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**Biodiversità e driver ambientali delle comunità  
ittiche nei differenti habitat delle coste Calabresi**

**Biodiversity and environmental drivers of fish  
assemblages in different habitats of the Calabrian  
coasts**

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## ABSTRACT

La stima della biodiversità è uno degli aspetti chiave per descrivere e preservare la diversità e funzionamento degli ecosistemi. La biodiversità degli ecosistemi marini e la distribuzione delle specie è modellata da una moltitudine di fattori che interagiscono tra loro, e negli ultimi decenni è stata osservata una riduzione della diversità specifica, con conseguenze su interi ecosistemi e sulle loro interazioni con gli esseri umani. In questo studio è stata applicata una metodologia di visual census per quantificare la diversità specifica della fauna ittica delle coste della Calabria, andando ad approfondire diverse sue sfaccettature, focalizzandosi sui popolamenti specifici degli habitat costieri (habitat rocciosi, sabbiosi e praterie di *Posidonia oceanica*). In particolare, sono state analizzate proprietà come la stima delle specie presenti, le loro interazioni e le differenze nelle comunità tra i vari habitat. Da queste osservazioni è emersa una maggior ricchezza specifica in habitat rocciosi, ma un contributo fondamentale di tutti gli habitat, quantificato con la capacità di portare un alto contributo alla  $\beta$ -diversità, specialmente da parte delle comunità sabbiose, nonostante la loro minor ricchezza specifica rispetto agli altri habitat. Anche le specie che contribuiscono maggiormente a creare queste differenze tra gli habitat sono state analizzate, con risultati che rispecchiano un alto contributo delle specie abitanti gli habitat sabbiosi, ma anche diffusa presenza di specie

generaliste e presenti in habitat rocciosi e/o praterie di *P. oceanica*. Inoltre, è stata modellata una predizione della ricchezza specifica su tutta l'estensione delle coste della Calabria, basata sui dati ottenuti durante i campionamenti, ottenendo una ricchezza specifica generalmente bassa su tutta la fascia costiera, ma caratterizzata da alcuni hotspot di diversità in aree che presentano elevata eterogeneità riguardante gli habitat.

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# 1. INTRODUCTION

## *1.1. The concept of biodiversity*

**Biodiversity**, defined as the “variability among living organisms from all sources, including, inter alia, terrestrial, marine, and other aquatic ecosystems, and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems” (UN Convention on Biological Diversity, 1992), has been highlighted in the last few decades as one of the key features to describe and understand the nature and functioning of ecosystems (Loreau et al., 2001; Midgley, 2012). The continuous challenges that natural systems are facing worldwide is requiring a deeper understanding of the attributes characterizing biodiversity, in order to better assess and manage the ecological consequences of changes occurring within those systems, also in relation to the Nature’s Contribution to People (NCP, Díaz et al., 2018), a recent concept that expands the one of Ecosystem Services (ES) provided by nature to humans (Bagousse-Pinguet et al., 2019). The NCP refers to “all the benefits and detriments that people get from their relationships with the rest of the living world” ( Hill et al., 2021). In fact, while the ES are the way by which people benefit from what the natural environment is able to provide them directly or indirectly and can be affected by every change occurring in the ecosystems themselves, deeply affecting the well-being of people all over the



world (Worm et al., 2006), the concept of NCP is wider and less economically driven, including many aspects which can have both positive and negative effects on humans. In broad terms, the NCP can be divided in three categories, material, non-material, and regulating NCP ( Hill et al., 2021).

There are a multitude of processes shaping species diversity and distribution in marine systems. Among the best known and acknowledged ones there are external drivers acting on them, both biotic (e.g. competition, predation; Van der Putten et al., 2010) and abiotic (e.g. climate and oceanographic features; Pearson et al. 2003). These drivers can act together in a synergistic way (Benton, 2009; Lewis et al., 2017), to model the structure and functions of marine ecosystems. There is still an ongoing debate on how such drivers contribute and the spatial scale at which they are more relevant in influencing biodiversity (Araújo and Luoto, 2007; Meier et al., 2010; Wiens, 2011; Lewis et al., 2017), but their overall importance is widely recognized. The general trend of the last decades has been a reduction in species diversity (McCauley et al., 2015) and in some cases even the loss of entire functional groups, hampering the ability of ecosystems to deliver ES to human communities, especially in some complex, delicate, and poorly known marine environments (e.g. the deep sea) (Danovaro et al., 2008).

## ***1.2. Fish as biodiversity indicators***

In marine ecosystems, fishes have received a special focus as they are often considered as a proxy of ecosystem biodiversity, because they represent a highly diverse group, cover a wide range of ecological functions, and their taxonomy and biological and ecological traits are relatively well known (Rice, 2003; Stuart-Smith et al., 2013; Duffy et al., 2016). Fish are among the most common organisms in the world's oceans, and overall the most diverse group of vertebrates, inhabiting all the possible aquatic ecosystems (Manel et al., 2020). Fish can exhibit a multitude of shapes and growth forms, from elongated and adapted for fast swimming, to flattened and suitable to camouflage under soft bottoms, but including an uncountable number of other forms standing in the middle. Such organisms optimized their biology over millions of years of evolution, acquiring the capability to survive in almost every ecosystem. Fish species are able to express a variety of life habits, differentiating from each other for reproductive, feeding, and behavioral features, depending on the conditions they live in and their life history.

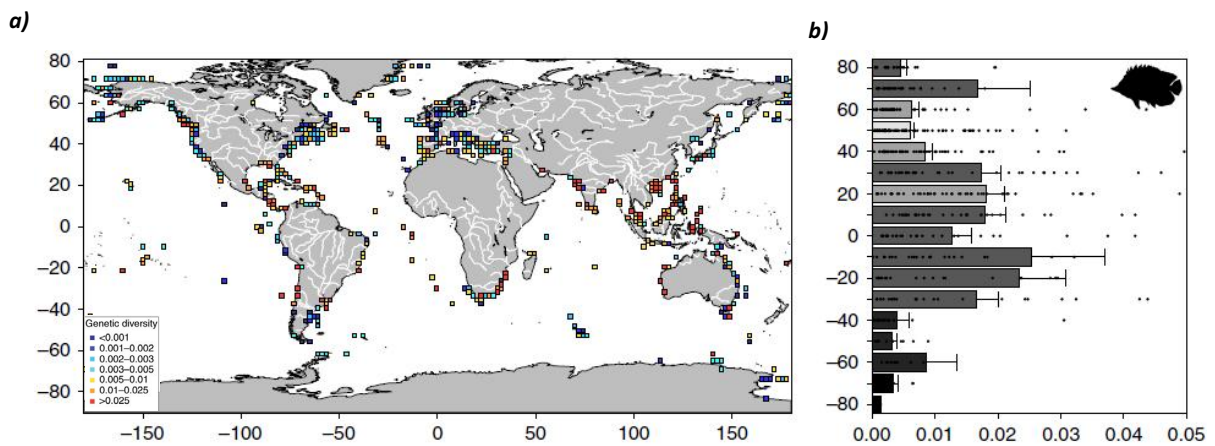


Figure 1.1. (From Manel et al 2020). Genetic diversity of marine fish in the world, estimated as the mean number of mutations per base pair for Cytochrome Oxidase Subunit 1 sequence across species (a) 514 cells for marine fishes. (b) Genetic diversity averaged across cells within latitudinal band of 10° and is plotted as a function of latitude for marine fish species.

The general classification under the name “fish” includes both cartilaginous fishes, named **Chondrichthyes** (i.e. sharks, rays, etc.), and bony fishes, named **Osteichthyes**, representing the vast majority of the total number of species (Frasca et al., 2018). Osteichthyes can be further divided into ray-finned organisms, or Actinopterygii, and lobe-finned fish, known as Sarcopterygii. The first bony fish currently identified has dated back around 425 million years (Zhao et al., 2021), and this can give us an idea of the longevity of this clade and the amount of evolutionary history they have been through, resulting in the species present now in our oceans with all the adaptations that they possibly exhibit to survive in very disparate conditions.

Many aspects of fish biology and biodiversity are still unknown, especially in extreme or remote habitats, but many times even the most accessible

environments can be associated with knowledge gaps. Recent estimates are of around 15.000 to 20.000 fish species for marine ecosystems, unevenly distributed and mainly concentrated in the shallow coastal ecosystems (within the first 200 m of depth) (Henseler et al., 2019). This is firstly due to more favorable living conditions, giving the presence of **light** (and so the presence of primary producers at the bottom of the trophic webs, that sustain all the higher levels), levels of **hydrostatic pressure** compatible with life (which could be instead a limiting factor in deep-sea ecosystems; Yancey et al., 2014), along with many other factors. A considerable part is also related to an evident gap in our knowledge regarding the deeper portions of the world's oceans, which needs to be addressed in future investigations (Ramirez-Llodra et al., 2011).

