Marine Coastal Ecosystems Biodiversity and Services in a Changing World

MaCoBioS

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Deliverable 1.1

Report on estimation of biodiversity dimensions at large scales in each targeted marine region and link with ecosystem services provision

WP 1 – Marine coastal ecosystems biodiversity, functions and services in a changing environment

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1. Roles of biodiversity and socio-environmental context to sustain ecosystem services

Humans have profoundly impacted Earth's ecosystems to the extent that we have generated a new geological era - the Anthropocene (Crutzen, 2016). Despite an ancient and profound link between humans and the sea, one of the main attributes of this era is the human footprint on marine ecosystems worldwide (Halpern et al., 2019; Norström et al., 2016). Human activities can affect marine and coastal areas due to direct, local- and regional-scale impacts on biodiversity, habitats, and ecosystem processes, or via global-scale changes such as climate change, which are pushing marine ecosystems towards their resilience limits, compromising overall ecosystem functioning and, therefore, the provision of ecosystem services (Singh et al., 2019).

Ecosystem services derive from ecological functions that sustain and improve human life (Daily, 1997) (Figure 1). Despite the increased popularity of ecosystem services research (Zhang et al., 2019), there is still limited knowledge of their ecological rationale (Bennett, 2017) and the consequences of biodiversity loss on ecosystem services provision (Bennett et al., 2015). Yet, the conservation and the sustainable management of ecosystems and their biodiversity, which provide services through ecosystem functions, are at the core of the 'Intergovernmental Platform on Biodiversity and Ecosystem Services' (IPBES) and the 'Conference of the Parties to the United Nations Convention on Biological Diversity' (CBD) preoccupations (Díaz et al., 2019). Understanding how ecosystems deliver services under existing and future threats is fundamental for sustainable development in the Anthropocene. To address this, it is essential to develop ecologically informed methods to ensure the impacts of biodiversity loss on ecosystem services provision can be assessed. These methods need to consider multiple interactions between biodiversity and socio-environmental factors and also encompass non-linear ecological responses.

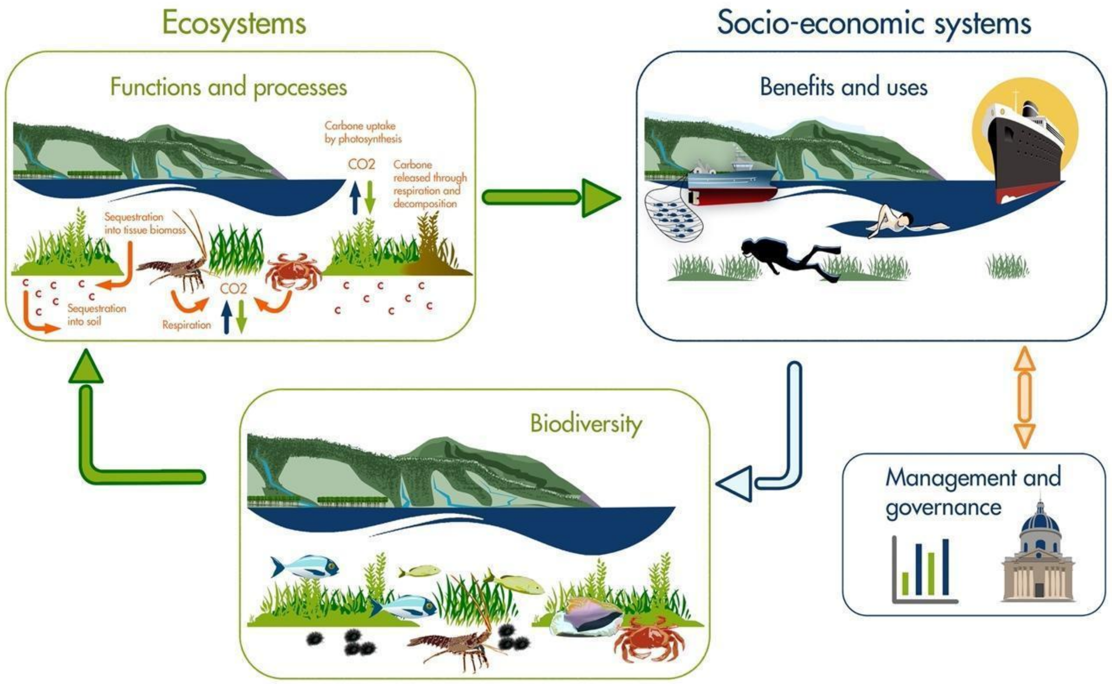

Figure 1. *The link between biodiversity, ecosystem functions and processes, and the benefits humans derive from ecosystems (conceptualised under the ecosystem services term). The management of human activities (e.g., the declaration of a marine protected area) has a direct impact on biodiversity and, thus, on ecosystem services.*

To date, experiments that quantitatively explore specifically biodiversity-function relationships in marine subtidal habitats are quite rare (but see Norkko et al., 2013; Thrush et al., 2014), but ecosystem models play an essential role in gaining scientific knowledge where empirical data are absent or partial. For instance, process-based models for community ecology, such as those based on Lotka–Volterra equations, can provide insights into the way that a loss of biodiversity may impact total biomass or abundance (Chalmandrier et al., 2021; Wang and Loreau, 2016). Population dynamics models also predict the consequences of biodiversity loss, including the local extirpation of rare species, on ecosystem functioning (Delalandre et al., 2022).

Despite these research efforts, knowledge gaps on inter-relations between human activities, biodiversity and service provision hinder the effective conservation of key marine ecosystems. Marine and coastal areas include some of the world's most heavily exploited ecosystems, as coastal zones host more than a third of the world’s population. Marine ecosystems such as seagrass beds, mangroves, coral reefs, and salt marshes have been widely acknowledged as crucial carbon sinks with a key role in climate regulation mechanisms on Earth (Duarte et al., 2013). They also provide climate change adaptation and mitigation through coastal protection, flood control, or biodiversity reservoirs, as well as non-material benefits for society (e.g., recreational space, aesthetics, cultural, and spiritual places) (IPCC, 2019). Nevertheless, marine and coastal ecosystems are threatened globally by ever-increasing environmental pressures, with negative consequences for human well-being (IPBES, 2018).

Marine and coastal ecosystems researched in MaCoBioS are among the most threatened globally, and yet, they are crucial for securing food supplies (e.g., fish communities from coastal hard substrates and continental shelves) and contributing to climate change mitigation (e.g., coral reefs and bioconcretions in continental shelves). In this context, it is fundamental to understand the links between human activities, biodiversity, and the provision of services in these areas, so that management can be effectively informed based on scientific data.

Based on scientific knowledge acquired before the start of the MaCoBioS project, it is known that different forms of biodiversity (species diversity, functional diversity, and phylogenetic diversity) are key to the provision of ecosystem functions and services at short spatial-temporal scales. The role of biodiversity in providing services at ecosystem and landscape scales is the focus of investigations in Task 1.1 of MaCoBioS. The study considers the sensitivity of these services to anthropogenic disturbance (extraction of resources, pollution, climate change) as well as to gradients (artificial or natural) across the system.

The methodological approach developed under Task 1.1 focuses on identifying the contribution of marine faunal diversity to functional diversity and, thus, the potential contribution to the provision of ecosystem services. Therefore, this work requires comprehensive diversity inventories, with a sufficient number of replicates to be able to estimate the relationships between biodiversity and functions. In addition, the study focuses on identifying the effects of human activities by considering variability in biodiversity over gradients of impact or protection.

This study relies on existing biodiversity inventories in four key marine coastal ecosystems in the three MaCoBioS ecoregions (Northwestern Mediterranean, Northern Europe, and the Lesser Antilles in the Caribbean) characterised by key coastal ecosystems (coral reefs, maërl beds, rocky subtidal habitats, and essential fish habitats over continental shelves).

2. Measuring the complementary facets of biodiversity and their links with Ecosystem Services

In this work, to establish a quantitative relationship between the biodiversity recorded in an ecosystem and its capacity to provide services, different dimensions of biodiversity, from specific to functional, were estimated. Due to the lack of empirical knowledge on the provision of regulating services that can be directly related to biodiversity in our case studies, we considered fish biomass as a proxy for the provisioning service. As quantitative information was obtained at the scale of biodiversity heterogeneity, the proposed model can be replicated in the future with additional variables representing different ecosystem services (e.g., carbon sequestration, hydrodynamic mitigation, nutrient flux).

2.1 The multiple facets of biodiversity

Biodiversity, i.e., the diversity of living organisms, is a multifaceted concept encompassing different scales (from landscape to individuals) and different biological attributes (from genes to ecological features)[1].

To unravel the drivers of ecosystem services, the most relevant level of biodiversity is species assemblage, that is, the scale at which species respond to environmental constraints and affect ecosystem processes (Hooper et al., 2005).

Hereafter, we provide an overview of the three dimensions of biodiversity that are relevant for studying its relationship with ecosystem services: taxonomic, functional and phylogenetic (Naeem et al., 2012) (Table 1).

Table 1. *Overview of the biodiversity facets assessed.*

		Information on species attributes		
		Biological units	Evolutionary lineages	Ecological traits
Information on assemblages	Species Presence	Taxonomic richness (number of species)	Phylogenetic richness (standardised sum of branch length linking all species on the phylogenetic tree)	Functional richness (standardised sum of trait-based distances between all species pairs)
	Species Dominance	Taxonomic entropy (exponential of Shannon index)	Phylogenetic entropy (extension of Shannon index to account for the evolutionary distance between species)	Functional entropy (extension of Shannon index to account for the trait-based distance between species)

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[1] IPBES; https://ipbes.net/glossary/biodiversity.

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2.1.1 Taxonomic diversity

Surveys for biodiversity assessments most often consist in identifying all (or a representative subset) of the organisms present in a standardised sampling unit (e.g., quadrat, transect, net) to the species level based on relevant taxonomic keys.

Hence, the simplest and oldest metric used to quantify biodiversity is the number of species present in an assemblage. This metric quantifies the taxonomic richness and depends only on the composition (i.e., presence of species), not on their respective dominance.

Because species dominance, expressed as cover, abundance, or biomass, could have a significant impact on processes supported by an assemblage, it is important to account for it using a complementary index. This facet is measured with the taxonomic entropy computed as the exponential of the Shannon index (Jost, 2006).

Taxonomic richness and taxonomic entropy are both Hill numbers indices. Hill numbers indices match key properties (e.g., doubling property) that make them operational and are all expressed in the same unit, allowing comparisons between indices from different facets (Chao et al., 2014).

2.1.2 Functional diversity

Taxonomic diversity considers all species ecologically distinct from each other to the same degree. However, species have different ecological attributes (e.g., size, diet) that determine their contribution to an ecosystem's functioning. Therefore, biodiversity assessments should also consider the diversity of functional traits, which are ecological attributes of organisms that drive their response to environmental factors and/or effects on ecosystem functioning (Violle et al., 2007).

Traits must be selected according to the taxa and ecosystem services studied and measured on all species present in the studied area.

Functional diversity is the variability in species trait values and is multifaceted (Mouillot et al., 2013), and thus, several functional diversity indices have been proposed for the last two decades (see review in Mouchet et al., 2010), mostly to unravel the rules driving community structure.

Recently, functional richness and functional entropy indices based on the Hill numbers framework have been proposed (Chao et al., 2019). Functional richness accounts only for the trait-based distance between species present in an assemblage, while functional entropy accounts for both the distance between species and their dominance.

