *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 phylogenetic tree of studied species.

## 2 Morphological measurements and functional traits

In lab, fish were thaw and 24 morphological measurements were taken on individuals, using an electronic caliper with a precision up to 0.01mm. Part of these measurements had previously been taken by students from La Rochelle University during practical class from 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 (see Table 1).

Following what had been made on similar studies and according to our measurements, a total of 21 functional traits were computed from morphological measurements and informs on 3 main functions: food acquisition, locomotion and habitat (see Table 2).

Table 1: Number of individuals measured for each species, with their size mean and range values

Species	Previous measurements from students	Data acquired during this study	Total	Mean standard length (mm)	Size range (mm)
Lampanyctus crocodilus	39	0	39	107.60	73.3 - 146.5
Xenodermichthys copei	38	0	38	109.68	82.3 - 132
Normichthys operosus	0	38	38	104.69	75.64 - 131.62
Argyroteleus olfersii	37	0	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	0	30	30	546.17	373 - 879
Ceratoscopelus maderensis	0	30	30	62.72	53.29 - 78.95
Stomias boa	0	26	26	239.00	144 - 311
Myctophum punctatum	8	17	25	65.48	52.53 - 80.14

### 3 Data analysis

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

#### 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 SL) were standardized by SL to get rid and the interquartile range (IQR) method of outlier detection was applied to remove outliers. According to this method, for each variable (measurement) and for each species, outliers are defined as every value outside this interval:

$$[Q1 - 1.5 * IQR, Q3 + 1.5 * IQR]$$

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

Missing values that were previously presents in the data set ( $n=52$ ) and those induced by outlier removal function ( $n=307$ ), are then imputed following k-Nearest Neighbor (kNN) method, which as proven to be effective (Zhang 2012). Based on non-missing values points, kNN algorithm computes Euclidian distances between points, and assumes that missing value can be approximated by the values of points that are the closest. To this end *tidymodels* R package and *step\_knnimpute* function (Kuhn & Wickham 2020) were used, with a number of nearest neighbors ( $k$ ) of  $\sqrt{N}$ , with  $N$  being the number of observations, i.e individuals, of the dataset. Accuracy was then checked with linear regression of each variable with SL. From this cleaned dataset, functional traits were computed using formulas in Table 2.

#### 3.2 Factorial Analysis of Mixed Data (FAMD)

To assess similarity or differences in species in terms of traits, FAMD was performed. This type of analysis is suited for dataset containing a mix of qualitative and quantitative variables, and performs PCA (Principal Component Analysis) on quantitative variables and MCA (Multiple Correspondence Analysis) on qualitative variables. In the same way that PCA, FAMD is used to assess similarity/difference of individuals and to check for association between the variables. To this end, *FactoMineR* and especially *FAMD* function were used. Because *Serrivomer beanii*



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 B.2, B.3 & B.4. OGA, GIT, PC, PHT are categorical variables directly provided by raw measurements with GIT and OGA scores detailed respectively in appendices B.5 & B.6.

Function	Functional trait	Description	FORMULA
<b>Feeding</b>	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
	Operculum volume	Operculum volume (chercher à quoi ça sert)	OD/OW
	Head length	Maximum prey size	HL/SL
	Pyloric caeca	Presence/Absence of pyloric caeca	PC
	Anus position	Digestive tract length	PAL/SL
	Body depth	Swimming capacities of fish linked to their food prospection behavior	BD/SL
<b>Locomotion</b>	Pectoral fin position	Maneuvrability of fish	PFI/PFB
	Pectoral fin insertion	Insertion de la pectorale (chercher à quoi ça sert)	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 behavior (chercher à quoi ça sert)	PDL/SL
	Eye position	Position in the water column (pelagic/sedentary)	EH/HD
<b>Habitat</b>	Presence photophores	Presence/Absence of photophores (chercher à quoi ça sert)	PHT

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. AJOUTER LE FAIT QU'ON AIT FAIT DES ACP AVEC/SANS cette espèce et AVEC/SANS ces variables.

TROUVER COMMENT JUSTIFIER LE NOMBRE D'AXES A RETENIR. A HCPC

## 4 niche area overlap

Justifier qu'on calcule la surface des niches sur la 1ere FAMD car ce sont les axes qui portent le + d'infos etc...