Organisms belonging to this taxon can therefore represent a very useful proxy to assess the biodiversity of marine environments effectively and rapidly, thanks to the relatively high knowledge of their diversity and ecological characteristics compared to other less known groups.

### ***1.3. Assessing biodiversity***

For the reasons above-described, it appears necessary to move forward the knowledge about biodiversity in order to properly assess the diversity of an

area, but also to highlight multiple shades of it, completing the evaluation by using multiple aspects and estimates, including the **species richness**, meaning the number of species in a given area (Solan et al., 2012; Gotelli et al., 2013), and **species abundance**, which is instead the number of fish individuals for a species in a given area (Verberk, 2011), giving the possibility to assess diversity using a compound approach, that provides more accurate answers to our questions (Stuart-Smith et al., 2013). For example, it is widely known that biodiversity generally positively influences the productivity and the stability of a system, enhancing the possible usage spectrum of the available resources (Cardinale et al., 2011). But different ecosystems react in different ways and with different magnitude to the oscillation in biodiversity that can be driven both by natural and anthropogenic stressors (Hooper et al., 2005), highlighting the necessity to increase knowledge on such relevant issues, to finally enhance the power to make inference regarding this complex topic. Furthermore, the consideration of more than one aspect is a good way to reduce biases, which is a critical issue to account for when we aim to obtain biodiversity estimates. Moreover, to assess the diversity of an area under investigation, as in any kind of scientific approach to the test of a hypothesis, there is a need to perform replicates of the measurement of interest (e.g. diversity). Replicates are repeated measurements of the same sample that represent independent

measures of the random noise associated with protocols or equipment (Blainey et al., 2014). Replication provides a gain of information, which justifies the costs related to the increased effort for the measurements (Dennis et al., 2010). More specifically, among the possible measurements related to biodiversity, also a large set of diversity indices focusing on the **taxonomical** dimension of biodiversity is available. A **diversity index** is a quantitative measure that reflects how many species (or other biological entities) there are in a given community and that can consider different aspects of the relations between the considered species.

Among the possible indices, one of the most used in marine ecology is the **Shannon-Wiener index** (Loiseau et al., 2015), which allows to assess the evenness of species in a community, while emphasizing the diversity component of that community (Shannon and Weaver, 1949). Another widespread used metric is the **Simpson index**. This index is a dominance index giving more consideration to common or dominant species of a community (Simpson, 1949).

Beside considering the diversity of a specific area, which is also known as  **$\alpha$ -diversity** (Magurran, 2004), a complete and comparative spatial evaluation should also include  **$\beta$ -diversity**, which refers to a measure of the difference in species composition either between two or more local assemblages or between

local and regional assemblages (Koleff et al., 2003). Using such scale of the species diversity allows to efficiently compare the communities inhabiting the different habitats or sampling units. The  **$\beta$ -diversity** can be also considered as driven by different components to highlight the differences between the sites, which are both regarding the spatial differences between each replicate. This measure can inform on the “uniqueness” of each individual site relative to the entire seascape community, also known as Local Contribution to Beta Diversity (Legendre & de Cáceres, 2013), and the Species contribution to Beta Diversity (Legendre & de Cáceres, 2013), which is a different way of considering the differences in diversity based on the species rather than on spatial entities such as sites, still relevant for contributing to the heterogeneity of the seascape (Harper et al., 2022). This kind of approach could be a powerful instrument that allows to highlight interesting patterns in a comparative spatial investigation.

Also, other very useful descriptors that can be assessed are the species in common among all the different areas or habitats, or just between some of them, and the species present in just one habitat (“unique species”), which are good quantitative estimators as well of the degree of change between them, giving a more detailed picture about the shades and the gradients that biological diversity is formed by (Harper et al., 2022).

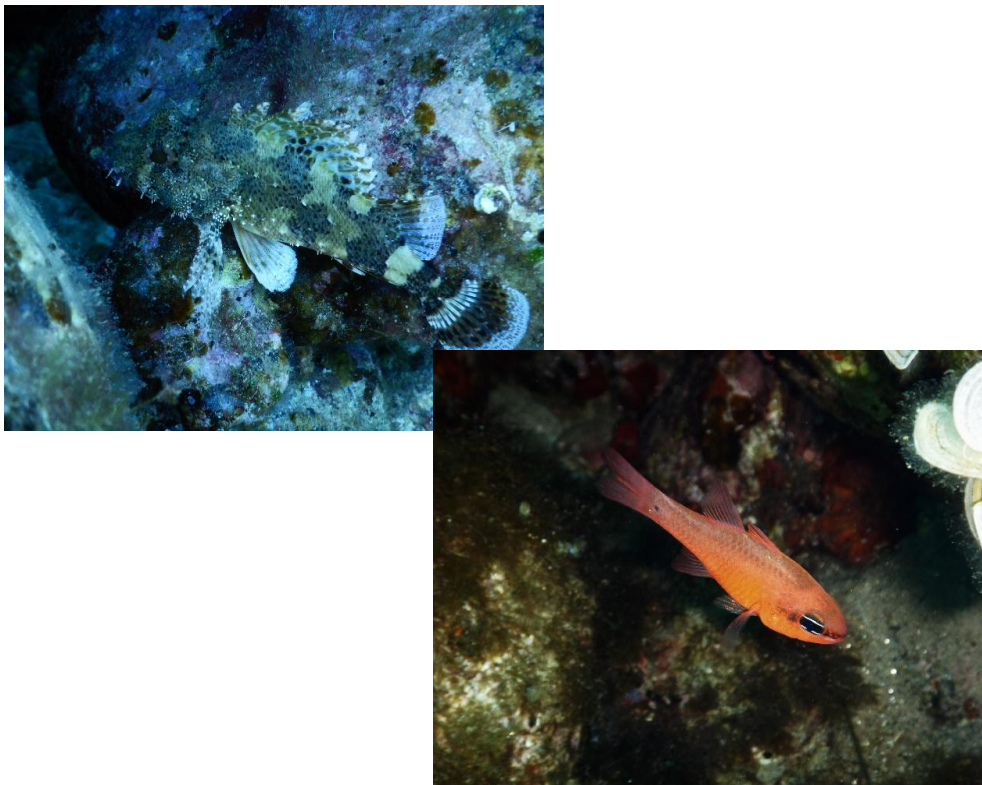
To enhance the potential to estimate the biodiversity of the community under study, a sound assessment should also include **biomass** measurements, defined as the total wet weight of individuals by area, that could be a possible descriptor to estimate the actual stability of a community (Cardinale et al., 2013). Regarding biomass, marine ecology assessments usually elaborate information to obtain a group's or population's biomass, which are historically of interest to ecologists and resource managers (Duffy et al., 2016). Biomass increases the capacity to evaluate the actual quantity of organisms, as it also considers the size of the organisms rather than just their presence as individuals (Fiorella et al., 2019). Furthermore, the consideration of the physical parameters in its calculation (e.g. length), biomass is also a useful metric for quantifying taxa and/or species whose members are of very different sizes (Bar-On et al., 2018), and so to give a very “readable” parameter for the assessment of the actual fish presence in an area or habitat.

The macroscopic nature of fish allows a non-destructive approach in their assessment, enabling the possible application of methods associated with reduced disturbance to species and ecosystems. This could be important when thinking about the eventual use of such organisms in the evaluation areas under any restriction or of particular biological interest, or just in order to improve the sustainability of this kind of studies. The best techniques to put these



theoretical concepts into practical terms are those which rely on visual tools, such as **Underwater Visual Census (UVC)**, **Baited Underwater Videos (BUVs)**, and related procedures (Colton et al., 2010; Caldwell et al., 2016). These techniques can be complementary for several reasons, such as the different operative depths at which they can be applied, and the species targeted by each method (Lowry et al., 2012).

In fact, literature suggests that UVC holds the potential to sample a wide spectrum of species, including more cryptic ones, while BUVs sampling



*Figure 1.2. Two fishes sampled over the study. Top-left: Scorpaena porcus; bottom-right: Apogon imberbis*

usually majorly focuses on the predatory fishes (Lowry et al., 2012; Cheal et al., 2021), due to the presence of attractive bait.

These types of data should ideally be combined to fishery-dependent data, that can give information on wider spatial and temporal scales but are generally less precise regarding the location of the fishing ground and the classification of species caught (Pennino et al., 2016), while fishery-independent data (or survey-based methods, e.g. UVC) have a more limited spatial and temporal extension, leading to a lower quantity of data but potentially higher quality, because of the specific sampling design of the study (Hilborn et al., 2013). The synergistic use of the two approaches allows to obtain more continuous, realistic, and robust assessments over time (Aglieri et al., 2021), but the use of survey-based methods (e.g. UVC and BUUV) already effectively combines both quantitative and qualitative results if properly performed and appears to be a useful approach to start estimating poorly known communities.