2.1.3 Phylogenetic diversity

Functional diversity considers only the subset of traits for which information is available for all species. Hence, some traits that are hard to measure (e.g., physiology) could be missed or described roughly (e.g., through categories). As species with a similar evolutionary history tend to share similar biological and ecological features, accounting for the evolutionary lineages of species could explain links between species assemblage and ecosystem processes (Mouquet et al., 2012).

The first step towards measuring such phylogenetic diversity is to build the tree describing the evolutionary relationships between species (nodes being common ancestors and branch length time since divergence).

As for taxonomic and functional dimensions of biodiversity, phylogenetic diversity gathers richness and entropy facets that could be measured using the Hill numbers framework (Chao et al., 2010).

Phylogenetic richness accounts only for the sum of the lengths of all branches on a phylogenetic tree linking all species present in an assemblage. Hence, it is low when all species from an assemblage belong to the same genus and increases when species belong to distinct evolutionary lineages (i.e., distant on the tree). Phylogenetic entropy accounts for species dominance by weighting the length of branches linking species and thus increases when the dominant species are from distinct lineages.

Other phylogenetic diversity indices have been proposed but are either correlated to those based on Hill numbers or mostly relevant to test evolutionary or ecological rules (see review in (Tucker et al., 2017).

2.2 Computing biodiversity indices

A new R library to compute and illustrate functional diversity

Computing the many functional diversity (FD) indices published for the last decade is a key step in most ecological studies. However, there are several methodological pitfalls (e.g., selecting the best functional space) that could make such computation a challenging process.

The University of Montpellier's team has been coordinating the writing of an open-source library for the free software R, which is the most used software by ecologists. The library is named *mFD* and is available on a public repository (https://cran.r-project.org/web/packages/mFD/index.html).

This *mFD* library gathers 18 functions that allow to compute all FD indices with any type of traits and to illustrate those indices in a safe (through internal check of data) and reproducible way.

The key methodological aspects to consider when computing FD indices and the main features of the *mFD* R library are presented in an Open-access software paper published in 2022 in the *Ecography* journal (Magneville et al., 2022).

To further help ecologists and ecosystem managers to compute FD indices using the *mFD* package, we released a set of tutorials online presenting the different workflows (given types of traits available) with examples of codes (https://cmlmagneville.github.io/mFD/index.html)

2.3 Models to test links between biodiversity facets and ecosystem services

Structural Equation Modelling (SEM) is a rising statistical approach in ecology that allows to resolve complex multivariate relationships among a suite of interrelated variables. SEMs differ from classical statistical models in two main ways. First, they explicitly hypothesise causal relationships between variables instead of being based only on correlations. They are often represented using path diagrams to map the assumed causal links between all variables. Secondly, variables can be considered both as predictors and responses, allowing to test quantitatively indirect or cascading effects. Variables that are included only as predictors are called exogenous variables, whereas variables that are responses (they can also be predictors in other models) are called endogenous variables.

In the project, we took advantages of these aspects to analyse the potential multiple links between biodiversity, socio-environmental factors and ecosystem services in each case study (see section 3 for a detailed description of these factors). More precisely, we considered both direct and indirect links between socio-environmental forcing factors (e.g., temperature or protection measures) and ecosystem services, i.e., mediated or not by biodiversity.

The analyses were conducted with the R package *piecewiseSEM*, which uses the local estimation method. In this method, relationships for each endogenous variable are estimated separately and then pieced together. As such, we first performed a set of analyses using linear models where we predicted each biodiversity index separately with social-environmental factors as predictors. Next, to simplify these models and then the social-environmental factors predicting ecosystem services, we selected a parsimonious set of factors predicting each biodiversity index based on the AIC criteria. Then, the final model of each case study is parsimonious and includes direct links between socio-environmental variables and ecosystem services, but also indirect links between socio-environmental variables and ecosystem services through biodiversity indices. We finally assessed the goodness-of-fit of all SEM using the R-square that represents the explained variation in ecosystem services across samples for each case study.

2.4 Overview of the analyses done for the MaCoBioS project

The biodiversity dimensions and their link with ecosystem services provision were studied in 4 case studies (CS) (see Table 2 and the detailed description of each CS in Section 3).

These CS span the three ecoregions targeted in MaCoBioS (Caribbean, Mediterranean, Northern Europe) and exemplify different key subtidal ecosystems: coral reefs, rocky subtidal habitats, mäerl beds and continental shelf habitats. These biogenic and complex habitats host high species diversity and are nurseries for numerous marine species, including species of commercial interest. The inclusion of different case studies with variable data sets and sampling strategies aims at assessing the performance of the developed methodology in different scenarios.

These ecosystems studied were surveyed with either a spatial or a temporal design and include teleost fishes and benthic invertebrates (3 case studies with fish biodiversity inventories and 1 case study with benthic species inventories; Table 2). The study areas are also under the influence of human activities and/or subjected to protection measures, which allow to assess the effects of management and conservation schemes over diversity (and therefore, ecosystem functions and services).

Table 2. *Overview of the case studies.*

Case study	Country - Location	Survey design	Number of taxa
Mediterranean Sea - Benthos	Spain - Catalan coast and Balearic archipelago	104 sites over a trawl fishing effort gradient	304 invertebrate taxa with trait and phylogeny available
Mediterranean Sea - Fishes	France - Marseille area	Single site (“Podestat calanque”) with 3 zones surveyed using 4 Underwater Visual Censuses, once a year for 9 years (2012-2021 but 2018) before and after protection measures - 27 surveys	42 taxa, 40 fish species with trait and phylogeny available
Caribbean Sea - Fishes	Netherlands - Bonaire Island	115 sites surveyed at 2 depths (5 and 10m) with 2 Underwater Visual Censuses. Single year (2017) - 230 surveys.	83 taxa, 72 fish species with trait and phylogeny available
Northern Europe - Fishes	Ireland	Scientific trawling in 163 sites	100 taxa, 73 fish species with trait and phylogeny available

For the three CS with fish data, phylogeny was taken from the most complete and accurate source available to date (Rabosky et al., 2018) and that is available online (https://fishtreeoflife.org/), and through the *fishtree* R package (Chang et al., 2019). Fishes were described with 6 traits linked to fish roles (Villéger et al., 2017): size, home range, diel activity, gregariousness, vertical habitat and diet. The Caribbean and Mediterranean CS values were taken from a public dataset (Quimbayo et al., 2021). The Northern Europe CS values were coded by experts from Ireland using information from *FishBase* (http://www.fishbase.org).

In the CS with benthic species data in Spain, the vast diversity of invertebrate lineages prevents from accounting for a true phylogeny of all the taxa. We thus computed a cladistic tree based on taxonomic relationships (Phylum/Class/Order/Family/Genus/Species) using the *ape* R package (https://rdrr.io/cran/ape/man/as.phylo.formula.html). Traits considered for this CS then were size, lifespan, morphology, external structure, vertical habitat, mobility and feeding type. Values were coded by the experts in Mediterranean benthos from Consejo Superior de Investigaciones Científicas (CSIC, Spain).

The key ecosystem service considered for the three CS with fish data was the total fish biomass, as it is known to be a driver of provision, regulation, and cultural services. For the CS with benthos data, we considered fish diversity as a service linked to food provision (considering that the higher the fish diversity, the higher the availability of resources to the mixed demersal fisheries in the Mediterranean).

We assessed the richness and entropy facets of the three dimensions of biodiversity using indices from the Hill numbers frameworks (Table 1) for all CS. The dominance of species was then assessed as biomass for the three fish CS and was assessed through cover for the benthos CS.

All data processing was done following a reproducible workflow taking advantage of the R language and *Git* version controlling and of the open-source *RStudio* software and a *GitHub* online repository service.

In addition, we wrote a R function to compute the 6 biodiversity indices described in Table 3, taking advantage of already available R libraries (*entropart*, *mFD*); https://cran.r-project.org/web/packages/mFD/index.html. The package has now reached its 6th version through continuous progress during the project's lifetime. The related paper has already been cited 52 times at the time this report is being submitted.

All output variables listed in Table 3 for all case studies will be made available through the appropriate data repository upon publication of the deliverable.

Table 3. *Biodiversity indices computed in this study.*

Index	Meaning	Reference
BIO_Taxo_Ric	biodiversity index: taxonomic richness (number of species)	Chao et al. 2014
BIO_Taxo_Ent	biodiversity index: taxonomic entropy (exponential of Shannon index)	Chao et al. 2014
BIO_Func_Ric	biodiversity index: functional richness (sum of transformed pairwise trait-based distances between all species present)	Chao et al. 2019
BIO_Func_Ent	biodiversity index: functional entropy (weighted sum of transformed pairwise trait-based distances between all species present, an extension of the Shannon index with distances between species)	Chao et al. 2019
BIO_Phyl_Ric	biodiversity index: phylogenetic richness (sum of branch length linking species on the phylogenetic tree)	Chao et al. 2014
BIO_Phyl_Ent	biodiversity index: phylogenetic entropy (weighted sum of transformed pairwise trait-based distances between all species present, an extension of the Shannon index on a tree)	Chao et al. 2014
meth_qual	methodological indicator: percentage of total biomass (or cover) made by species with both traits and phylogenetic position known	
ES_biomfishes	ecosystem service: total biomass of commercial fishes	

2.5 Biological traits assigned to the species in MaCoBioS' case studies

A biological trait is a component of an organism's phenotype that influences ecosystem processes and its response to environmental factors (Petchey and Gaston, 2002). The biological traits approach applied to marine fauna uses morphological, life history and behavioural species characteristics to indicate aspects of their ecological role and performance of ecosystem functions (Bremner et al., 2003; Hinz et al., 2021; Törnroos and Bonsdorff, 2012). As roles performed by organisms are important in regulating ecosystem processes, a traits approach is useful to assess these processes and related ecosystem services (Bremner et al., 2006). It is generally accepted across a variety of ecosystem types and taxa that when the biological traits are carefully chosen, they extrapolate to function. For example, in marine systems, deep burrowing fauna increase the oxygen flow into the sediment and extend the total zone of denitrification, stimulating nutrient cycling as an important ecosystem service (Beaumont et al., 2007; Norling et al., 2007). Other traits such as body size and life span are related to ecosystem productivity (Jennings et al., 2001) and to food production services (Beaumont et al., 2007), while dispersal information is related to the ability of organisms to recover from a disturbance (de Juan et al., 2014).

While we did not intend to assess in details trophic interactions in the studies ecosystems, for both fish and invertebrate case studies, the main diet of species (coded as categories) was accounted for as well as other traits (activity, position, mobility) that affect roles of species in controlling food-web. In our case studies, based on benthic habitats, most trophic interactions occur across taxons (e.g., fish, benthic invertebrates, primary producers). Indeed, for each of the fish case study, very few species are piscivorous while most fishes are feeding on plants or invertebrates (including many sessile and mobile clades). We consider that functional diversity metrics are a proxy of trophic interactions between species and other biotic compartments. We would however suggest future studies should assess biodiversity metrics for each of the main compartments (plants, zooplankton, benthic invertebrates, mobile vertebrates) of marine ecosystems, which require further monitoring efforts to estimate biomass and relevant traits for each compartment based on their expected contributions to ecosystem services.

2.5.1 Fish traits

Fish play important roles in aquatic ecosystems, mainly through the regulation of food webs and nutrient cycling (Villéger et al., 2017). The ability of each species to impact these ecosystem processes depends on several biological traits linked to food acquisition and locomotion. For instance, the trophic impact of a species depends on its foraging activity: i.e., which prey items it targets, when, and how many. More particularly, an ambushing solitary benthic predator (e.g., scorpionfish) will not have the same trophic impact as a mobile pelagic gregarious predator (e.g., barracuda) on small fishes. Therefore, describing fish's functional niche requires considering a set of complementary functional traits. Here, we selected six traits that describe the main facets of fish ecology and that are available for a wide range of reef species (Villéger et al., 2017).