# Results

## 1 Factorial Analysis of Mixed Data

The first 5 FAMD components explained 80% of the total variation (Table 3). The first axis (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 ( $a = 8.21$ ) (Table 3). Along this axis, all traits have increasing values toward the right (see C.7 for details). As can be seen on Figure 4, this axis clearly separates 3 groups of fishes. For low PC1 values, fishes have a low transversal shape (meaning that both BD and BW have similar values, consistent with an elongated body), short lower jaw and small oral gape surface, such as *A. risso*, *S. boa* and *S. beanii*. On the right of this axis, fishes display high body depth values suggesting a laterally compressed form, such as *A. olfersii*. The second axis (21.6% of explained variance) is correlated with habitat, through food prospection behaviour 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 axis separates the 3 species on the left, *A. risso* 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. Because *S. beanii* does not have pectoral fin, same analysis has been run without traits referring to pectoral or pelvic fins to look if discrimination between species were highly dependant if these traits. Same results than Figure 4 were obtained. Thus, without the entire *S. beanii* species, it seems that *A. risso* and *S. boa* are no longer overlapping. The third axis (explaining 12.2% of total variance) mainly carries traits linked to the diet, 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 axis, species are characterized by a rather high pectoral fin insertion and close-to-head dorsal fin insertion and anus position (see Figures 5 and C.8). Finally, the fourth axis (explaining 7.9% of variance) is mainly related to traits linked to prey selection, with *pyloric caeca* ( $a = 31.6$ ), *operculum volume* ( $a = 17$ ) and *presence of photophores* ( $a = 10.9$ ) (Table 3). The remaining PC scores (20% of variance) are mainly

linked to food acquisition. Overall, several species' ellipses are overlapping in both Figure 4 and Figure 5. In the first, all 4 Myctophidae and 2 Platytrocidae species, plus *X. copei* are more or less overlapping, not displaying much differences along PC1 nor PC2. On the same figure *A. risso* and *S. boa* seems to slightly overlap each other niches, which are mainly separated along PC2. *S. beanii* and *A. olfersii* are the only two species not showing any overlap. In Figure 5 *A. risso* and *A. olfersii* are showing some overlap. On the same figure, the same species (except *X. copei*) than Figure 4 overlaps. Especially, *N. operosus* and *S. koeoedi* 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* niches.

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

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

## 2 Functional niche area and overlap

The niche area estimation showed that *N. kroyeri* had the smallest niche, with *N. operosus* and *S. koeoedi* having slightly bigger ones (Table 4). In fact, all Myctophidae (except *L. crocodilus*) and Platytrocidae have rather small niches and are the one overlapping in Figure 4. Conversely, *A. olfersii* is the species with the biggest niche, more than 7 times wider than *N. kroyeri*. Bootstrapped niche area estimation function did not show any difference in the surface of estimated