The habitat-based characterization of fish diversity can possibly have a good potential to assess the biodiversity of an area, because the differences found in biodiversity (both  $\alpha$ - and  $\beta$ -diversity) for each habitat can inform on the importance of underrated portions of complex ecosystems, composed by more than just one habitat. Furthermore, the connectivity between the habitats is another aspect to account for when trying to achieve sound protection of species, especially if quite highly mobile organisms with a complex ecology such as fishes are considered. It is known that different life stages of fishes can

occur in different habitats: for example, seagrass meadows are well known to be nursery areas (Madi Moussa et al., 2020), hosting a number of juveniles that will then move to other habitats when they become adults, because they offer a very good shelter, and stable and productive environment for them to increase their survival chances during the most delicate period of their life. This suggests that habitats should not be considered as isolated compartments, but more on their completeness, to have a more comprehensive estimate of their true contribution to the overall diversity.

#### ***1.4. Aim of the study***

The overall aim of this study is to assess pattern of coastal fish diversity and its drivers in different habitats. To do so, we used as a case study the coastal waters of the Calabria Region, Southern Italy (see a description in Methods section 2.1.).

The investigation proceeded following a multiple and progressive stepped approach, developed around three main goals:

1. Evaluate the **fish diversity of each habitat** under consideration.
2. Assess the **contribution of each habitat** on the overall  $\alpha$ -diversity.
3. **Scale up the biodiversity assessment**, especially based on how the biotic and abiotic drivers can shape fish assemblages.

More specifically, the first goal is to evaluate the fish diversity of each habitat under consideration (i.e. rocky, sandy, *Posidonia* meadows, see Section 2.1 for further details), possibly providing useful information for future assessments of similar habitats and enhance the comparative potential with already present investigations, even using different approaches about the habitat-based fish diversity assessments (Thiriet et al., 2016; Clarkson et al., 2021; Arndt et al., 2018; Bolgan et al., 2022). It is believed indeed, also based on previous studies (Guidetti, 2000; Gratwicke et al., 2005), that each habitat hosts a specific diversity, composed of many exclusive species that rely on food sources present or that developed the ability to use resources of the habitat where they live, also depending on the biotic and abiotic drivers acting on the habitat, and so all of them deserve adequate consideration. This does not only mean the simple assessment of species richness, which remains still very important but also to check which species are present and how their niches could possibly overlap and how could they interact, to see the specific potential of every area under study.

The second expected goal is to “use” the obtained knowledge about the habitat-specific fish biodiversity to assess the contribution of each habitat on the overall  $\alpha$ -diversity. In fact, this is still one of the first facets of biodiversity analyzed on a small scale investigation, and a key feature of an environment to then

expand to other components of diversity (e.g.  $\beta$ -diversity; Lazzari et al., 2020). The relative contribution of a habitat to the  $\alpha$ -diversity is also a good measure of the potential of every habitat to provide diversity to a larger system and its specific contribution to people (Díaz et al., 2018), especially in coastal habitats (Henseler et al., 2019), being the first step to investigate the connectivity between the habitats and their relative value in determining the overall biodiversity of a larger area (e.g. the Calabrian coasts), that can be expressed as  $\gamma$ -diversity (Whittaker, 1960).

Regarding this, scaling up the biodiversity assessment on the specific study locations, based on how the drivers can shape fish assemblages and the possible changes occurring in the ecological relationships between them becomes fundamental.

The final aim of this process is to increase the knowledge not only regarding the habitats, but also concerning the potential of this important portion of the Mediterranean Sea in contributing to the spatial distribution of biodiversity in the entire basin (Edgar et al., 2016).



*Figure 1.3. An UVC (Underwater Visual Census) transect performed on a sandy habitat (source: EC).*

The last step will be subsequently the prediction of the distribution of the fish species with a modeling approach, that allows to expand the spatial scale in which the species presence can be assessed. In fact, this could inform on any possible hotspot of biodiversity, and eventually on other areas with lower values of fish diversity, (i.e. “coldspots”), but also areas with rare or vulnerable species that should be managed, especially if a reduction in their density is noticed.

To do so, both data taken from the field (e.g. depth) and derived from online

databases (e.g. temperature, salinity) are of vital importance to correlate possible fish diversity patterns found to biotic and abiotic drivers (see Section 1.1 for more detailed information) in the different habitats. Their importance is relevant also considering the different spatial units, to model fish distribution in the whole Calabrian coastline and try to develop a predictive distribution model (Rodrigues et al., 2022) of the considered fish species.

The findings of this study could inform management and conservation strategies, such as the 30x30 commitment that will likely engage countries in protecting 30% of their waters (with at least 10% of strictly protected waters, European commission, 2020). In fact, it is widely recognized that protected areas are one of the foundations for the conservation of biodiversity (Bleeker et al., 2011). However, at present time, the portion of adequately protected sea surface is insufficient and not evenly distributed (Claudet et al., 2020), so immediate efforts are needed to reach the aimed goals.

More specifically, identifying patterns of diversity and locating diversity hotspots could help guiding site selection for the implementation of new Marine Protected Areas (MPAs) and designing sound management strategies. This means that, if necessary, reduced fishing pressure, as well as other management initiatives, could be suggested to prevent the occurrence of possibly irreversible effects both on the ecosystem and in the services provided to people.

## **2. MATERIAL and METHODS**

### ***2.1. Study area***

#### ***2.1.1. The Mediterranean Sea and the basins surrounding the Calabrian coastlines***

The Mediterranean Sea covers an area of slightly over 2.5 million km<sup>2</sup> and it is a semi-enclosed basin, with the only openings to connect with the other oceans being represented by the Gibraltar Strait on the western side, where Atlantic water flows (Poulos, 2020), and the Suez Canal on the eastern side, opened in 1869 and connecting the Mediterranean to the Red Sea. The Suez Canal was opened to facilitate the commercial routes from Asia, but created a number of different new threats for the native biodiversity, such as the increased extinction rate (Gurevitch et al., 2004; Bellard et al., 2016) resulting from this connection (Zenetos et al., 2017). Average depth of Mediterranean Sea is ~1547 m (Barale, 2008), which is quite low compared to other world's oceans, averaging ~3850 m. Despite of its relatively small extension, the Mediterranean Sea hosts a large number of inhabitants surrounding it, divided into 28 different countries that belong to three continents (Europe, Africa, and Asia). Thus, also the anthropogenic impact level on the marine environment is high compared to larger basins around the world. Nonetheless, because of its intrinsic natural and



historical features, this basin is well known as a biodiversity hotspot (Coll et al., 2010), and in particular, the Calabrian coasts present of a variety of habitats and bio-oceanographic conditions. The biodiversity potential of this area is thus really high, but robust assessments need to be made to characterize fish diversity, including comprehensive data about the fish assemblages of the area. In fact, partial, fragmented, and often just catch-based data are present about this area (Busalacchi, 2010; Carlucci et al., 2018), not covering all the coastline extension (Tyrrhenian and Ionian Seas, Messina Strait).

This thesis was based on a large-scale survey which encompassed the Calabrian coasts, Southern Italy, central Mediterranean area. The Calabria Region has a marked peninsular shape and coastlines extend for almost 800 kilometers. In particular, the sampling design included five main locations, where the team could take fast boats from to reach the points chosen for sampling activities, selected also to reduce sampling constrains due to logistic issues.

The locations under study represent very important and strategic sites as they are at the center of the biogeographic border between the Eastern and the Western Mediterranean (Nicolaidou et al., 2012; Sperone et al., 2012). Overall, the three basins surrounding Calabria are: The Western Ionian Sea, the Messina Strait, and the Southern Tyrrhenian Sea.

The **Ionian Sea** is an extremely important region in terms of biodiversity and

coastal geomorphological heterogeneity (Galli et al., 2022), located between the Western basin limit and the southernmost portion of the Adriatic region, shaping its unique geomorphological features, such as some of the deepest trenches of the entire Mediterranean and a marked interannual variability in its conditions (Kalimeris et al., 2020). This reflects the high diversity potential of this sector resulting from variable abiotic and biotic drivers that can change their relative contribution over time (Benton et al., 2009; Meier et al., 2010). Also, negative aspects must be considered when discussing such various influxes, for example, the high number of Non-Indigenous Species (NIS) recorded in this area, majorly coming from the eastern basin through the Suez Canal, and also known as Lessepsian species. Some of these species are currently jeopardizing native fish assemblages and entire ecosystem dynamics all over the Mediterranean Sea (Carlucci et al., 2018), so assessing and knowing how widespread the problem is in this area could be crucial to design sound management strategies.

The **Messina Strait** is probably one of the most peculiar spots of the entire Mediterranean basin, connecting the Tyrrhenian and the Ionian Sea while separating Sicily from the Italian mainland. The area is characterized, as a consequence of the hydrological properties, by upwelling phenomena of the Levantine Intermediate Waters (LIW), coming straight from the Eastern

Mediterranean and passing through the Ionian Sea, and finally resulting in a large amount of organic matter in addition to that arriving from the shallower layers. This leads to strong current flows and a steep slope of the sea bottom, which are factors that widely affect the distribution and presence of fish assemblages, both larval and adult stages (Rattray et al., 2016). The biological result of the abiotic factors acting is a high biodiversity and abundance of species, in many cases very similar to the Atlantic fauna, due to the resemblance of the oceanographic conditions (Spanò et al., 2017).