Body size has a primary role in defining a fish's ecological niche. More specifically, size determines the amount of energy required per unit of body mass and constrains prey-predator relationships because predator mouth opening width, which determines prey size, scales with predator body size. Size also influences growth rate, with small fishes growing faster than larger ones. Furthermore, the mortality rate tends to be higher for smaller fishes, whereas temperature tolerance is at least partly related to body size in reef fishes.

Diet, like size, is an essential component of a reef fish's ecological niche. Diet determines a fish's impact on ecosystem functioning through trophic interactions with other food-web components and, consequently, on nutrient cycling. Diet also mediates habitat requirements because some resources are restricted to certain habitats (e.g., epilithic algae).

Mobility determines energy needs, with mobile species requiring a lot of energy by mass unit compared with sedentary species. Mobility also affects the spatial extent over which fishes control their resources and transfer nutrients, especially between habitats around reefs.

The period of the day during which fishes are active has implications on the trophic role a species plays in the food web through both bottom-up controls (i.e., the set of resources it can target) and top-down controls (i.e., the susceptibility it has to being preyed upon). For instance, most nocturnal species escape predation during the day and vice versa.

The level in the water column occupied by a fish is critical for determining its ecological niche as it influences the set of potential prey available and the fish's impacts on nutrient transfer between vertical strata.

The gregariousness of fish is an important component of their behaviour that determines the ability to (i) escape from predation and (ii) impact local ecological processes, with schooling species inducing potentially massive nutrient cycling and resource depletion.

2.5.2 Benthic invertebrates' traits

Invertebrate species' biological attributes that describe certain aspects of their morphology and behaviour are used with the aim of approximating the ecological role of the species (de Juan et al., 2022). The combination of biological traits can inform functional roles in the ecosystem. For example, the abundance of large sessile suspension feeders increases habitat complexity and nutrient cycling, whereas the dominance of large burrowing deposit feeders increments the bioturbation potential of an area (Hinz et al., 2021). In this work, we selected a set of seven biological traits that cover aspects of the benthic organisms' morphology, feeding patterns and life histories, and are proxies for the benthic ecosystem functional potential.

These seven traits were broken down into categories. For example, feeding type was separated into the category's primary producer, deposit feeder, suspension feeder, grazer, opportunist/scavenger and benthivorous or piscivorous predator. Life history traits were not included in the analysis due to the limited data availability for Mediterranean benthic invertebrates (de Juan et al., 2007).

Size and age: inform the magnitude of the impact on ecosystem function that an organism can have, depending on other key biological traits exhibited by the organism.

Morphology and external structure: inform the sensitivity of the organisms to physical damage (e.g., storm, predatory aggression, fishing), but also on the ability of the organism to perform a particular function (e.g., habitat provision).

Habitat: the position of a benthic invertebrate over or within the sediments is related to biogeochemical requirements, niche creation, refuge, nursery, below sediment oxygenation and organic matter re-distribution, and habitat provision.

Mobility: this trait is related to the foraging mode, ability to escape predation, migratory requirements, and dispersal.

Feeding: this trait is related to the interaction of the organisms with their environment (e.g., species interaction through predation but also the interaction with the substrate through deposit feeding).

The combination of these biological traits is considered a proxy for the potential functional diversity of the benthic system (Degen et al., 2018).

3. Case studies description

3.1 Shallow coastal habitat in the western Mediterranean (south of France)

Marseille, a port city in the South of France, hosts nearly 900 000 people. The fisheries activity is a historical pattern of the city, mainly with small-scale boats using artisanal techniques near the coast. The fishing fleet is globally stable around 120 small-scale boats for net fishing and long-liners and 10 fishing trawlers.

It is in Marseille that the famous “calanques” are located. They are large or small bays surrounded by massive and steep limestone cliffs. The most represented coastal marine habitats in these calanques were subtidal rocky assemblages and seagrass meadows of *Posidonia oceanica*. As a result of coastal development, wastewater discharges and polluted rainwater runoffs, the seagrass meadows of the area were largely degraded and replaced by dead ‘matte’ and sandy beds. In addition, the remaining seagrass meadows are in poor ecological condition (Figures 2 a and b). The subtidal rocky assemblages are, therefore, a key habitat for the productivity of this area. This habitat hosts a photophilic algae canopy. The sessile primary producers and invertebrate filter-feeders assimilate the energy, while mobile biota occurs in the water column (Keith et al., 2020). This coastal habitat is referenced as an important nursery for the fish community (Cheminée et al., 2021, 2017), stressing its potential importance for the fishing stocks.

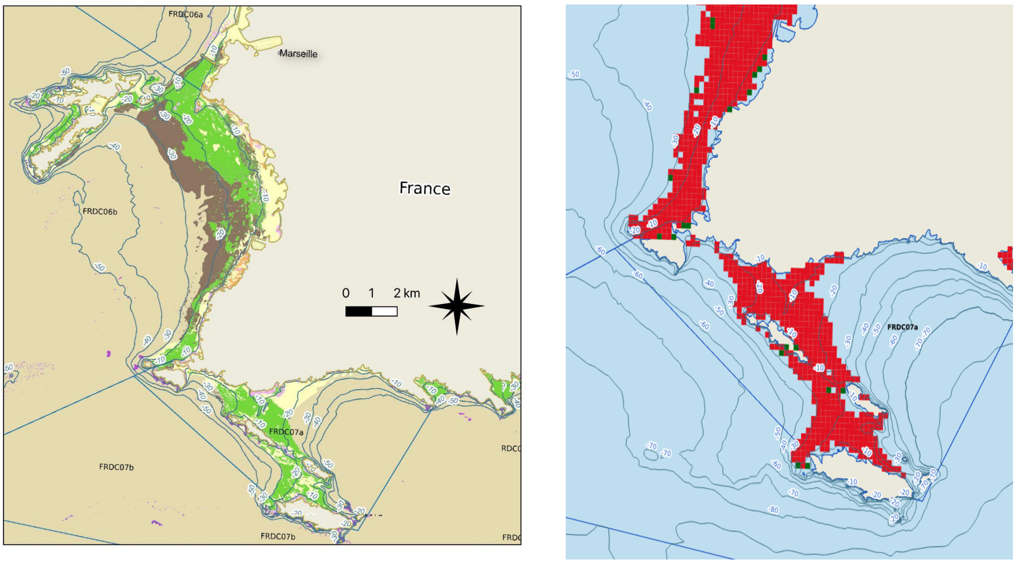

Figure 2. *Cartography of the marine and coastal habitats near Marseille. On the left (a), in yellow, sand beds; in brown, muddy areas; in pink and purple, rocky and coralligenous assemblages; in green, seagrass beds; in orange, shingles. On the right (b) ecological condition with, in red, bad ecological condition and, in green, good ecological condition (extracted from Medtrix, Andromède).*

The National Park of the Calanques was created in 2012. It is the only peri-urban National Park in Europe and the only one to be shared between mainland, insular and marine areas in the Mediterranean Sea. Due to the high level of cumulative pressures in this area, this Marine Protected Area (MPA) needs to address numerous challenges to increase biodiversity while preserving human activities. Several no-take areas were implemented inside this MPA. The main coastal No-take area is delimited by the “Pointe du Vaisseau” on the east coast, the “calanque de Podestat” on the west coast and the islands “Plane” and “Riou” on the south (Figure 3). This area includes the historical outlet of the Marseille wastewater. This outlet has the specificity to end at the surface along the shoreline, which reduces the dilution potential for marine and coastal habitats compared to the classical piped flow away from the shore. Even if a wastewater treatment plant was built in 1987, the remaining wastewater treated flow still impacts this coastal area. Interestingly, this is an unusual No-take area, including the high pressure of the wastewater flow that may drive the ecological condition, fauna communities and ecosystem services in a specific way.

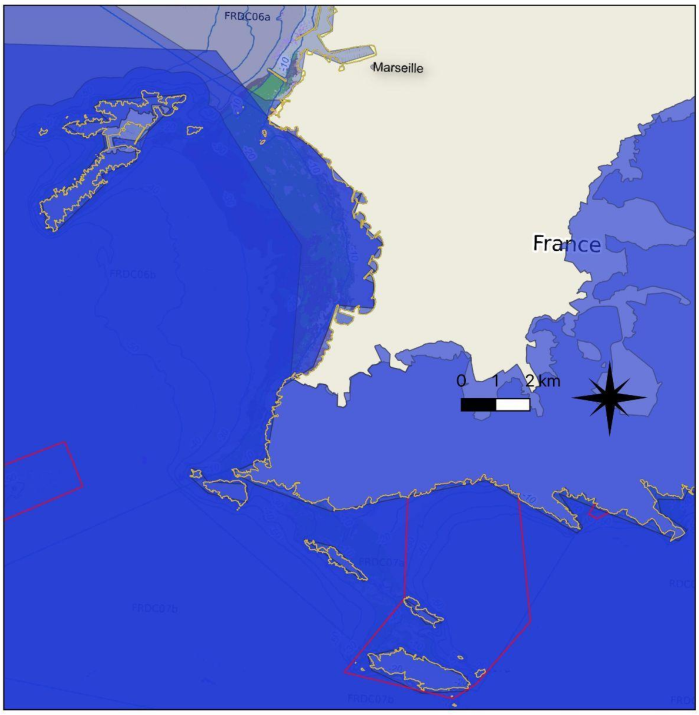

Figure 3. *In blue, Marine and Terrestrial protected areas around Marseille. In red, No-take areas of the National Park of the Calanques.*

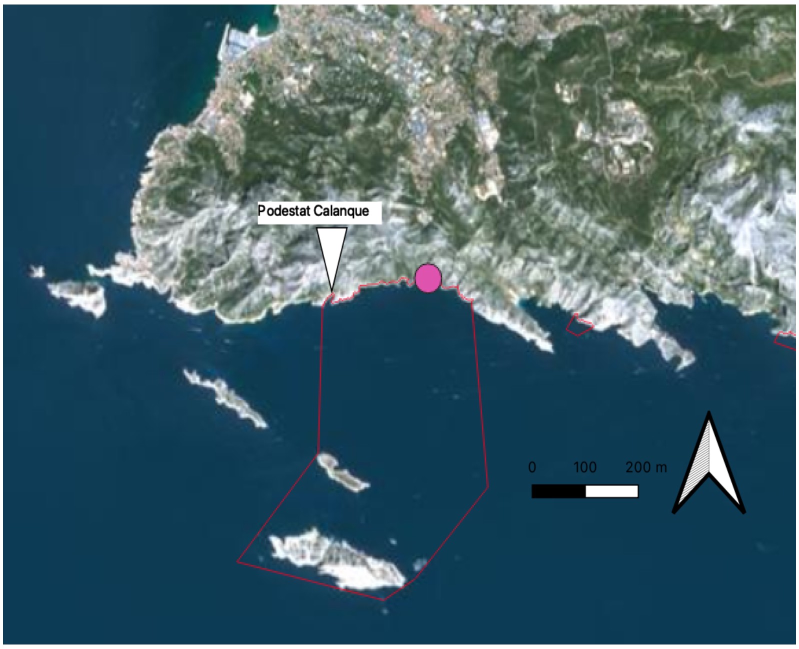

Figure 4. *France Case Study (Northwestern Mediterranean) showing the location of the sampling site that has been surveyed with underwater fish censuses for 9 years (white arrow). The pink dot shows the location of the outflow pipe from the wastewater treatment plant. The red line indicates a No-take area of the National Park of Calanques.*

3.1.1 Data collection and data sources

The survey (still ongoing) started in 2012 in the Podestat Calanques. The same year, the National Park of the Calanques was created and the Podestat Calanques became a fully protected area with the prohibition of all fishing activities (in red on the map, Figure 2). However, before 2015 enforcement of the surveillance and control of activities was not fully in place. The Podestat Calanques is located less than 2 km from the outflow pipe of the wastewater treatment plant of Marseille (Figure 4). This water flow was fully out of the norms until 2015, partially on the norms in 2016 and 2017 and in the norms since 2018 (the improved remaining flow is still impacting due to the quantity of water and the legal days without active treatment).