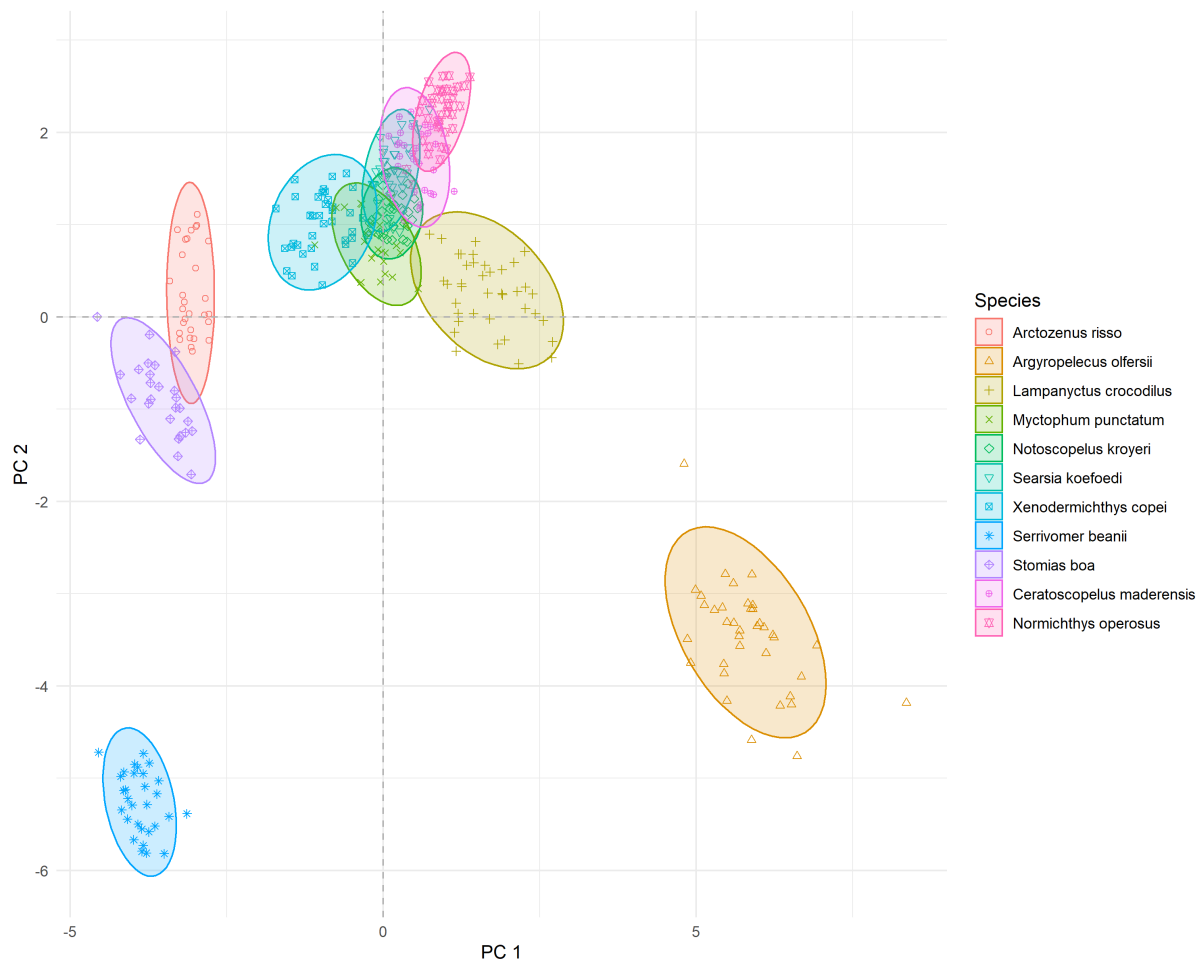


Figure 4: FAMD results for PC 1 and 2.

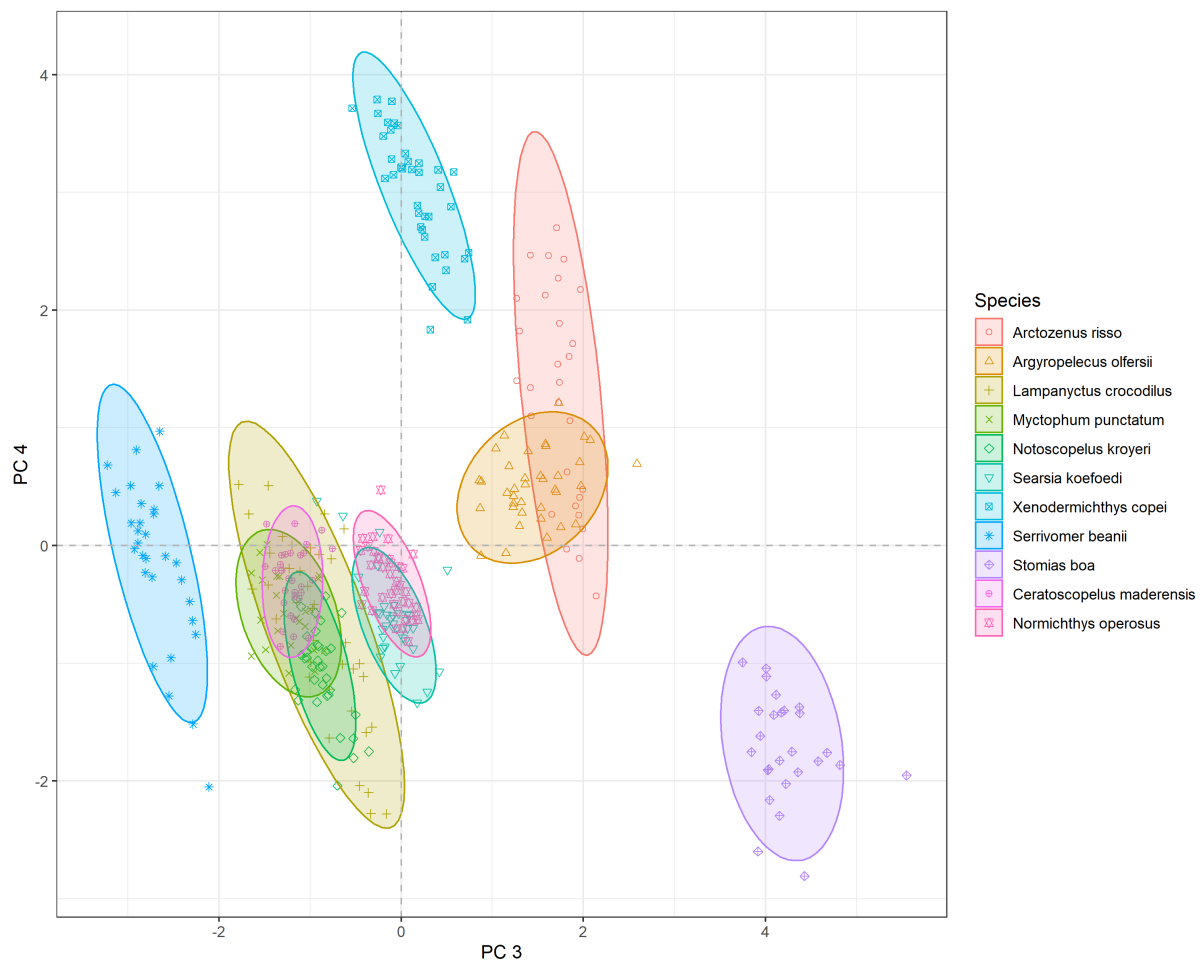


Figure 5: FAMD results for PC 3 and 4.

niche through sample size  $n$ . Areas values seems to be more influenced by the individuals sampled for estimation rather than the number of individuals itself. Yet, estimated niche area value are tightly converging for  $n = 30$ .