The last sector on focus is the **Tyrrhenian** portion of the Calabrian coasts, also characterized by high oceanographical and environmental complexity along the coastlines considered (Iacono et al., 2021). Due to these features, it supposedly holds some very interesting features that shape the regional diversity of its faunal assemblages, like the occurrence of many seamounts and the persistent influence of the Messina Strait currents (Busalacchi et al., 2010).

### ***2.1.2. The sites***

The sampling sites have been chosen from a wider set of potential sites, in order to cover the maximum geographic range possible in relation to the environmental gradients present in the area and increase the range of values associated to the predictors that could shape biodiversity patterns along the Calabrian coasts. The original set of potential sites was compiled in QGIS

software (version 3.24.2) using data from the EUNIS (European Nature Information System) database. These data provide information on European habitats and has been a key tool to have reliable information on a quite wide spatial scale. The cells have been designed using a grid with a resolution of ~ 4 km, correspondent to the spatial division of the Copernicus Marine Environment Monitoring Service (CMEMS, <http://marine.copernicus.eu>) environmental data, that allowed to maximize the spatial range covered in relation to the environmental data correspondent to each cell. At the end of this process, each site was associated to a habitat-type. Nonetheless, before starting the sampling process, an echo sonar was used to precisely assess the depth and the kind of bottom, as well as a surficial visual inspection by snorkel, also known as ground-truthing. Any discrepancy from the original habitat of the sampling design has been recorded and replaced from the previous one, to be used in all the following analyses performed in the study.

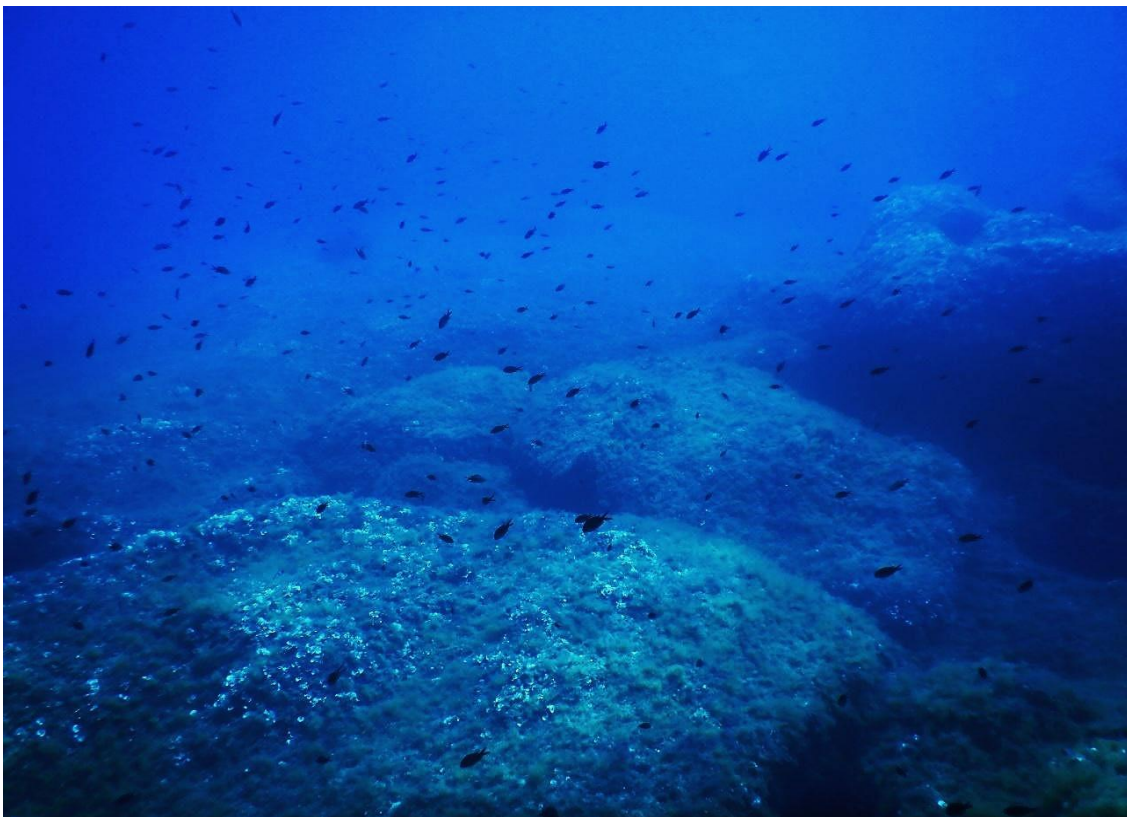
## ***2.2. The habitats of the Calabrian coasts***

The extreme variety in the biotic and abiotic characteristics of the Calabrian coastal waters results in three possible categories of habitats that can be found (at the depths < 25 m). These habitats can be listed as: rocky bottoms, seagrass meadows (mainly *Posidonia oceanica*), and sandy bottoms.

### *2.2.1. Rocky bottoms*

**Rocky bottoms** are usually very heterogeneous and diverse, thanks to their complexity and the creation of micro-habitats that can be exploited by organisms, offering shelter to juveniles, and allowing the simultaneous presence of a wider spectrum of species (Guidetti, 2000), thus bringing to the maximization of biodiversity when dealing with fish assemblages.

Of course, the definition of rocky bottoms remains pretty general, because of the multitude of shapes and the degree of complexity that may fall under this category, as well as the various benthic assemblages that cover the abiotic portion of the seascape, so the possible variety of organisms that can be found



*Figure 2.1. A typical Mediterranean rocky habitat (source: EC)*

depends more on the specific conditions that change case by case (Di Franco et al., 2021).

### ***2.2.2. Posidonia meadows***

*Posidonia oceanica* is the most represented and renowned seagrass species of the Mediterranean basin. *Posidonia oceanica* is a plant, so it relies on light to grow, and it can be found within the photic zone of sandy and mixed sea bottoms (Marbà et al., 2014; Balestri et al., 2015).



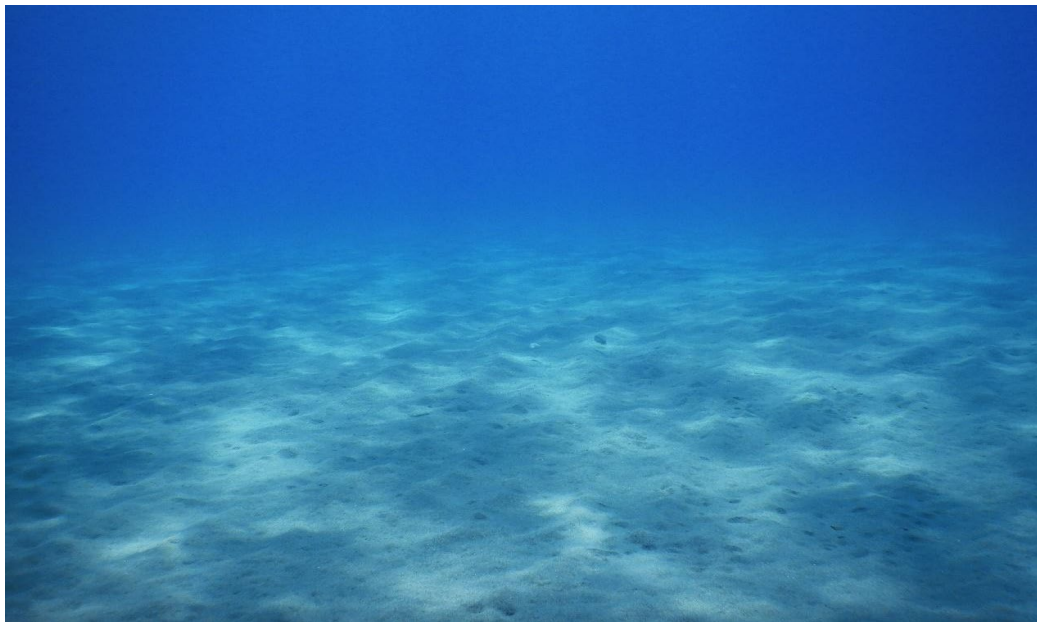
*Figure 2.2. A typical Mediterranean Posidonia habitat on rocky bottom (source: EC)*

In some cases, *Posidonia* can have a patchy distribution with some of the patches embedded inside other habitats. The structures formed by its roots and rhizomes can stabilize the sediments, and this is one of its most important

characteristics, along with numerous other benefits resulting from the habitat it forms. Even if the species' decline has been widely reported over the last decades (Chefaoui et al., 2018) mainly due to anthropogenic pressures, including the spread of invasive species (Telesca et al., 2015), *Posidonia* still has an extremely important role in providing services and represent a suitable habitat for multiple life stages of many organisms, especially mollusks and fishes. In fact, it is particularly considered a sensitive habitats used as nursery areas by many species, including those of commercial value. Being a nursery area, this habitat has a high seasonal variability in abundance and diversity of the associated fauna, which needs to be accounted for when performing biodiversity studies. The high sensitivity of *Posidonia* to a number of abiotic and biotic stressors (Pergen-Martini et al., 2006; Waycott et al., 2009; Telesca et al., 2015) requires immediate actions to quantify their potential to provide services and protect the associated diversity, and this can be done also by assessing the organisms that exploit this ecosystem and the relations occurring in it.