The area is surveyed a maximum of twice a year. Fish inventories were achieved by underwater visual census on permanent transects, mainly in rocky bottom areas with photophilic algae (the nature of the substrate was surveyed in 2012). The observations were performed along 4 transects of 25 x 5 meters, representing a total of 1500 m². Within each transect, all visible fish were counted except for small cryptobenthic species. The size (total length) of the individuals encountered is estimated to the nearest 2 cm or 5 cm for large individuals.

In summary, in the French case study, the data used for computing the diversity indices and the diversity-ecosystem services models came from one site (Podestat Calanque) that includes three zones that have been surveyed annually for 9 years, including a before-after protection scheme (Table 2). Functional traits were assigned to 40 fish species identified in the samples.

3.2 Coral reefs in the Caribbean: Bonaire Island

Coral reefs are hotspots of marine biodiversity. Despite occupying just 0.1% of the Earth's surface, they host 35% of known marine species. In the Caribbean coral reefs, this includes over 60 species of corals and 1500 different species of fish (Spalding et al., 2001). Corals are *the* foundation species for these ecosystems. Their calcium carbonate skeletons form the main reef structure that houses most other reef dwellers and attract visitors. Therefore, this ecosystem depends on the health of its coral engineers. Coral reefs are typically found in the tropical areas of the Indo-Pacific and Caribbean, providing a range of ecological and socioeconomic services, including coastal protection, supporting fisheries and tourism industries, and being a source of biomedical products.

Tropical reefs are at risk by the combined effects of global and local stressors. Global stressors to coral reefs include temperature increase, ocean acidification and sea level rise. Warming is currently the most concerning and widespread stressor, affecting corals from tropical to temperate environments (Hughes et al., 2003). Marine heatwaves are increasing in frequency and intensity and are triggering thermal stress events that induce bleaching and mortality, as well as several sub-lethal impacts on processes like growth or reproduction. While temperature has impacted corals during at least the last 20-30 years, ocean acidification is expected to increasingly impact these ecosystems in the future by impeding calcification. Although less studied, sea level rise can also result in changes to wave energy propagation and light at the benthos (Browne et al., 2021). Local stressors impacting coral reefs include overfishing, habitat destruction, eutrophication, pollution, sedimentation, diseases, invasive species, and physical damage (Andrello et al., 2022).

Bonaire, Caribbean Netherlands, is a special municipality of the Kingdom of the Netherlands, situated in the Southern Caribbean (12°9 N, 68°16'W, Figure 5). The island's surface area is 286 km^2 and the coastline is 127 km in length. In 1961, Bonaire had a population of 5 800, which increased to 15 000 in 2010. After Bonaire became a special Dutch municipality in 2010, the population further increased to 22 573 inhabitants on 1 January 2022, which equals 76.8 inhabitants/km^2. The urban area covers 6.1%, which is mainly restricted to Kralendijk, the capital city and main port located on the leeward side of the island (Mücher and Verweij, 2020).

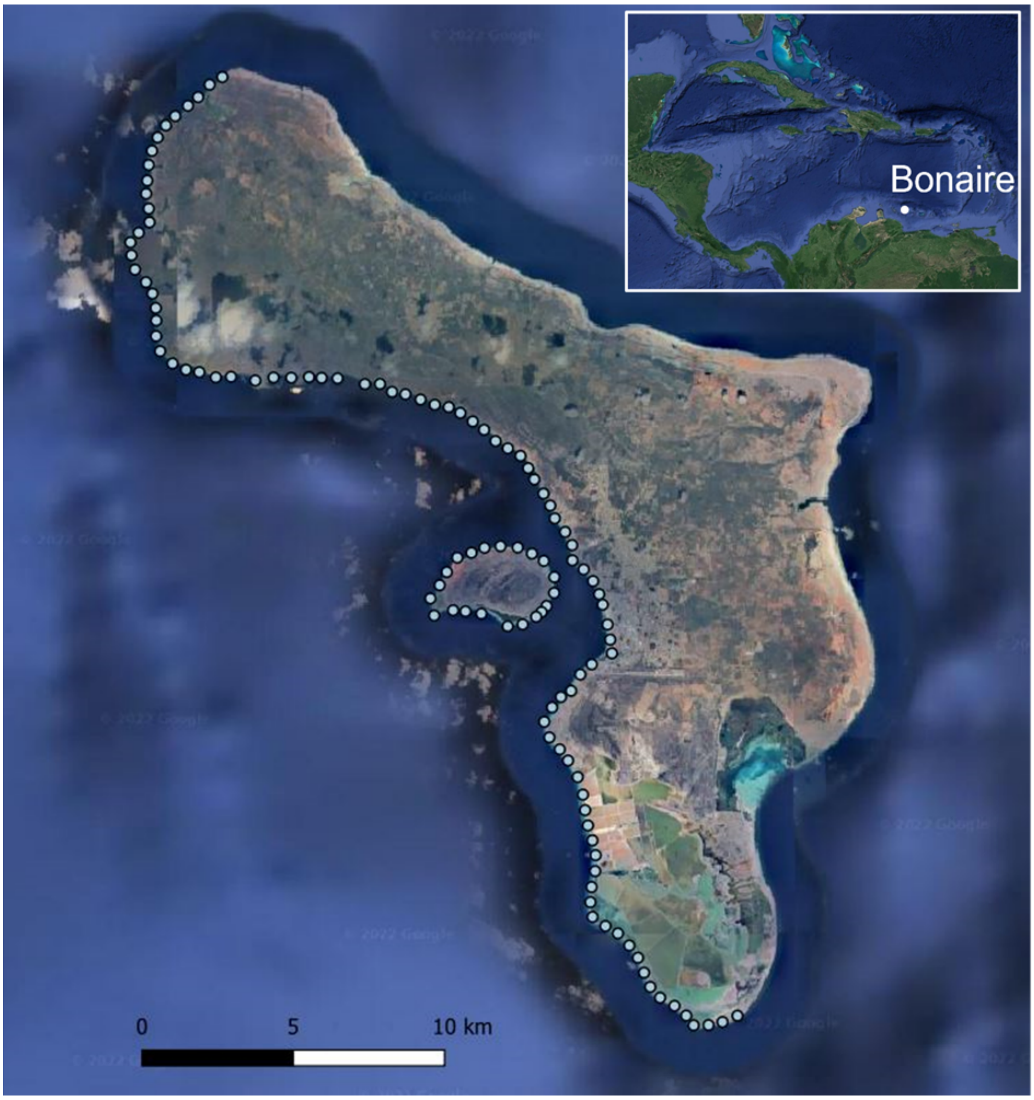

Figure 5. *Location of Bonaire, Carribean Netherlands, and its 115 coral reefs monitoring sites (blue dots). Google Earth Pro 2020 imagery date 14 December 2015.*

Bonaire's economy relies largely on tourism, with 405 000 visiting cruise tourists and 128 500 stay-over tourists in 2017. Direct tourism expenditure is estimated at around 40% of the Gross Domestic Product of 428 million US dollars in 2017. In contrast, current practices of agriculture in Bonaire are very small-scale, mainly due to the small domestic markets and limited access to freshwater, electricity, human capacity, and know-how, while the widely used practice of extensive husbandry results in suboptimal yield and severe grazing-induced erosion issues and poor soils. As a result, 99% of consumed food is imported, which represents a major risk to food security in Bonaire (van der Geest and Slijkerman, 2019).

Coastal and marine ecosystems on Bonaire cover 61.2 km^2. They fall into five categories: salt ponds, crystallised ponds and saliñas (38.14 km^2 – 62 %); lagoons and shallow coastal waters containing mixed communities of seagrass and macroalgae (870 ha – 14.3%, mainly in Lac Bay in the south of Bonaire); coral communities (866 ha - 14.1% - mainly west side of the island); beaches (305 ha – 0.05%); mangroves covering 365 ha (0.06%), most of which are located in Lac Bay.

Bonaire's coral reefs are amongst the healthiest reefs in the Caribbean relative to historic baselines (Jackson et al., 2014). The leeward reefs of Bonaire are, however, known to display a wide range of ecological degradation from almost pristine configurations to reefs that are approaching full functional collapse, which is attributed to local variation in the degree of anthropogenic impact (De Bakker et al., 2017). The reef-fronted coastline of Bonaire has several centres of high anthropogenic activity, which include the capital (Kralendijk), oil storage facility in the north, and salt pans in the south, which all reduce water quality at a local scale due to inputs of nutrients, sediments, or chemical pollutants. These anthropogenic impacts are likely to increase in the future due to the rapidly growing population and tourism industry, expansion of the built-up environment and associated coastal run-off, and ongoing climate change, the latter resulting in sea-level rise and more frequent storm and coral bleaching events. As a result, the ecosystem services provided by the coral reefs to the people of Bonaire, which include coastal protection, fisheries, and tourism, as well as erosion control and increased socio-economic resilience to climate change, are at risk.

3.2.1 Data collection and data sources

Dedicated surveys to quantify coral reef status were carried out on the shallow reefs of the southern Caribbean Island of Bonaire (12°9′N, 68°16′W) (Figure 5). Survey efforts generally followed the GCRMN monitoring guidelines and protocols (https://gcrmn.net/resource/caribbean-guidelines-integrated-coral-reef-monitoring/) and were confined to the leeward side of the island and conducted between September and December 2017. Substantial reef formations are concentrated on this side of the island, where human activity is the highest as well. The general reef profile on the leeward side comprises a lower-terrace zone (LT, ~3 to7 m depth) that gradually slopes from the shore to the upper drop-off zone (DO) at approximately 10 to 15 m depth, after which the reef steeply runs down (usual angle between 20° and 50°) to a depth of 25 to 50 m towards a second terrace. Data on benthos and fish composition was collected from 115 sites (including Klein Bonaire), separated by a predefined distance of approximately 500 m and covering most of the leeward reef stretch. Per site and in each zone (LT and DO), two replicate transect lines (25 m) were positioned in series (starting points 10 m apart) and parallel to the orientation of the reef front. In total, 460 transects were collected, divided over 115 sites at 5 and 10m depth (Table 2). This data was used to estimate diversity indices, and the ecosystem services considered are the biodiversity associated with coral reefs and fish biomass (as a proxy for potential fisheries production).

Body size (fork length) and numerical densities of all reef fish were recorded within a 4-m wide belt transect centred on the main 25-m transect lines. Each transect was surveyed twice, once to count conspicuous species and a second time to count demersal and cryptic species. To ensure consistency, all fish surveys were conducted between at least 2 hours after sunrise and 2 hours before sunset. The encountered fish were identified to species level or lowest recognisable taxon. The weight of each individual fish was calculated based on the estimated length using the equation as defined by Bohnsack and Harper (1988). Species-specific values for constants a and b were taken from the Atlantic and Gulf rapid reef assessment (AGRRA: http://www.agrra.org/).