Table 4: Standardized area of functional niches.

Species	Area
<i>Argyropelecus olfersii</i>	7.39
<i>Lampanyctus crocodilus</i>	4.00
<i>Xenodermichthys copei</i>	2.60
<i>Stomias boa</i>	2.54
<i>Myctophum punctatum</i>	2.13
<i>Serrivomer beanii</i>	1.89
<i>Arctozenus risso</i>	1.78
<i>Ceratoscopelus maderensis</i>	1.75
<i>Searsia koefoedi</i>	1.33
<i>Normichthys operosus</i>	1.18
<i>Notoscopelus kroyeri</i>	1.00

Niche overlap analysis confirms that 7 species have overlapping niches and that smallest niches overlaps each other the most (Table 5). The maximum overlap is found between *M. punctatum* and *N. kroyeri*, as almost 76% of the latter's niche is covered by the first. In total, these two species share nearly 27% of their niches. Same observation is made between *S. koefoei* whose niche is 71% covered by *C. maderensis*. Finally, *N. kroyeri* and *S. koefoedi* are the species for which total overlap is the highest, with nearly 30% of their niches overlapping. As can be seen on Figure 4, these two species display rather similar niches, rather neutral in terms of differentiation along PC1 and PC2. Finally, *N. kroyeri* and *N. operosus* show minimum total overlap value of 0.31%. This is due to some individuals of the latter in *N. kroyeri*'s ellipse (see 4).

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

Species1	Species2	Overlap of Species 2 over Species 1 (%)	Overlap of Species 1 over Species 2 (%)	Total overlap (%)
<i>Searsia koefoedi</i>	<i>Ceratoscopelus maderensis</i>	65.44	49.64	28.23
<i>Notoscopelus kroyeri</i>	<i>Searsia koefoedi</i>	65.38	49.17	28.06
<i>Myctophum punctatum</i>	<i>Notoscopelus kroyeri</i>	32.28	68.69	21.96
<i>Myctophum punctatum</i>	<i>Xenodermichthys copei</i>	44.86	36.64	20.17
<i>Ceratoscopelus maderensis</i>	<i>Normichthys operosus</i>	31.77	47.10	18.97
<i>Notoscopelus kroyeri</i>	<i>Ceratoscopelus maderensis</i>	41.58	23.72	15.11
<i>Myctophum punctatum</i>	<i>Searsia koefoedi</i>	20.27	32.44	12.48
<i>Searsia koefoedi</i>	<i>Normichthys operosus</i>	15.02	16.89	7.95
<i>Notoscopelus kroyeri</i>	<i>Xenodermichthys copei</i>	22.93	8.80	6.36
<i>Searsia koefoedi</i>	<i>Xenodermichthys copei</i>	17.47	8.92	5.90
<i>Lampanyctus crocodilus</i>	<i>Myctophum punctatum</i>	6.49	12.20	4.24
<i>Arctozenus risso</i>	<i>Stomias boa</i>	9.41	6.60	3.88
<i>Myctophum punctatum</i>	<i>Ceratoscopelus maderensis</i>	5.78	7.01	3.17
<i>Lampanyctus crocodilus</i>	<i>Ceratoscopelus maderensis</i>	2.50	5.70	1.74
<i>Lampanyctus crocodilus</i>	<i>Notoscopelus kroyeri</i>	1.20	4.79	0.96
<i>Notoscopelus kroyeri</i>	<i>Normichthys operosus</i>	0.46	0.39	0.21

### 3 Kernel density estimation

The estimation of kernel density overlap for functional traits of the 7 overlapping species of Figure 4 and concludes that these species are all overlapping for 7 of the 17 computed traits (see figure 6). 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* and *M. punctatum* have very similar distributions. When looking at these 2 species only, analysis show that they are overlapping for every 17 traits, with particularly high values for eye size ( $o = 0.915$ ), gill outflow ( $o = 0.882$ ), operculum volume ( $o = 0.901$ ), pectoral fin insertion ( $o = 0.828$ ) and caudal throttle width ( $o = 0.782$ ).