### 2.2.3. *Sandy bottoms*

**Sandy bottoms** are expected to be the less diverse habitats among the ones described in terms of specific richness (Guidetti, 2000; Schramm et al., 2021), because of the reduced heterogeneity due to the absence of spatial subdivisions over large surfaces, that can form micro-habitats like in the other cases, resulting in apparent monotonous bare substrates. Despite this, they are preferential homes for many fish species (e.g. *Lithognathus mormyrus*, *Xyrichtys novacula*, *Bothus podas*, etc.), using them also as feeding grounds or just transit areas (Guidetti, 2000), and other taxa such as mollusks. Soft bottoms can be the target for destructive anthropogenic activities, such as dredging and bottom trawling, and the consequences of those practices on the associated target and non-target fauna are potentially considerable.



*Figure 2.3. A typical sandy bottom of the Mediterranean Sea (source: EC)*



The investigation of soft bottoms assemblages is quite challenging because of the patchy distribution of organisms and the relative difficulties in detecting them, so most of the available data come from fishery-dependent information-FDI (Boudouresque et al., 2004). However, the use of visual methods, which has been rarely applied to sandy bottoms in the past, could be the key to better observing and correctly discriminating how different organisms interact, also based on their specific life habits.

### ***2.3. Sampling locations and sites***

Sampling locations included in the study were five: **Cetraro, Vibo Valentia, Capo Rizzuto, Amendolara, and Scilla**. These locations were chosen in order to cover different areas along Calabrian coasts, and also for logistic reasons as they are close to harbors, thus facilitating the access to boat for sampling.

The total number of sampled sites was **62**, of which:

- **4 rocky** sites
- **23 sandy** sites
- **15 *Posidonia*** sites

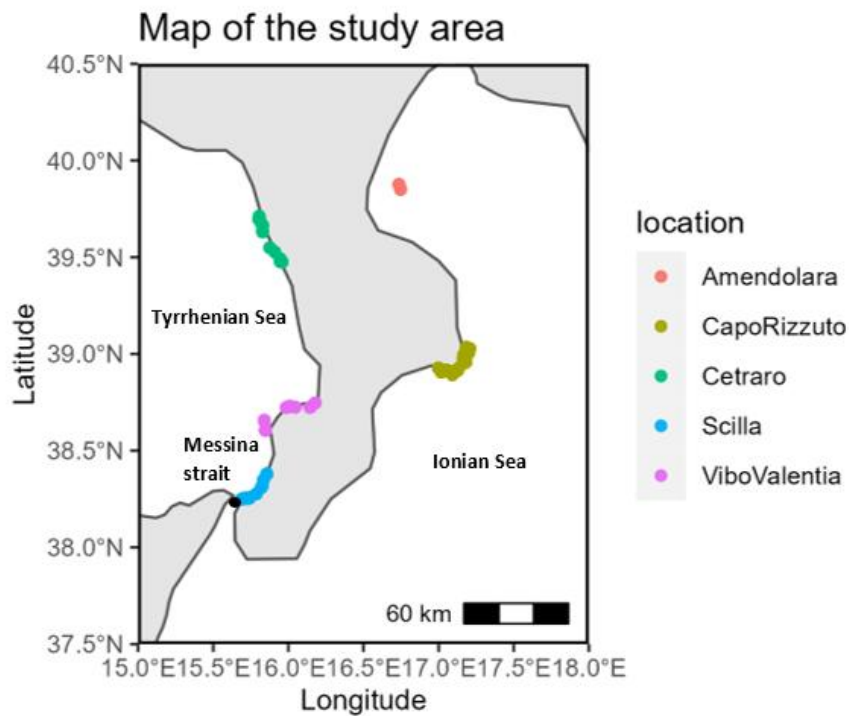


Figure 2.4. Map of the sampled sites (the colors are correspondent to the starting locations)

In particular, we sampled 14 sites in Cetraro, 11 in Vibo Valentia, 21 in Capo Rizzuto, 2 in Amendolara, and 14 in Scilla. The reduced number of sites in Amendolara was due to the smaller area suitable for UVC sampling (established during the sampling design at around – 25 m), despite the large area covered by the bank, i.e. the off-shore rocky bank “Secca di Amendolara”, also included because of its potentially high biological interest. Capo Rizzuto is also an area of special interest for Calabrian waters, being the only Marine Protected Area (hereafter MPA) in the region. Our study did not aim to assess MPA effectiveness, but the area has been chosen because of its good fit with the sampling design.

#### ***2.4. Sampling method***

The method chosen for collecting data on fish assemblages was **Underwater Visual Census (UVC)**. UVC is a widespread technique used for non-invasive sampling of community-level data in shallow, nearshore habitats (Sale, 1980), including many techniques used to quantify fish populations (Thresher and Gunn, 1986). This sampling method was proven a reliable one in shallow waters to assess fish diversity, thanks to its unique features, i.e. short data processing times, accurate estimates for diversity, abundance, and specific traits of fish assemblages. UVC is comparable with other visual techniques (e.g. BRUVs), even if their complementarity enhances to a higher level their overall performances (Cheal et al., 2021).

The divers involved in sampling operations were five (ADF, MDL, AC, SG, EC), trained to perform UVC transects in the most consistent way possible and to ensure a correct estimation of fish abundances and sizes (Lowry et al., 2012) despite of the possible biases known for this technique, such as fish mobility, meteorological and water conditions of the site and the mentioned differences between the observers' knowledge and the critical judgment of assemblages.

The depth range at which transects were carried out was between 0 m and around -25 m, which has been recognized as the maximum depth to complete all the observations planned for every sampling day and remain within the safe

limits regarding SCUBA diving activities.

Within each of the 62 sites, 8 replicates (from now on referred to as “**transects**”) were performed. In every site, one or two divers performed the transects, and the number of transects carried out by each operator has been assessed in the pre-diving briefing, based on many variables (depth of the site, number of dives already made during the day, etc.). Every operator was provided with a pencil, a blank sheet (on a slate) to annotate the information, and a reel to measure the transect. The divers proceeded in opposite direction to avoid covering the same areas over the replicates. At each transect, sampling was carried out according to the UVC (Underwater Visual Census) protocols described by Harmelin-Vivien et al. (1985), which has been commonly applied in the whole Mediterranean basin in the last years (Di Franco et al., 2009; Sala et al., 2012; Di Lorenzo et al., 2020). In particular, each transect was sampled using a **strip transect** of 25 m × 5 m, with a total surface of 125 m<sup>2</sup>.

Along each transect, a trained diver operator swam one way at a constant speed (covering each transect in approximately 6–8 min) using SCUBA equipment and quantified several aspects of fish encountered (see below).



*Figure 2.5. diver finishing a UVC transect (source: EC).*

The transect was physically identified by a polyethylene line rolled up in a reel and ending with a small weight to keep it steady, with a fixed length of 25 m, to avoid any bias related to distances miscalculation underwater. The line was laid as the diver moved forward during its replicate to avoid excessive disturbance on fish (Dickens et al., 2011; Emslie et al., 2018).

Because of the cryptic nature of some benthic species in the Mediterranean assemblages (e.g. Blenniidae, Gobiidae, Scorpaenidae) (Thiriet et al., 2016),

during the way back to the starting point of each transect, the operator usually looked for any additional fish occurrence under rocks, in crevices and in other hidden portions of the sea bottom, to ensure a complete census of all species. For every transect, the diver also noted any deviation from the supposed habitat (noting it with a percentage of the dominant habitat).

#### ***2.4.1. Fish metrics measurements***

During each transect, the diver recorded all fish species, estimating **abundance** whenever there was more than one individual at the same time, and the size of all fishes encountered. Actual number of fish encountered was recorded up to 10 individuals, whereas larger groups were recorded using categories of abundance (i.e. 11–30, 31–50, 51–200, 201–500, >500 ind.; see Harmelin-Vivien et al., 1985). Fish size (total length, TL) was recorded within 2 cm size classes for most of the species, and within 5 cm size classes for large-sized species (maximum size > 50 cm) such as *Epinephelinae*, accounting for a minimum level of visual error by the operator (Bortone and Mille, 1999; Edgar et al., 2004; Mallet and Pelletier, 2014).