3.3 Continental shelf habitats in Northern Europe (Ireland)

Ireland is an island nation in Northwestern Europe, located on the edge of a shallow continental shelf that slopes rapidly to the deep-sea plain of the North Atlantic. The marine area of the state covers 880 000 km^2, which is 10 times the land area. The Irish continental shelf is one of the largest in the Northeast Atlantic and includes a variety of seafloor habitats characterised by different depths, substrate types and oceanographic conditions (Marine Protected Area Advisory Group, 2020). Three major habitat types, offshore circalittoral sands, offshore circalittoral coarse sediments and offshore circalittoral muds, account for over 65% of the shelf seafloor (Marine Protected Area Advisory Group, 2020). These conditions involve a high biodiversity, with 563 marine fish species described in 2010, 245 inshore species (<200 m depth) and 435 offshore species (>20 m depth).

Ireland is located in one of the most important fishing areas of the UN Food and Agriculture Organisation (FAO). This area corresponds to Area 27, Atlantic, Northeast, which covers 4% of the world´s ocean surface and accounts for 10% of the world's capture fisheries (Norton et al., 2018). The shelf waters (<200 m deep) of Ireland are very productive and can be divided into two principal water types, seasonally stratified and permanently mixed waters. Some of the most extensive and valuable marine fisheries resources in Europe are located off the Irish coast.

As an island nation, fisheries resources are important to the Irish economy and society. In 2020, Irish vessels landed a total of 188,994 tons of fish catch in Irish ports, with an estimated value of €220.5 million (ICES, 2020), and another €31.5 million were landed abroad (ICES, 2021). According to the Irish Seafood Development Agency, Bord Iascaigh Mhara (BIM), 16,430 people were employed directly and downstream in the Irish seafood sector in 2020. The 2020 Ireland's environmental assessment conducted by the Environmental Protection Agency (EPA) reported that the statuses of commercial fish and shellfish stocks were not fully compatible with Good Environmental Status (EPA, 2020). The Irish Fisheries Ecosystems Advisory Services (FEAS) found that the number of sustainably fished stocks has slightly decreased, and 13 stocks remained overfished in 2020 (ICES, 2021).

Fishing can cause disturbance and displace species from preferred habitats. Fishing activities are physically degrading 13 % of Ireland´s maritime area (DHPLG, 2020), although the impact of this disturbance depends on the sensitivity of receiving habitats and species and the intensity of bottom fishing activity. The high level of bottom fishing activity in mud and sand-mud habitats and the low resilience of the organisms living there may make these habitats particularly vulnerable. Emergent epifauna and cold-water corals are also very sensitive to such disturbances. Recent reports on the subset of habitats mapped and assessed under the EU Habitats Directive indicate that many are in unfavourable condition (NPWS, 2019a; NPWS, 2019b; NPWS2019c).

In addition to anthropogenic pressures such as overfishing, fish populations are also affected by environmental changes. Several studies address the effects of climate change on marine species and marine ecosystems (Boyce et al., 2010; Mills et al., 2013) and directly link temporal and spatial changes in climate variables in fish abundance (Bellido et al., 2001; Cheung and Oyinlola, 2018). The waters of the Northeast Atlantic have warmed at a faster rate compared to the global ocean, and the distribution and changes in the relative abundance of various fish species have been observed at local, regional, and global scales (Nye et al., 2009; Simpson et al., 2011). At the regional scale, Irish waters have warmed in recent decades at 0.3 °C decade^{-1} (Casal and Lavender, 2017), and some significant trends have also been observed for chlorophyll and diffuse attenuation coefficient, which is a proxy for turbidity (Casal et al., 2022). These changes in water column properties could have implications for fish populations around Ireland, which should be considered in fisheries management.

3.3.1 Data collection

Finding available databases of biodiversity metrics (more than 50 sampling stations) in Ireland is challenging. In this case, we used a dataset provided by the Marine Institute, the state agency responsible for marine research, technology development and innovation in Ireland. The dataset belongs to the Irish Ground Fish Survey (IGFS) that takes place within the International Council for the Exploration of the Sea (ICES) surveys and that are coordinated by the International Bottom Trawl

Survey (IBTS) Working Group. These surveys aim for the long-term monitoring of demersal fish to provide data on commercial species for stock assessments and for examining changes in fish distribution and abundance. Data is collected under the Data Collection Framework (DCF), which is the main instrument used by the European Commission to collect scientific data for the Common Fisheries Policy (CFP).

The IGFS has been registering these data in their current form since 2003 onboard a 65-m research vessel, the R.V. Celtic Explorer. Historically, surveys were conducted on commercial fishing vessels and small research ships. The IGFS forms part of an internationally coordinated bottom trawl survey program where Ireland covers part of the Celtic Sea and the West of Ireland. In total, around 170 stations are allocated annually using a "semi-random, depth stratified survey design" (Marine Institute, 2012) (Figure 6). The survey is conducted annually, with the northern area being undertaken in early October and southern and western areas being carried out in two legs during November-December (Marine Institute, 2012).

The survey trawl uses a high headline, "*Grand Overture Verticale*" (GOV 36/47), in order to sample species just off the seabed as well as those foraging upon it. This practice became a standard fishing gear amongst the countries that were International Bottom Trawl Surveys (IBTS) participants, which allows us to compare the results across surveys. The GOV trawl normally maintains a headline height of 4.5 m and is towed at a speed of 4 knots by 30 minutes over the ground using otter boards (Morgere FP 10 doors). Due to the generally harder and more difficult trawling grounds off the northwest coast, all hauls in Area VIa of the survey are carried out using a GOV rigged with 16" hoppers to minimise gear damage. The remaining survey is completed using GOVs in their more traditional A-gear configuration (8" disks centre). During fishing operations, the trawl is continually monitored using real-time trawl sensors giving details of wing-end spread, headline height, symmetry, trawl speed through the water, footrope touchdown, lift-off and door spread (Marine Institute, 2012). Once the trawl is on board the vessel, the species are classified in the fish room, registering length, age, and maturity. Special attention is paid to length measurements, as one of the main objectives of the survey is to establish the proportion of juveniles to adults for each species. For more detailed information about how the data is registered, the reader can refer to the Atlas of Irish Groundfish Trawl Surveys (Marine Institute, 2012).

From the IGFS database, we extracted a subset of data to be analysed by the models (Table 4). This subset of data corresponds to three months (September to December) of 2016. This selection was made considering the highest number of sampled species in a short period of time and to avoid seasonality issues. These data include 163 stations along the coast of Ireland, apart from the Irish Sea (see Figure 6). The stations cover coast strata (0-80 m), medium strata (81-120 m), deep strata (121-200 m) and slope strata (201-600 m).

The data used in the models correspond to fisheries-independent data collected in specific scientific surveys. As previously mentioned, these surveys used standardised methods of data collection, which provide consistent information that is used to build a "time series" of fish abundance. Groundfish surveys use standard nets to sample fish species found on or near the seabed, collectively referred to as "demersal fish or groundfish" (Marine Institute, 2012).

The dataset used in the models includes 100 taxa (6 not at the species level). Information about biological traits and commercial value was mainly taken from *FishBase* (www.fishbase.se) and complemented with other online available sources and expert knowledge.

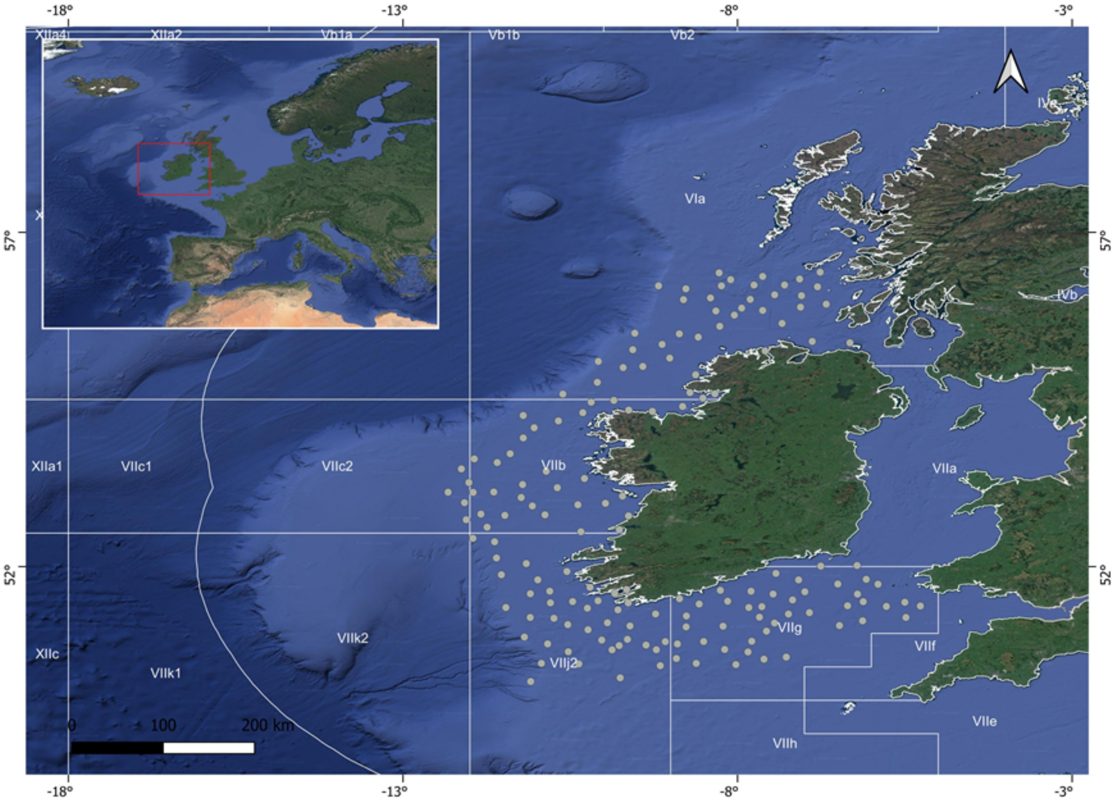

Figure 6. *Map of the Irish study area with ICES divisions overlapped. Grey dots represent the sampling stations.*

Table 4. *Summary of sampling sites and environmental variables in the study area (overview; entire table to be provided in a repository).*

Strata	Number of sampling stations	Measured variable	Environmental variables
Coast	36	Biomass (Kilograms per hour)	Sea Surface Temperature, Sea bottom temperature, chlorophyll, optical depth, salinity, net primary production, Substrate_EUSM2019
Medium	64	Biomass (Kilograms per hour)	Sea Surface Temperature, Sea bottom temperature, chlorophyll, optical depth, salinity, net primary production, Substrate_EUSM2019
Deep	41	Biomass (Kilograms per hour)	Sea Surface Temperature, Sea bottom temperature, chlorophyll, optical depth, salinity, net primary production, Substrate_EUSM2019
Slope	22	Biomass (Kilograms per hour)	Sea Surface Temperature, Sea bottom temperature, chlorophyll, optical depth, salinity, net primary production, Substrate_EUSM2019

3.3.2 Environmental context

Sea Bottom Temperature, Sea Surface Temperature, Chlorophyll concentration, Euphotic zone, Salinity, Net Primary Production and type of substrate were extracted for each sampling station to describe the environmental context. The information on these environmental variables was extracted from the following products:

- Sea Surface Temperature (degrees Celsius): Sea Surface Temperature and Sea Ice Analysis (SST_GLO_SST_L4_NRT_OBSERVATIONS_010_001) downloaded from the Copernicus Marine Environment Monitoring Service (CMEMS).
- Sea water potential temperature at sea floor (degrees Celsius): Atlantic- European North-West Shelf- Ocean Physics Reanalysis (NWSHELF_MULTIYEAR_PHY_004_009) downloaded from the Copernicus Marine Environment Monitoring Service (CMEMS).
- Mass concentration of chlorophyll-a in seawater (mg/m^3) and Net primary production of biomass expressed as carbon per unit volume in seawater (mg/m2/day): Atlantic- European North-West Shelf- Ocean Biogeochemistry Reanalysis (NWSHELF_MULTIYEAR_BGC_004_011) downloaded from the Copernicus Marine Environment Monitoring Service (CMEMS).
- Euphotic zone (m) a: Global Ocean low and mid trophic levels biomass content hindcast (GLOBAL_MULTIYEAR_BGC_001_033) downloaded from the Copernicus Marine Environment Monitoring Service (CMEMS).
- Sea water salinity (PSU): Atlantic- European North-West Shelf- Ocean Physics Reanalysis (NWSHELF_MULTIYEAR_PHY_004_009) downloaded from the Copernicus Marine Environment Monitoring Service (CMEMS).