Table 6: Kernel density overlap values for the 17 computed traits. 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	<b>0.12</b>
3	Oral gape surface	0.00
4	Oral gape shape	0.00
5	Oral gape position	<b>0.34</b>
6	Lower jaw length	<b>0.16</b>
7	Gill outflow	0.00
8	Operculum volume	0.00
9	Head length	0.00
10	Anus position	0.00
11	Body depth	<b>0.25</b>
12	Pectoral fin position	<b>0.20</b>
13	Pectoral fin insertion	<b>0.01</b>
14	Transversal shape	0.00
15	Caudal throttle width	0.00
16	Dorsal fin insertion	0.00
17	Eye position	<b>0.29</b>

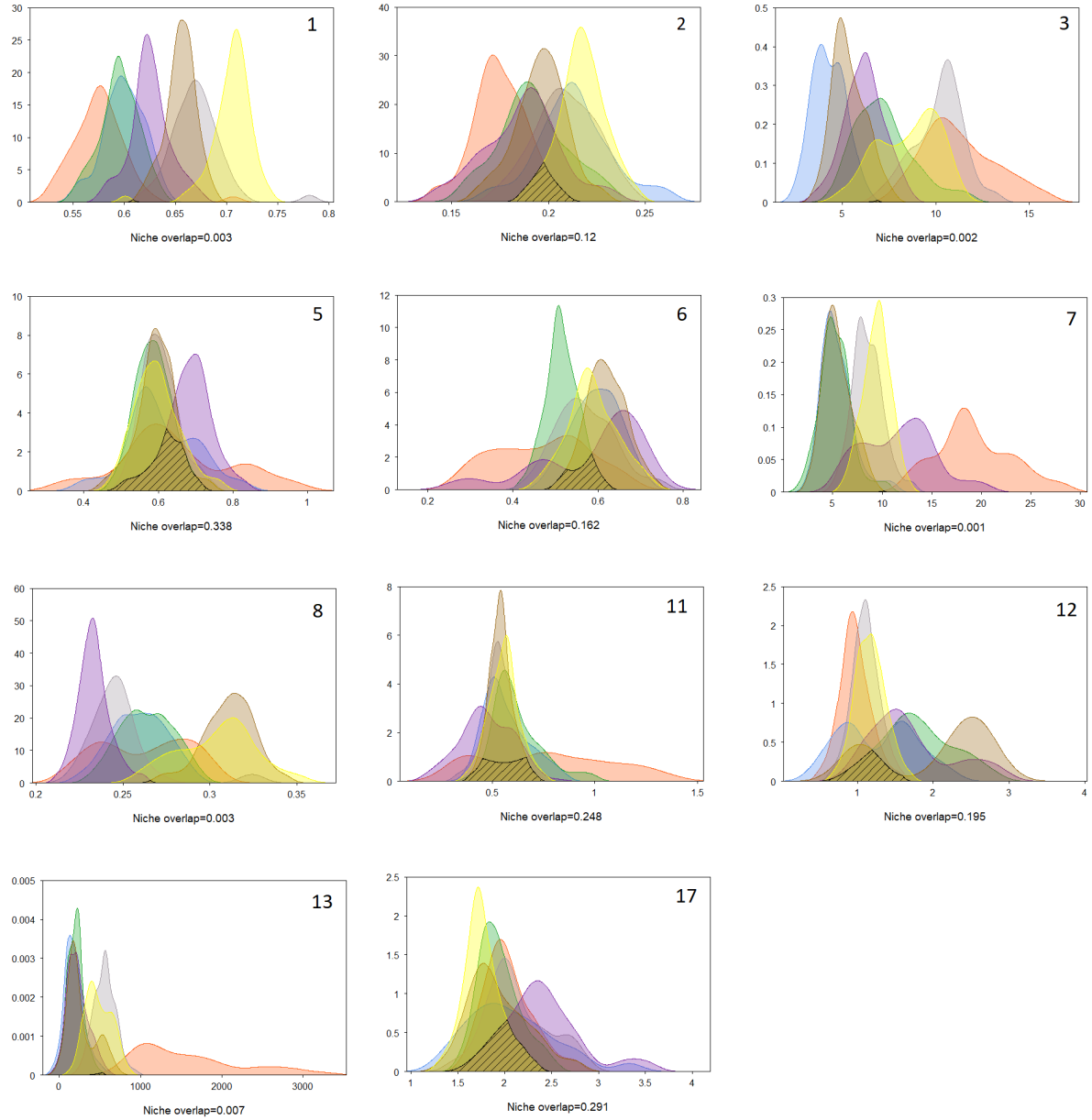


Figure 6: Kernel density overlap for 11 functional traits and overlapping species. Colors correspond to following species: orange - *L. crocodilus*; brown - *C. maderensis*; yellow - *N. operosus*; purple - *X. copei*; green - *N. kroyeri*; blue - *M. punctatum*; grey - *S. koefoedi*. Here, every traits that showed non-null overlap is displayed.