#### ***2.4.2. Additional measurements***

The diver also noted for each transect several other information to have a complete assessment of useful metrics to use in the data analysis process. Measures included some general information, i.e. **date** of the observation,

**diver's name**, and information about the site, such as its **code**, **latitude** and **longitude**, fundamental to geo-locating the observation, **initial** and **final depth**, that were averaged to obtain a mean depth for each transect. Lastly, the actual **type of habitat** sampled (Rocky, Sandy, *Posidonia*) was recorded, after visual confirmation of the EUNIS prediction. Any additional note about the transects was written too, to have it stored and available in any required case.

### ***2.4.3. Environmental variables***

Apart from all the variables recorded *in situ*, many others were taken from online databases, made available by Copernicus Marine Environment Monitoring Service (CMEMS).

The retrieved data included:

- **Sea Surface Temperature (SST)**
- **Sea Bottom Temperature (SBT)**
- **Sea Surface Salinity (SSS)**
- Concentration of **dissolved molecular oxygen** in sea water ( $O_2$ )
- Sea water **pH** (pH)
- Concentration of **ammonium** in sea water ( $NH_4$ )
- Concentration of **nitrates** in sea water ( $NO_3$ )
- Concentration of **phosphates** in sea water ( $PO_4$ )
- Concentration of **silicates** in sea water (Si)

- Concentration of **chlorophyll-a** in sea water (Chl)

Moreover, also the concentration of **phytoplankton** (PHYC) and the concentration of **zooplankton** (ZOO), both expressed as carbon in sea water, were retrieved. The **bathymetries** were obtained from the EUNIS database, that has a higher resolution compared to other sources available, which is fundamental for the purposes intended in this kind of investigation, to have precise data about the depth of the shallow layers (< 30 m, sampled by UVC). The bathymetric data were used to obtain the **slope** and the **roughness** of the sea bottom, that could be useful variables to relate with fish diversity metrics. Finally, another driver considered was the **human impact score**, always spatially referenced and available from Micheli et al. (2013), which compounds estimates of 22 anthropogenic drivers (e.g. trawling, coastal population density, hypoxia, etc.) in the Mediterranean and the Black Sea. Each one of the data with a temporal variability has been handled by averaging the monthly values of the previous year at each location.

### ***2.5. Data Handling and Analyses***

All the subsequent analyses were conducted using Rstudio 2022.07.2 unless otherwise stated.

The abundances and biomasses were put into matrices in Microsoft Excel



(Version 2210) along with all the mentioned variables to have them ready to be analyzed.

### ***2.5.1. Diversity metrics calculation***

From the starting data, many metrics and indices were calculated, with the goal of obtaining robust data to characterize fish diversity, also decomposing the information for the specific diversity of each habitat, and their relative contribution. In particular, using the ‘vegan’ package in R, the **species richness** was computed for each transect. This is a basic diversity metric that reflects the number of different species in each replicate, giving an accurate estimate of the taxonomic diversity. Fish biomass (i.e. wet weight, in g) was estimated from size data by means of length–weight relationships from the available literature, selecting coefficients referring to Mediterranean samples whenever possible (Bayle-Sempere et al., 2002, [www.fishbase.org](http://www.fishbase.org)). The biomass for each individual in each transect was then summed, to obtain the total biomass of each transect (community biomass, Cardinale et al., 2013) and also the total biomass of each species for other analytical procedures. Biomass, along with the abundance of every species in a transect, was calculated both for each site and also for each singular species within the sites, to have complete information on the presence and density of the fish species. **Shannon-Wiener** index and **Simpson’s index of Diversity** were also computed by using the ‘vegan’

package. Shannon-Wiener index measures the evenness of species in a community, meaning how similar the abundances of different species are in a given community. Its value rises with the number of species and the evenness of their abundance, and it is calculated as follows:

$$\text{Shannon Index } (H') = \sum_{i=1}^s p_i \ln p_i$$

Where “ $p_i$ ” is the frequency of the  $i^{\text{th}}$  found on the total number of organisms in a sample ( $n_i / N$ ),  $\ln$  is the natural log, and “ $s$ ” is the number of species.

The Simpson’s Index of Diversity is a dominance index, because it gives more weight to common (or dominant) species, and it is calculated as:

$$\text{Simpson's Index of Diversity } (D) = 1 - \sum_{i=1}^s p_i^2$$

Where “ $p_i$ ” is the proportional abundance of one particular species “ $i^{\text{th}}$ ” found, and “ $s$ ” is the number of species.

This index represents the probability that two individuals randomly selected from a sample will belong to different species. Following this definition, the greater the value is, the greater will the diversity be.

All the metrics were calculated for each replicate (transect), to then be possibly pooled per habitat type (Rocky, Sandy, *Posidonia*) when specifically analyzing

the differences between the habitats or kept separate when there was a need to have the information in an extended way.

Finally, the total density (total number of individuals recorded within each transect) was calculated to have an overview of the mean number of fish counted over the transects, and eventually the number of “null transects” (i.e. transects without any observation).

Another part of the study focused more on the metrics for each separate species. To do so, the abundances and biomasses of each species in every transect were considered. The same procedure was also performed for the subsets that just include the observations from one habitat, to have a more straightforward information about the occurrence and density of species in every habitat.

Furthermore, the study aimed at finding any differences and uniqueness of the considered habitats. To do so, the “**dominant habitat**”, intended as the habitat in which the abundance of a species was the highest, was identified. This value can give useful information about the habitat preference of a species and has been done also following Harper et al. (2022). To highlight this concept even more, also the species that were found in just one habitat, named “**unique species**”, and the percentage of them on the total number of species found in that habitat, were detected (Harper et al., 2022). On the other hand, to assess potential similarity between the habitats, the species in common to two or all

of them were identified.

To find the species that have the highest “probability” of being observed associated in the same replicate, a **ranked crossed-correlation** was compiled and then plotted for the 20 most relevant “couples of species” ( $p < 0.05$ ).

All these results have been graphically visualized using the ‘ggplot2’ package in RStudio.

### ***2.5.2. $\beta$ -diversity estimates***

Following this path, started by considering the  $\alpha$ -components of diversity, intended as the local “richness”, the  **$\beta$ -diversity** was evaluated, following the approach by Harper et al. 2022.  $\beta$ -diversity is intended in this study as “the extent of change in community composition” (Whittaker, 1960), in this case between the different habitat types. The  $\beta$ -diversity provides useful information about the contribution of each habitat in shaping the fish biodiversity and highlights the differences between them.  $\beta$ -diversity estimates were computed using the R package ‘adespatial’, which contains the function ‘beta.div’. This function automatically calculates the two components of  $\beta$ -diversity of interest, based on the proposed division of the total  $\beta$ -diversity by Legendre and Cáceres (2013): **Local Contribution to Beta Diversity (LCBD)**, that quantifies the ecological uniqueness of each site in relation to a wider ecosystem network (Heino and Grönroos, 2017), and **Species Contribution to Beta Diversity**

(**SCBD**), considered as the relative importance of each species in affecting beta diversity patterns (da Silva et al., 2018). **LCBD** is an index for the “community uniqueness” of each site compared to the entire seascape (Legendre and de Cáceres, 2013). A high **LCBD** is indicative of the high dissimilarity between two habitats. This decomposition of the total change in community composition well fits one of the goal of the study, which is the evaluation of the habitats’ contribution to diversity. In this case the **LCBD** values were plotted by grouping them per habitat type, just considering the significant values ( $p < 0.05$ ), calculated following the Holm’s method (Holm, 1979). Regarding the species, high **SCBD** values for one species indicate that a species highly differs in its distribution between the habitats of the study area (Legendre and de Cáceres, 2013). We then plotted the 10 species with the highest **SCBD** in `ggplot2`. The initial data were scaled using “Hellinger transformation” to obtain more suitable values for the analyses.

### ***2.5.3. Analysis of variance (ANOVA)***

To test putative difference in univariate diversity metrics (see above) between habitats and accounting for our experimental design (including locations and sites), we used the analysis of variance (**ANOVA**, package ‘nlme’ in R), designed with a mixed-effects model, in which the sites (62 levels) were nested in the locations (five levels), being both random factors, and being nested in the

habitat (fixed, with 3 levels: rocky, sandy, *Posidonia*). This design was chosen to assess variability among habitats, accounting for spatial replication at the two spatial scales considered. To assess whether the inclusion of the nested factors improved the ANOVA or not, also models where each of the factors was gradually removed were performed, and the best model has been chosen looking at the AIC results. Post-hoc tests on the main factor (habitat) were performed using pairwise comparisons among the groups through “emmeans” package in R.

#### ***2.5.4. Permutational Multivariate Analysis of Variance (PERMANOVA)***

To analyze the differences in multivariate densities between habitats, a **PERMANOVA** (Anderson, 2001) was carried out. This method belongs to the family of the “ANOVA-like tests” and constructs an output from a Bray-Curtis resemblance matrix calculated among the sample units and obtain “p-values” using random permutations of observations among the groups. The same experimental design used for ANOVA was adopted. Before running the PERMANOVA, data were square root-transformed, followed by the addition of a “dummy value”, to tackle the problems regarding the many zeros in the data matrix, which is a common issue in ecological data (Zuur et al., 2010). The PERMANOVA analyses have been computed using PRIMER software, version 7.