The type of substrate was then downloaded from the EMODnet Seabed Habitats-EUSeaMap 2019 EUNIS Broadscale.

Several depth levels (0 m - 200 m) were also used in some of the variables, such as chlorophyll-a concentration, net primary productivity or salinity, to better represent the water column values and avoid possible stratification issues.

3.4 Maërl in the Northwestern Mediterranean (Balearic Islands, Spain)

Rhodolith beds are aggregations of free-living red coralline algae (Rhodophyceae) that cover extensive areas of sedimentary continental shelves; these are also known as maërl beds (Figure 7). These beds are highly productive and are responsible for the main biogenic deposits of $CaCO_3$ on the planet (Steller and Cáceres-Martínez, 2009). Maërl beds are considered hotspots of biodiversity. They can harbour high densities of spawners of certain species and function as nursery areas for the juvenile stages of commercial species of fish, crabs, and scallops. The regenerative capacity of maërl-forming species is relatively low, and, in addition, these habitats are particularly sensitive to increases in suspended sediment, physical disturbance by bottom fishing gears, temperature increase and acidification (Ragueneau et al., 2018).

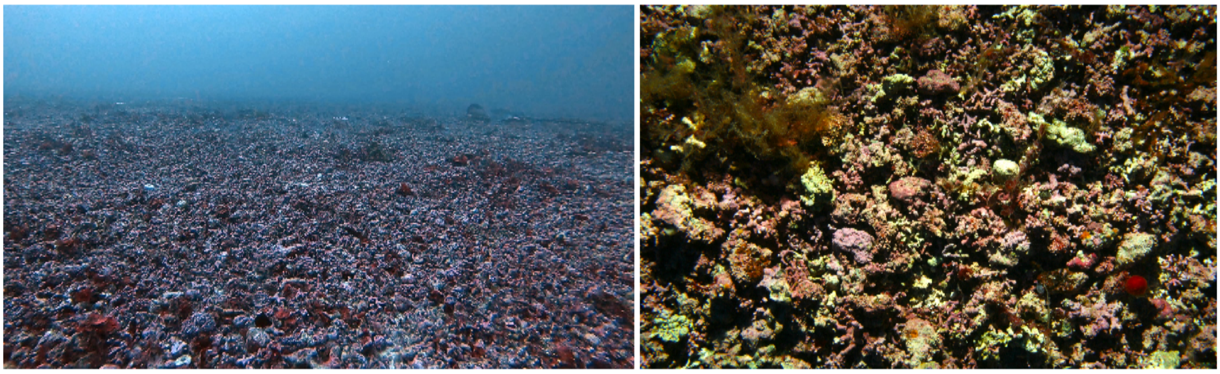

Figure 7. *Maërl bed in the Menorca Channel, Balearic Islands (Northwestern Mediterranean). The photos correspond to a well-preserved maërl bed in an area adjacent to underwater cables that prevent trawling activities. Source: LIFE+INDEMARES (Moranta et al., 2014), and MaCoBioS.*

Maërl requires light to photosynthesise, so the depth at which we can find maërl is determined to a large extent by water turbidity. This biogenic habitat has been recorded in Europe on the southern and western coasts of the British Isles, north to Shetland, France, and other western European waters, and in the Mediterranean Sea, particularly in the Western basin around the Italian peninsula, Corsica, Sardinia, Sicily, and the Balearic Islands. Some Mediterranean maërl beds extend down to 100 m due to the oligotrophic nature of the Mediterranean that allows light penetration at these depths (Barbera et al., 2012). The deeper distribution of Mediterranean maërl beds makes them less accessible to scientific fieldwork and experiments than other marine and coastal ecosystems; in consequence, there is a general lack of knowledge on maërl functional roles in Mediterranean coasts and their protection is deficient.

Aiming to focus on these important habitats for both biological production and ecosystem functions, the Spanish case study investigates maërl beds on Mediterranean continental shelves spanning from 50 to 100 m. In the case study, we include some of the best-preserved continental shelf habitats in the NW Mediterranean (i.e., the Menorca Channel) and areas off the Iberian Peninsula, where maërl beds have been identified despite prevalent trawling impacts in the area (i.e., Cabo de Palos and Cap de Creus - Figure 8).

Figure 8. Maërl beds in the Spanish case study, Northwestern Mediterranan: Cabo de Palos, Cap de Creus and Menorca Chanel. Blue dots indicate the sampling sites.

In the Menorca Channel, despite an overall good conservation status, a fishing impact gradient exists, with trawling activities traditionally operating in all the area except for an exclusion area close to underwater cables. In 2016, a trawling ban was established in a large proportion of the channel based on the uniqueness of the Menorca Channel seascape (de Juan et al., 2023).

In Cabo de Palos and Cap de Creus areas, coastal Marine Protected Areas provide partial protection over the maërl beds, with fishing impacts increasing as the bed goes deeper and further from the MPA border (de Juan and Demestre, 2012). In these areas, off mainland Spain, the light penetration is lower than the Balearic Islands and the studied maërl beds span between 40 and 70 m.

3.4.1 Data collection and data sources

Sources of data:

- Menorca Channel: data collected in the framework of LIFE+INDEMARES (Moranta et al., 2014). Sampling cruises were conducted in 2009, 2010 and 2011.
- Cabo de Palos and Cap de Creus: data collected in the framework of Spanish research project COMSOM (de Juan and Demestre, 2012). Sampling cruises were conducted in 2009.

104 sites were included in the study that cover an environmental gradient and fishing pressure gradient.

The same sampling protocol was conducted in the 104 study sites. Epibenthic fauna samples were collected with an epibenthic sledge (2 m wide and a 20 mm cod-end) towed at 1.5 knots for 5-10 minutes at each site. All samples were standardised to 1 m^2. The retained organisms were identified to the minimum taxonomic level possible, generally to species level (<1% identified to genera or higher level) and counted. At the same sites, grab sediment samples were collected to record sediment grain size and to categorise the habitat type per site.

Sediment samples were collected with a van Veen grab at each site. The sediment particle size was analysed with laser diffraction (using Horiba La- 950 v2 particle size analyser). In the sites with a high density of rhodoliths, only the estimated rhodolith density was provided. To complement the identification of rhodolith density types in Cabo de Palos and Cap de Creus sites, acoustic surveys covered the sampling sites. The integration of acoustic data with seafloor samples allowed defining the composition and spatial heterogeneity of substrata at the study sites (de Juan et al., 2013). In the Menorca Channel, the information provided by epibenthic samples and sediment grabs was combined with side-scan sonar and photo images to classify the seabed into different habitat types (Barbera et al., 2012). These data sources allowed the classification of the habitat types on maërl density groups: <10%, <25%, <50% and >50% of rhodolith coverage.

The trawl fishing effort data was also collected from various sources. In Cabo de Palos and Cap de Creus sites, fishing effort was accurately measured by monitoring the daily activity of the trawling fleets (monitoring the fleet distribution by observers on-board the vessels and interviews with the fisherman); by recording the characteristics of the fishing fleet at each harbour (Gross Tonnage of the fishing fleet, GT); and also by gathering data from the fishermen associations, e.g., fleet fishing hours per day which can be used to estimate the monthly average of fishing hours in a specific area. These data sources allowed estimating the fishing effort as fishing hours × GT/month (Martin et al., 2014). In the Menorca Channel, trawling fishing effort data were assessed based on Vessel Monitoring System registers for the years 2005-2010. The number of records (annual density and annual average) per 3x3 km2 was estimated using ArcGIS v. 9.2 (Moranta et al., 2014). Fishing effort data allowed to categorise the sites in a gradient from no-fishing (e.g., within the Cap de Creus and Cabo de Palos MPA or around the underwater cables in the Menorca Channel) to high fishing impact (i.e., high density of trawl tracks or trawling activity in a site).

3.4.2 Maërl bed sites: benthic communities

The sampling sites covered a range of environmental conditions, where bathymetry, rhodolith coverage and fishing effort were selected as the variables that were homogeneously estimated in all study sites (Table 5). This gradient in rhodolith coverage, depth and fishing intensity allowed us to assess the effects of environmental variability on the diversity associated with maërl beds.

A total of 448 species were identified in the case study; the species list includes benthic invertebrates like ascidians, sponges, bivalves, crustaceans, and benthic fish like flatfish or gobies. A set of 7 biological traits were assigned to these species (Table 6). The ecosystem services considered are the biodiversity associated with maërl grounds and the fish biomass (as a proxy for potential fisheries production). The density of maërl beds (spanning from <10% to >50% rhodolith coverage) is also a proxy for potential carbon storage; this function is currently being tested in the project by estimating the dimension of the maërl bed deposit over the sediment column (penetrating to 2m in the seabed) in the study area; the deposit of dead rhodoliths under the living surface layer is expected to have a significant role in carbon deposit (Amado-Filho et al., 2012).

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No 869710

Table 5. *Summary of environmental data in the study sites.*

Environmental variables	Levels	Nº samples
Depth	35-110 m	104
Habitat	Sand/sandy-mud	7
	Sand with rhodoliths	21
	Sand with rhodoliths and brown algae	27
	Maërl beds	40
	Maërl with brown algae	9
Maërl coverage	<10%	48
	<25%	7
	<50%	27
	>50%	22
Fishing effort	No fishing	12
	Low effort	33
	Moderate effort	33
	High effort	26

Table 6. *List of traits and trait categories assigned to the benthic community.*

Size	Age	Morphology	External structure	Habitat	Mobility	Feeding
Small (<1cm) Medium (1-5 cm) Large (> 5cm)	Long (> 10 yrs) Medium (>3 yrs) Short (>1 yrs) Annual	Arborescent, articulate, bivalve, crustose, cushion, flat, globose, pisciform, stellate, turbinate, vermiform	Calcareous Chitinous Cuticula None	Emergent Surface Sub-surface	Swimmer Crawler Sedentary Sessile	Primary producer Planktivorous Benthivorous Piscivorous Deposit feeder Suspension feeder Grazer Scavenger/opportunistic

4. Results for MaCoBioS case studies

4.1 Shallow coastal habitat in the Northwestern Mediterranean

We used 27 underwater visual surveys along the French Mediterranean coast in subtidal habitats to model the total biomass of fish as a function of the 6 biodiversity indices (Table 3), mixing species relative abundance, traits, and phylogeny, and 5 habitat factors (depth, block, scramble, rock, sand). We first log10-transformed fish biomass to obtain a Gaussian distribution.

The selection of factors and biodiversity indices, based on the AIC criteria, selected a parsimonious model with only sandy habitat coverage and two out of six biodiversity indices (taxonomic richness and phylogenetic entropy). We then fitted the piecewise structural equation model that explains 43% of the variation (R-square: 0.43) in the log10-transformed total fish biomass (Figure 9). The path analysis shows that total fish biomass is not directly influenced by sandy habitat coverage but indirectly through the negative influence of sandy coverage on both taxonomic richness and phylogenetic entropy. Taxonomic richness has a strong and positive influence on fish biomass, while phylogenetic entropy has a negative impact.