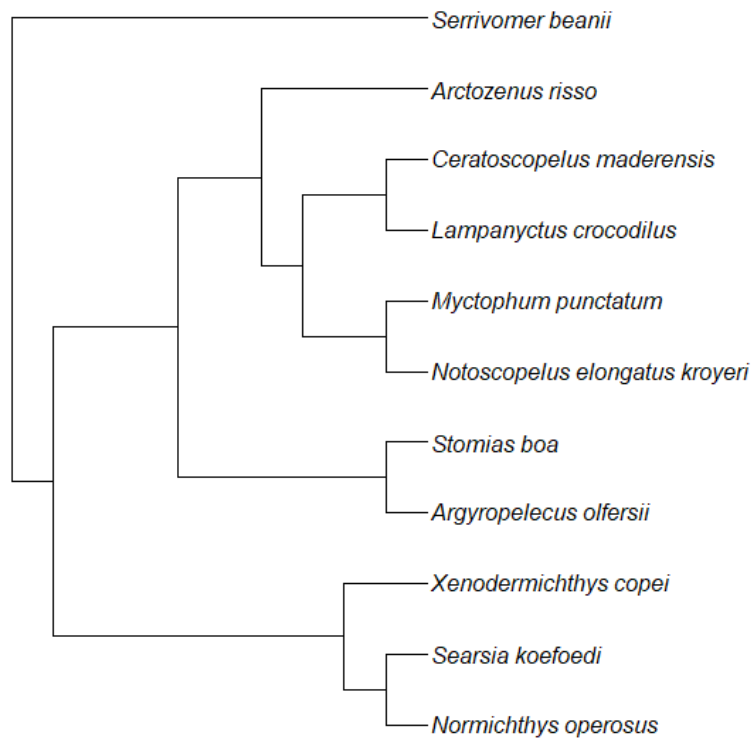


Figure A.1: Phylogenetic tree of studied species, using R *rotl* package (OpenTreeOfLife *et al.* 2019) .

## Phylogenetic tree

## Morphological measurements

## Correlation plot

## References

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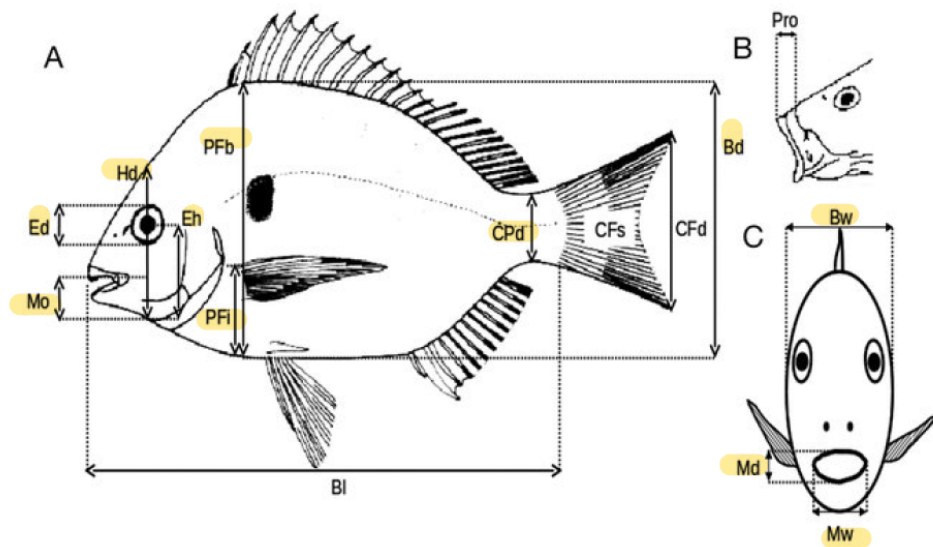


Figure B.2: Morphological measurements, from Albouy *et al.* (2011). BD, body depth; BW, body width; CPD, caudal peduncle minimal depth; ED, eye diameter; EH, distance between the bottom of the head and the eye center along the head depth axis; HD, head depth along the vertical axis of the eye; MD, mouth 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.

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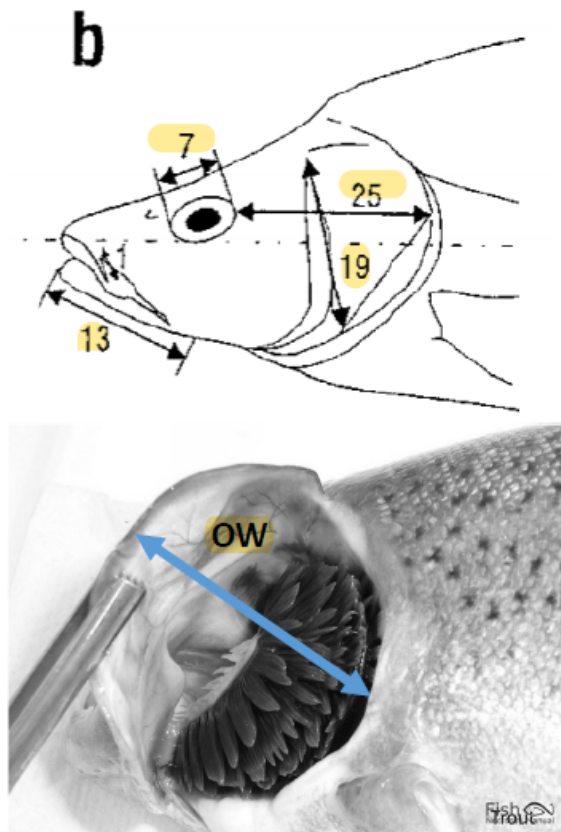