### ***2.5.5. Nonmetric Multidimensional Scaling (nMDS)***

To graphically represent the multivariate information about the diversity in species composition and highlight the features of the different sites belonging to different habitats, a **Nonmetric Multidimensional Scaling** (nMDS) was carried out. This technique allows to represent the original position of communities in multidimensional space as accurately as possible using a reduced number of dimensions, using the rank orders rather than the absolute abundances (distances) and can be applied with every dissimilarity matrix (in this case using Bray-Curtis dissimilarity). The matrices were scaled using “Hellinger transformation”, to avoid excessive effects related to very large values. Also in this case, a “dummy value” was added to the original data for computational reasons. To perform the nMDS in R, the ‘metaMDS’ function of the ‘vegan’ package was used.

### ***2.5.6. Species Distribution Model (SDM)***

The last step to analyze the obtained data about diversity was to relate it to the pressures and the environmental variables obtained as described before and geographically referenced for each spatial unit, to see how these variables shape fish diversity in the study area, and to make projections regarding the distribution of the considered fish species along the entire Calabrian coastal waters, possibly highlighting areas with high or low species richness

(respectively “hotspots” and “coldspots”). This was done by developing a **Species Distribution Model (SDM)**, a common tool in quantitative ecology (Thuiller et al., 2009), In our case, the SDM was implemented by using the specific richness of each transect, in order to relate the richness to the several drivers into account. Moreover, the general nature of this metric was used to predict the richness of the entire Calabrian coasts, always considering the spatial behavior of the drivers obtained from the CMEMS database and the ones from the field sampling. The drivers used were all the ones described in the paragraph 2.4., and the habitat type (categorical), that was highly relevant for our study purposes.

Firstly, all the spatial data concerning the possible drivers to investigate were gathered to check on the collinearity between them (Zuur et al., 2010), that can possibly result in a reduced performance and precision of the model, because of the “masking” of the real effect of one variable. The variance-inflation factor (VIF, Allison, 1999), which is a measure for the increase of the variance of the parameter estimates if an additional variable is added to the linear regression, was used for this purpose, and only the variables with a VIF value lower than 4 have been retained for further analyses. After this preliminary “filter”, 3 different models have been fitted to our data: a linear model, a Generalized Linear Model (GLM), and an Additive Linear Model (GAM), with the Poisson



error distribution type. The three models were tested based on the Akaike information criterion (AIC) results and the graphic inspection of the residuals to select the best one.

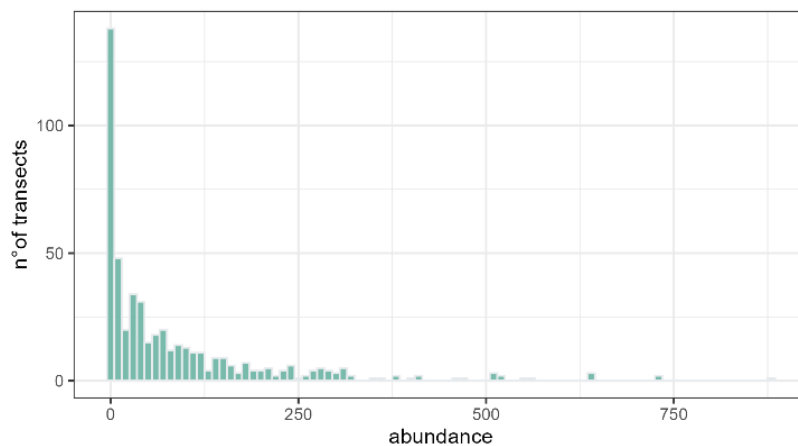
Moreover, we used a backward selection approach, useful to fit the regression models in which the choice of predictive variables was carried out manually. To this end, the stepwise model selection was performed by comparing the AIC of the full model and the ones of all the possible combinations of reduced models, to finally select the model with the lowest AIC value and the lowest number of variables. Finally, an ANOVA on the terms selected was performed to check on their significance.

To predict the richness of the entire Calabrian coasts, the results of the model developed beforehand were extended, by using the georeferenced rasters regarding the area, obtained as previously mentioned from the CMEMS database (<http://marine.copernicus.eu>), and mapped on the cartography of interest. Also the errors associated to the model were computed and mapped to see whether their contribution could influence the results of the model itself.

### 3. RESULTS

Considering the total number of sites sampled (62), divided into 24 rocky sites, 23 sandy sites, and 15 *Posidonia* sites, 58 of them belong to the 0 – 20 m stratum (surficial), while 4 of them to the 20 – 30 m stratum (intermediate). The average depth of the sites was assessed at around 9.77 m, obtained by averaging the initial and the final depth recorded for each transect at each site.

First of all, a brief revision of the number of observations for each transect has been plotted (figure 3.1). In 8.5% of the total transects (42), no individuals were recorded (all the 42 null transects belong to sandy habitat replicates), and in 28% of them (138), the number of observed fishes did not exceed 5 individuals (including the null ones). On the other hand, 138 transects recorded more than 100 individuals, and 220 transects (44%) recorded a number between 6 and 100 fishes.



*Figure 3.3. Number of fish observed for each transect (replicate) during samplings.*

To focus on the high number of null transects, these data were divided among the habitats, explaining that almost all of them belong to sandy transects, which was the case during the sampling operations. The very high abundances recorded for some transects were mainly due to big schools of small fishes (e.g. *C. chromis*).

### ***3.1. Species number***

In total, 72 species were recorded, belonging to 25 families (Table 3.1). The most represented families are Labridae (13 species), Sparidae (12 species), Gobiidae (10 species), and Serranidae (7 species). Some of the species were regularly observed in a relevant number of replicates (e.g. *C. julis*, 52.6 % of the transects), while others were observed on just a few occasions (e.g. the family *Tripterygiidae*, 3% of the transects). In a very limited number of cases, fishes were identified at genus (e.g. *Trachurus*, *Sphyræna*) or family (e.g. *Mugilidae*) level due to the limitations of visual identification.

Table 3.1. List of the species found during the UVC sampling. Also the habitat in which each species has been most commonly found (dominant habitat), is noted (column three).

<b>Family</b>	<b>Species</b>	<b>Dominant habitat</b>
<i>Apogonidae</i>	<i>Apogon imberbis</i>	Rocky
<i>Atherinidae</i>	<i>Atherina spp.</i>	Posidonia
<i>Blennidae</i>	<i>Parablennius rouxi</i>	Rocky
	<i>Parablennius tentacularis</i>	Sandy
	<i>Parablennius zvonimiri</i>	Rocky
<i>Bothidae</i>	<i>Bothus podas</i>	Sandy
<i>Callionymidae</i>	<i>Callionymus spp.</i>	Sandy
<i>Carangidae</i>	<i>Trachurus spp.</i>	Sandy
<i>Centracanthidae</i>	<i>Spicara maena</i>	Posidonia
	<i>Spicara smaris</i>	Sandy
<i>Dactylopteridae</i>	<i>Dactylopterus volitans</i>	Sandy
<i>Dasyatidae</i>	<i>Dasyatis pastinaca</i>	Sandy
<i>Gobiidae</i>	<i>Deltentosteus quadrimaculatus</i>	Sandy
	<i>Gobius bucchichi</i>	Rocky
	<i>Gobius cobitis</i>	Rocky
	<i>Gobius fallax</i>	Rocky
	<i>Gobius geniporus</i>	Rocky
	<i>Gobius incognitus</i>	Sandy
	<i>Gobius niger</i>	Sandy
	<i>Gobius xanthocephalus</i>	Rocky
	<i>Pomatoschistus sp.</i>	Sandy
	<i>Zebrus zebrus</i>	Rocky
<i>Labridae</i>	<i>Coris julis</i>	Rocky
	<i>Labrus merula</i>	Posidonia
	<i>Labrus viridis</i>	Rocky
	<i>Symphodus cinereus</i>	Rocky
	<i>Symphodus doderleini</i>	Rocky
	<i>Symphodus mediterraneus</i>	Rocky
	<i>Symphodus melanocercus</i>	Rocky
	<i>Symphodus ocellatus</i>	Rocky
	<i>Symphodus roissali</i>	Rocky
	<i>Symphodus rostratus</i>	Posidonia
	<i>Symphodus tinca</i>	Rocky
	<i>Thalassoma pavo</i>	Rocky