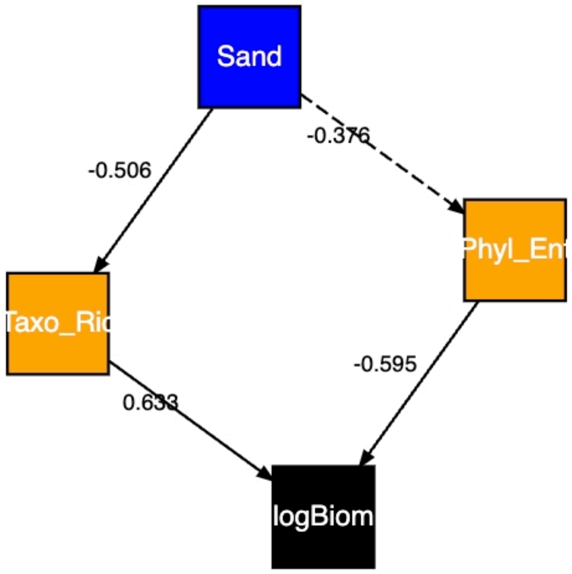

Figure 9. *Path diagram of factors influencing the log10-transformed total biomass of fish (logBiom in black) in Mediterranean subtidal habitats. Orange boxes correspond to biodiversity indices (taxonomic richness and phylogenetic entropy), while the blue boxes correspond to habitat (sandy bottom coverage). Solid lines represent significant partial effects, while dotted lines represent non-significant effects.*

4.2 Coral reefs in Bonaire

We used underwater visual surveys conducted on the shallow reefs of the southern Caribbean Island of Bonaire at 115 sites. We estimated the total fish biomass at each site which was log10-transformed prior to analyses to obtain a Gaussian distribution. For each site, we also calculated the 6 biodiversity indices (Table 3), mixing species relative abundance, traits, and phylogeny, and 9 environmental and habitat factors (no-take marine reserve, depth, wave energy, terrace width, hard substratum area, rugosity, vertical height, coral live cover, and hard coral cover).

Based on the AIC, the most parsimonious model explaining the log10-transformed fish biomass contained 3 factors (depth, terrace width and hard substratum area) and 3 biodiversity indices (taxonomic richness and entropy, and functional entropy).

We then fitted the piecewise structural equation model that explained 78% of the variation (R-square: 0.78) in the log10-transformed total fish biomass (Figure 10). The path analysis shows that the total fish biomass is directly and significantly influenced by only 3 environmental factors out of 9. Depth and coral live cover positively influenced fish biomass, while terrace width had a negative influence. The 3 biodiversity indices retained in the parsimonious model are significant drivers of fish biomass, with taxonomic richness having a strong positive influence, while taxonomic and functional entropy have a weaker negative influence. Another important effect is the link between the no-take zone and taxonomic diversity.

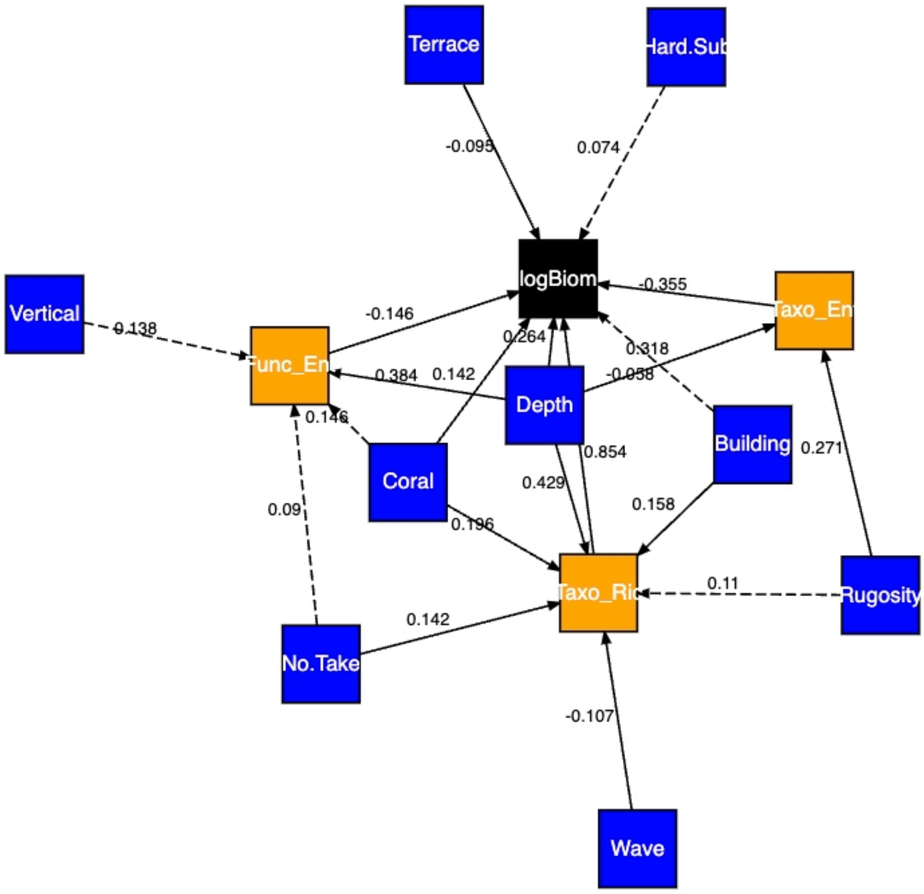

Figure 10. *Path diagram of factors influencing the log10-transformed total biomass of fish (logBiom in black) in Bonaire's coral reefs. Orange boxes correspond to biodiversity indices, while blue boxes correspond to environmental factors. Solid lines represent significant partial effects, while dotted lines represent non-significant effects.*

4.3 Demersal fish in Ireland (Northern Europe)

We used trawl surveys in 163 stations along the coast of Ireland to model the total biomass of demersal fish or groundfish according to the 6 biodiversity indices (Table 3), mixing species relative abundance, traits and phylogeny, and 9 environmental factors (Depth, Sea Surface Temperature or

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No 869710

SST, Bottom Sea Temperature or BST, Chlorophyll-a concentration or Chla, Euphotic zone or Eup, Salinity or Sal, Net Primary Production or NPP and type of substrate or Sub). We first log10-transformed fish biomass to obtain a Gaussian distribution (Figure 11).

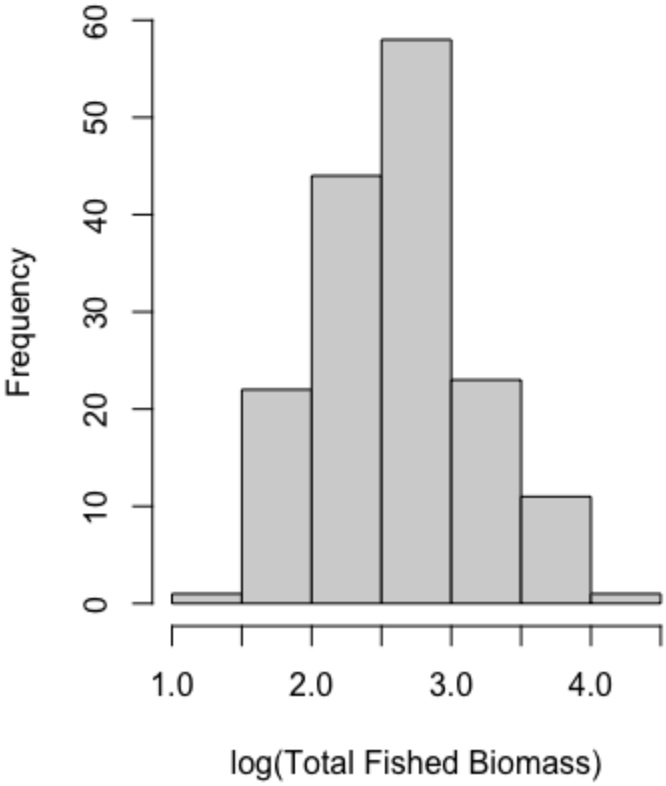

Figure 11. *Distribution of total fish biomass in trawl surveys along the Irish coast after log-transformation.*

The selection of factors and biodiversity indices, based on the AIC criteria from a linear model predicting log-transformed fish biomass, selected a parsimonious model with only 4 environmental and habitat factors (Depth, SST, Chla and NPP) and 5 biodiversity indices (taxonomic richness and evenness, functional richness and evenness, and phylogenetic richness).

We then fitted the piecewise structural equation model that explains 51% of the variation (R-square: 0.51) in the log10-transformed total fish biomass (Figure 12). The path analysis shows that total fish biomass is directly and significantly influenced by only one environmental factor, which is SST, with a positive and significant influence. Other factors (Depth, Chla and NPP) act on fish biomass through biodiversity indices. Among the 5 biodiversity indices, taxonomic richness has the strongest and most positive influence on fish biomass, while phylogenetic richness and taxonomic evenness have a significant negative impact. The euphotic zone acts positively on fish biomass through taxonomic and functional richness, while depth negatively influences taxonomic and functional richness, which negatively impacts fish biomass. We also observe a negative impact of NPP on functional richness, so an indirect negative effect on fish biomass, albeit not significant.

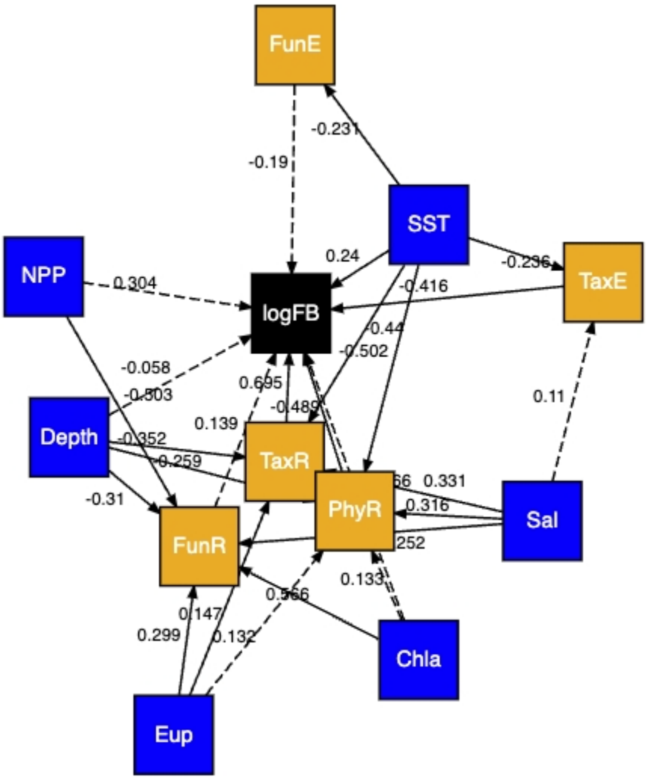

Figure 12. *Path diagram of factors influencing the log10-transformed total biomass of demersal fish or groundfish (logFB in black) in the Irish case study. Orange boxes correspond to biodiversity indices, while blue boxes correspond to environmental factors. Solid lines represent significant partial effects, while dotted lines represent non-significant effects.*

4.4 Maërl beds in Spain (Northwestern Mediterranean)

The benthos dataset has 104 observations or sampled species communities. We only kept 101 observations since we do not have the traits or the phylogeny of enough species for some communities, i.e., representing more than 70% of total biomass, so we cannot confidently assess functional and phylogenetic diversity indices.