Figure B.3: Morphological measurements of the head, from Diderich (2006), following Sibbing & Nagelkerke (2000). 7 being ED, eye diameter; 13 LJL, distance between the tip and the insertion point of lower jaw; 19 OD, depth of the operculum from point of insertion to bottom; 25 POL, shortest distance between the eye and the end of the head; OW, operculum maximum width.

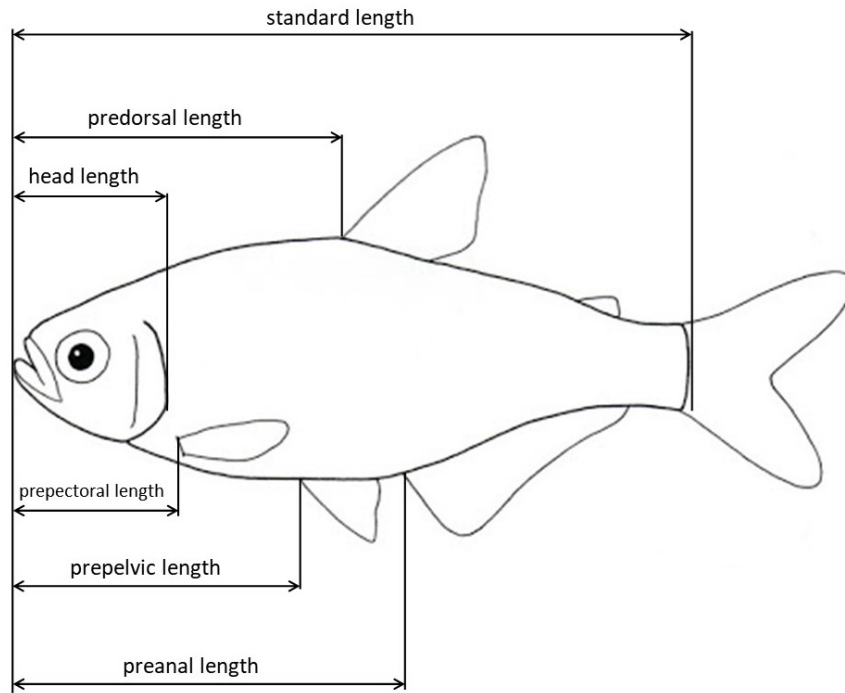


Figure B.4: Morphological measurements of the head, adapted from Keat-Chuan Ng *et al.* (2017); Habib *et al.* (2019). HL, head length, from the nose to the closest-to-caudal-fin point of the operculum; PAL, distance between the tip of the nose and the insertion of anal fin; PDL, distance between the tip of the nose and the insertion of dorsal fin; PPL, distance between the tip of the nose and the insertion of pectoral fin; PVL, distance between the tip of the nose and the insertion of pelvic fin; SL, standard length.

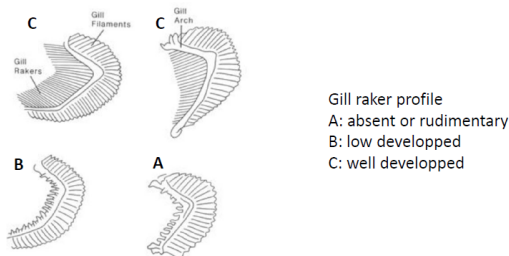


Figure B.5: Scores of gill rakers types GIT, based on their length.

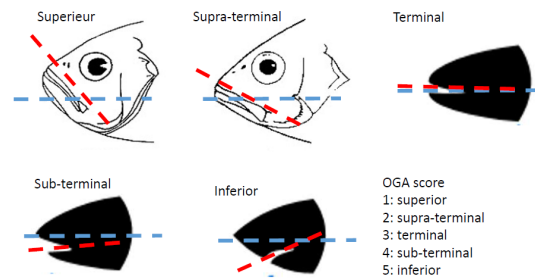


Figure B.6: Scores of oral gape axis OGA, based on the angle between mouth orientation (red) and a fictive mid-depth lateral line (blue).

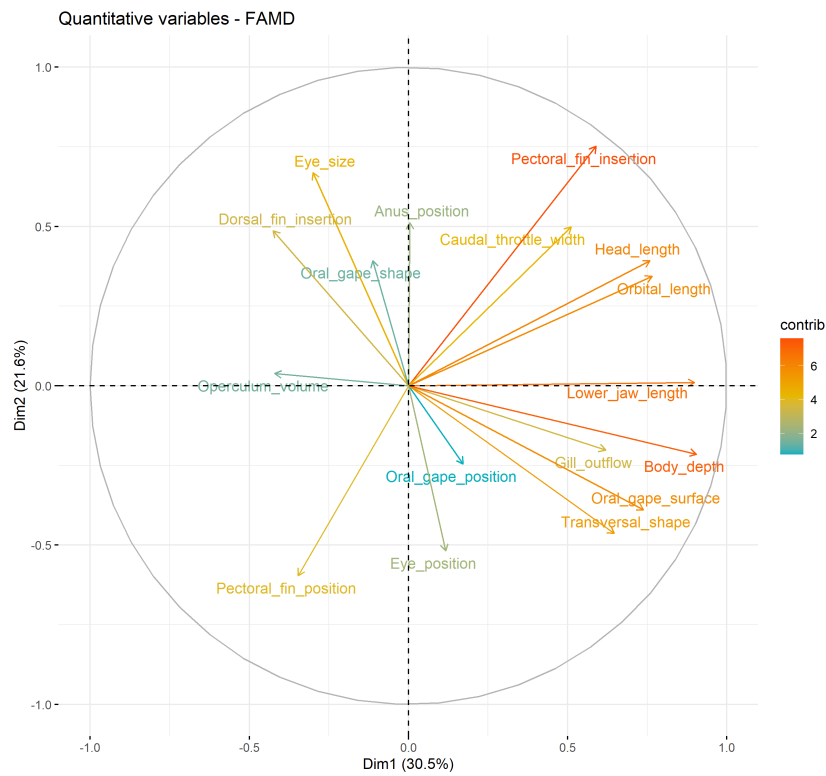


Figure C.7: Correlation circle of axis 1 and 2. The 'contrib' variable refers to the representativity of the variable on the axis. The higher the value is, the more the corresponding variable contributes to the axis.

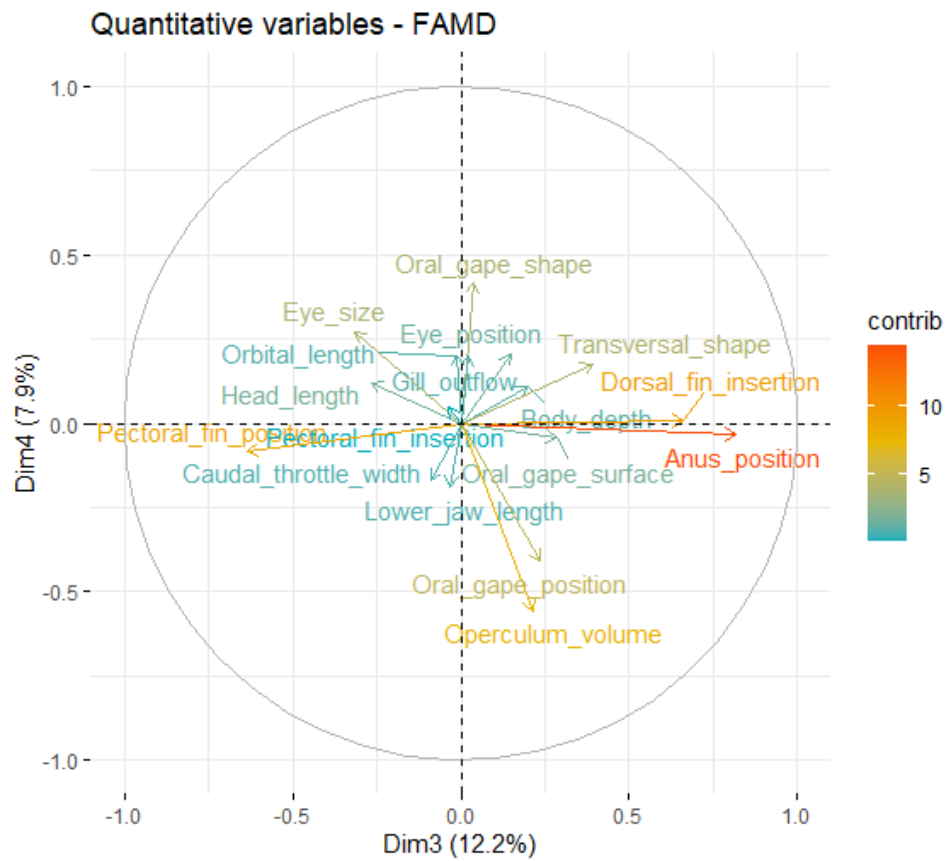


Figure C.8: Correlation circle of axis 3 and 4. The 'contrib' variable refers to the representativity of the variable on the axis. The higher the value is, the more the corresponding variable contributes to the axis.

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