We predicted the log10-transformed total abundance of fish, in terms of the number of individuals, using 5 socio-environmental factors (depth, the proportion of mäerl beds, trawl fishing effort and protection regime), the 6 biodiversity indices (Table 3) mixing species relative abundance, traits and phylogeny.

The selection of factors and biodiversity indices, based on the AIC criteria, selected a parsimonious model with the 4 factors (depth, the proportion of mäerl beds, fishing effort and protection) but only 2 biodiversity indices (taxonomic and functional richness).

We then fitted the piecewise structural equation model that explains 20% of the variation (R-square: 0.20) in the log10-transformed total abundance of fish (Figure 13). The path analysis shows

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that the total fish abundance is only directly influenced by both biodiversity indices (taxonomic and functional richness) but not by any of the 4 socio-environmental factors. It suggests that these 4 factors influence fish abundance through their direct link to biodiversity. This low percentage of explained variance is probably linked to the limited number of environmental variables included in the study (i.e., available at the site scale for the 104 sampling stations). Other variables are known to play a significant role in the distribution and density of maërl beds, and therefore, on the associated diversity, for example bottom currents, bottom geomorphology and sedimentation (Illa-López et al., 2023).

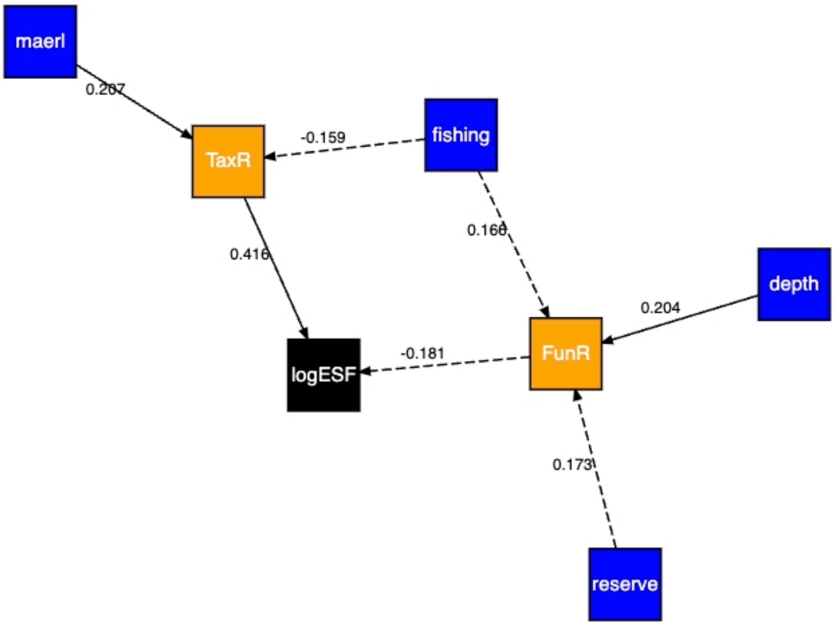

Figure 13. *Path diagram of factors influencing the log10-transformed total abundance of fish (logESF in black) in Mediterranean benthic communities. Orange boxes correspond to biodiversity indices, while blue boxes correspond to social-environmental factors. Solid lines represent significant partial effects, while dotted lines represent non-significant effects.*

When focusing on links in our path analysis, we show that taxonomic richness, which significantly and positively influences fish abundance, is significantly and positively influenced by the proportion of mäerl beds and negatively by fishing effort, albeit not significantly. Functional richness is only significantly influenced by depth, with more diverse traits in deeper habitats. We also show a positive reserve effect on functional diversity, albeit not significant.

5. Discussion and conclusions

5.1 Summary of findings per case study: implications for biodiversity conservation

5.1.1 Shallow coastal habitat in the Northwestern Mediterranean in France

The case study in France was limited by the number of sampling stations, 27. However, the model applied with a limited number of environmental factors allows the identification of relationships with diversity indices. This model detects the negative effect of sandy habitat cover on taxonomic diversity. In turn, taxonomic diversity has a positive effect on fish biomass. As for phylogenetic diversity, sandy habitat also has a negative influence, but this diversity also has a negative influence on fish biomass. In conclusion, in these heterogeneous subtidal habitats, fish biomass is higher in rocky habitats and positively linked to taxonomic diversity.

5.1.2 Coral reefs in Bonaire

Depth and coral live cover positively influenced fish biomass, while terrace width had a negative influence. Also, taxonomic richness had a strong positive influence, while taxonomic and functional entropy had a weaker negative influence. On the other hand, the no-take Marine Reserve had a positive link with taxonomic diversity. The shallow reef terrace has suffered from the White Band Disease (WBD) in the eighties of the previous century, that wiped out much of the *Acropora* species. Presently coral cover and coral complexity in this zone are low, which reduces the number of refuges for fish. The WBD did not happen deeper on the reef then because the affected species only occurred in shallow waters. This means that deeper coral cover is higher, and there are more hiding places for fish and would explain why depth and coral live cover positively influence fish biomass. Furthermore, terrace width is higher in the southern area of Bonaire, where the terraces were also dominated by two *Acropora* species (*A. palmata* and *A. cervicornis*). Thus, wider terraces were more affected by the WBD and nowadays have less structure, which would explain why terrace width is negatively related to fish biomass. Nature-based solutions such as coral restoration are now restoring mainly *A. cervicornis* in the shallow areas of Bonaire, which should hopefully lead to an increase in shallow fish biomass in the future.

5.1.3 Demersal fish in Ireland

Results from Ireland’s case study showed that the most parsimonious model for fish biomass included four environmental variables (Depth, SST, Chla and NPP) and five biodiversity indices (taxonomic richness and evenness, functional richness and evenness, and phylogenetic richness). Total fish biomass was found to be directly and significantly influenced by only one of the environmental variables considered, SST. This finding is in line with previous research, which has identified SST as a critical factor in determining the composition of the demersal community due to a variety of reasons, including the availability of food and fish physiology (e.g., metabolism and growth rates). With climate change resulting in rising SST, it is likely that the distribution of fish together with phytoplankton populations, the base of the food web, will suffer alterations leading to changes in fish biomass and abundance. This could have a major impact on species interactions and food web organisations and could ultimately result in a redistribution of resources available to fishers.

Regarding biodiversity indices, fish biomass was found to be strongly and positively influenced by taxonomic richness. A greater number of fish species favours better resource utilisation through reduced competition, improved trophic structure, enhanced ecosystem stability, and increased functional redundancy, which in turn could increase the total biomass supported by the ecosystem.

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As expected, the euphotic zone positively affected fish biomass through taxonomic and functional richness, as many of the species considered here were not exclusively demersal and relied on the euphotic zone for their diet. The productivity of the euphotic zone can promote the growth of phytoplankton and other prey species, which in turn can lead to higher demersal fish biomass. Consequently, depth negatively affected fish biomass through taxonomic and functional richness. As depth increases, available resources and environmental conditions may decrease, negatively affecting fish biomass. Only adapted species can optimally use the resources in these deep zones.

5.1.4 Maërl beds in Spain

The most parsimonious model included taxonomic and functional richness indices; the relative abundance of species was not a relevant indicator. In the high-diversity benthic communities associated with maërl beds, the presence/absence of species, and their biological traits, has been previously related to fishing activities (as the main impact in the area) (Barbera et al., 2012). Regarding environmental variables, the most parsimonious model included fishing and protection regime, and maërl coverage.

The abundance of fish was driven by taxonomic and functional diversity, but not by the environmental variables, likely because fish are mobile and not subject to the environmental conditions of the sampling site; however, fish rely on benthic invertebrates for food. Therefore, fish biomass is driven by the environment, including fishing activities, through the diversity of benthic invertebrates. Taxonomic and functional richness are significantly influenced by different factors, negative effects of fishing and positive effects of the reserve; maërl bed coverage also has positive effects over taxonomic richness, and functional richness is linked with depth, as the deeper stations had species characteristic from the shallower stations but also had the presence of species typical form deeper continental shelves.

In summary, the fishing regime and the presence of biogenic habitats are the main drivers of fish biomass through the increase of taxonomic and functional richness. Protection from fishing activities promotes a higher benthic invertebrate richness, which positively influences fish biomass. The maërl bed coverage is also an important driver of taxonomic richness, whereas functional richness increases with depth and slightly with protection.

5.2 Advantages and limitations of the functional diversity indices and the structural equation model approach

Since global and local pressures on biodiversity and negative consequences on ecosystems and human health are rising, we need better monitoring of biodiversity status and trends to preserve ecosystem functioning and associated Nature's Contribution to People (Díaz et al., 2018). While taxonomic diversity has long been used in ecological studies, it only represents one of the multiple biodiversity facets. Functional Diversity (FD), the diversity of traits in a given community, is the cornerstone between global change impacts and ecosystem functioning and has now become a key biodiversity metric to monitor (e.g., Trindade-Santos et al., 2020), while phylogenetic diversity, the diversity of evolutionary lineages in a given community, is also key to better understand the response of communities to disturbances and their functioning (e.g., Cadotte, 2013). Yet, our metrics ignore intra-specific variability of traits or genes, which can represent one-third of inter-specific variability (Xavier Jordani et al., 2019) but remains challenging to measure on many sites. This intraspecific genetic and functional diversity has been shown to shape how predator species can affect the community and ecosystem functioning of lower trophic levels (Raffard et al., 2021). So here, we make the assumption that intraspecific variability is not playing a key role in ecosystem services. The second main limitation of our set of biodiversity metrics is the lack of trophic interactions between species pairs which could inform a trophic diversity sustaining food webs (Gaüzère et al., 2022). Yet, taxonomic and functional diversity can be considered as proxies of trophic diversity since species number and their traits shape interactions (Coux et al., 2016). An emerging challenge is also to compute functional diversity across the Tree of Life (Luza et al., 2023), in our case for both vertebrate and invertebrate species, but common lists of relevant traits must be available, which has not been achieved yet.

Structural Equation Models (SEM) have the advantage of selecting parsimonious and both direct and indirect pathways to predict ecosystem services. Here we show that in most samples, the social-environmental context is not directly affecting ecosystem services but is influencing them through impacts on several biodiversity indices. These models cannot explicitly take into account space or time, but we can consider that our case studies are very local and synchronised sampling. SEM cannot predict ecological outputs as accurately as the new generation of Machine Learning models, but we obtained relatively high R-square values (>0.6) for some case studies (coral reefs – Bonaire) meaning that we collected most of the meaningful factors explaining biodiversity indices and ecosystem services. Yet, for the other case studies (maërl beds – Spain), we obtained low R-square values (<0.3) suggesting that important socio-environmental factors or spatio-temporal variations are missing from the models (e.g., bottom currents, seabed geomorphology and small-scale habitat heterogeneity; de Juan et al. 2023; Illa-López et al., 2023). On the other hand, SEM offer more explanatory links than Machine Learning approaches, which remain black boxes for most of them and are often over-parameterised.

In MaCoBios the most important aspect was not the explanatory power of the models but the assessment of links between socio-environmental factors, biodiversity indices, and ecosystem services providing causal pathways and identifying relevant bioindicators.

What is interesting about the study is the observed relationships in the different case studies, which are consistent despite the diversity of the communities studied. In all case studies, fish biomass, considered as a proxy for provisioning service, is positively related to taxonomic diversity, and in the case of benthic communities, also to functional biodiversity. These results indicate the importance of taxonomic richness for the provision of ecosystem services, which is in turn influenced by environmental factors, but also by human factors, such as the negative effect of fishing on maërl beds and the positive effect of the reserve in the protected area of Bonaire.

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