	<i>Xyrichtys novacula</i>	Sandy
<b>Mugilidae</b>	<i>Mugilidae</i>	Rocky
<b>Mullidae</b>	<i>Mullus surmuletus</i>	Rocky
<b>Muraenidae</b>	<i>Muraena helena</i>	Rocky
<b>Pomacentridae</b>	<i>Chromis chromis</i>	Rocky
<b>Scaridae</b>	<i>Sparisoma cretense</i>	Rocky
<b>Scophthalmidae</b>	<i>Lepidorhombus boschii</i>	Sandy
<b>Scorpaenidae</b>	<i>Scorpaena maderensis</i>	Rocky
	<i>Scorpaena notata</i>	Rocky
	<i>Scorpaena porcus</i>	Rocky
	<i>Scorpaena scrofa</i>	Posidonia
<b>Serranidae</b>	<i>Anthias anthias</i>	Rocky
	<i>Epinephelus aeneus</i>	Sandy
	<i>Epinephelus costae</i>	Rocky
	<i>Epinephelus marginatus</i>	Rocky
	<i>Serranus cabrilla</i>	Posidonia
	<i>Serranus hepatus</i>	Sandy
	<i>Serranus scriba</i>	Rocky
<b>Sparidae</b>	<i>Boops boops</i>	Rocky
	<i>Dentex dentex</i>	Rocky
	<i>Diplodus annularis</i>	Posidonia
	<i>Diplodus puntazzo</i>	Rocky
	<i>Diplodus sargus</i>	Rocky
	<i>Diplodus vulgaris</i>	Rocky
	<i>Lithognathus mormyrus</i>	Sandy
	<i>Oblada melanura</i>	Posidonia
	<i>Pagellus acarne</i>	Posidonia
	<i>Pagrus pagrus</i>	Sandy
	<i>Sarpa salpa</i>	Rocky
	<i>Sparus aurata</i>	Posidonia
	<i>Spondylisoma cantharus</i>	Posidonia
<b>Sphyraenidae</b>	<i>Sphyraena sp.</i>	Posidonia
<b>Syngnathidae</b>	<i>Hippocampus hippocampus</i>	Sandy
<b>Trachinidae</b>	<i>Trachinus araneus</i>	Sandy
	<i>Trachinus draco</i>	Sandy
<b>Tripterygiidae</b>	<i>Tripterygion delaisi</i>	Rocky
	<i>Tripterygion melanurus</i>	Rocky
	<i>Tripterygion tripteronotus</i>	Rocky
<b>Total families = 25</b>	<b>Total species = 72</b>	

As we can notice in Table 3.1, it is possible to find (column 3) the "dominant habitat" of each species. This parameter has been evaluated by calculating in which one of the three habitats the abundance of a species was the highest. In general, a total of 56 species were found in rocky habitats, 38 species in *Posidonia* meadows and 32 species in sandy bottoms. These numbers do not exclude the co-occurrence of one species in more than one of the habitats, as these aspects of "uniqueness" will be presented later on.

The total number of fish individuals (without distinctions for the species) found was 30,955 individuals for the rocky bottoms, 10,177 for *Posidonia* meadows, and 2,027 individuals for sandy bottoms, highlighting evident differences in the magnitude of fishes observed in each habitat.

### **3.1.1. The abundances**

Analyzing the species separately, some of them were found at high **densities** (mean  $\pm$  SE) most of the times they have been encountered. This is the case of species like *Chromis chromis* ( $44.8 \pm 4.19$  individuals/125 m<sup>2</sup>), *Boops boops* ( $8.2 \pm 1.6$  individuals/125 m<sup>2</sup>), and *Oblada melanura* ( $6.2 \pm 1.1$  individuals/125 m<sup>2</sup>) (those data are referred to the observations on the 3 habitats pooled). Those species typically form big schools. More in detail, in rocky habitats (figure 3.2a) the three species with the highest mean density are *C. chromis* ( $93.5 \pm 9.4$  individuals/125 m<sup>2</sup>), *B. boops* ( $9.8 \pm 2.8$  individuals/125 m<sup>2</sup>), and *S. sarpa* ( $9.4$

$\pm 1.3$  individuals/125 m<sup>2</sup>).

*Posidonia* meadows (figure 3.2b) showed similar trends in the densities of species, with the maximum values for *C. chromis* ( $35.1 \pm 4.2$  individuals/125 m<sup>2</sup>), *B. boops* ( $14.9 \pm 4.1$  individuals/125 m<sup>2</sup>), and *Oblada melanura* ( $9.9 \pm 2.3$  individuals/125 m<sup>2</sup>).

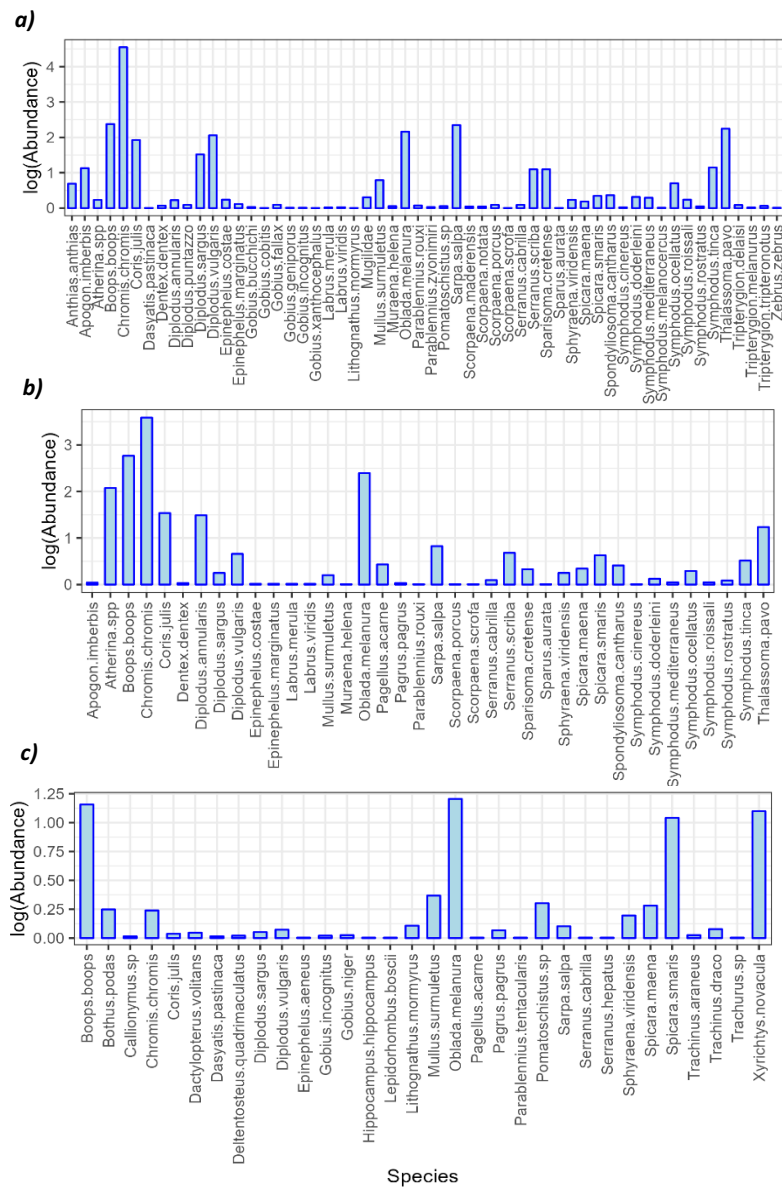


Figure 3.4. Mean number of individuals (abundance) for each species in rocky (a), *Posidonia* (b), and sandy (c) habitats.

Lastly, Sandy sites (figure 3.2c) deviated a bit in their most abundant species, represented by *Oblada melanura* ( $2.3 \pm 2.17$  individuals/125 m<sup>2</sup>), *B. boops* ( $2.2 \pm 1.6$  individuals/125 m<sup>2</sup>), and *Xyrichtys novacula* ( $2 \pm 0.23$  individuals/125 m<sup>2</sup>).

### **3.1.2. Fish biomass**

Also fish **biomass** (fish net weight) was estimated (figure 3.3) (mean  $\pm$  SE), to have a better idea of the actual quantity of organisms, and in this case, other organisms have been highlighted for their biomass, such as *Sarpa salpa* ( $770 \pm 132.1$  g/125 m<sup>2</sup>), *Diplodus vulgaris* ( $530.5 \pm 74.9$  g/125 m<sup>2</sup>) and *Chromis chromis* ( $410.8 \pm 58.01$  g/125 m<sup>2</sup>) on rocky substrates, *Oblada melanura* ( $70.9 \pm 68.8$  g/125 m<sup>2</sup>), *Xyrichtys novacula* ( $40.28 \pm 5.7$  g/125 m<sup>2</sup>), *Boops boops* ( $28.1 \pm 24.6$  g/125 m<sup>2</sup>) on sandy substrates, and *Chromis chromis* ( $109.5 \pm 16.5$  g/125 m<sup>2</sup>), *Oblada melanura* ( $86.1 \pm 33.9$  g/125 m<sup>2</sup>), and *Sarpa salpa* ( $78.4 \pm 26.2$  g/125 m<sup>2</sup>) in *Posidonia* meadows.



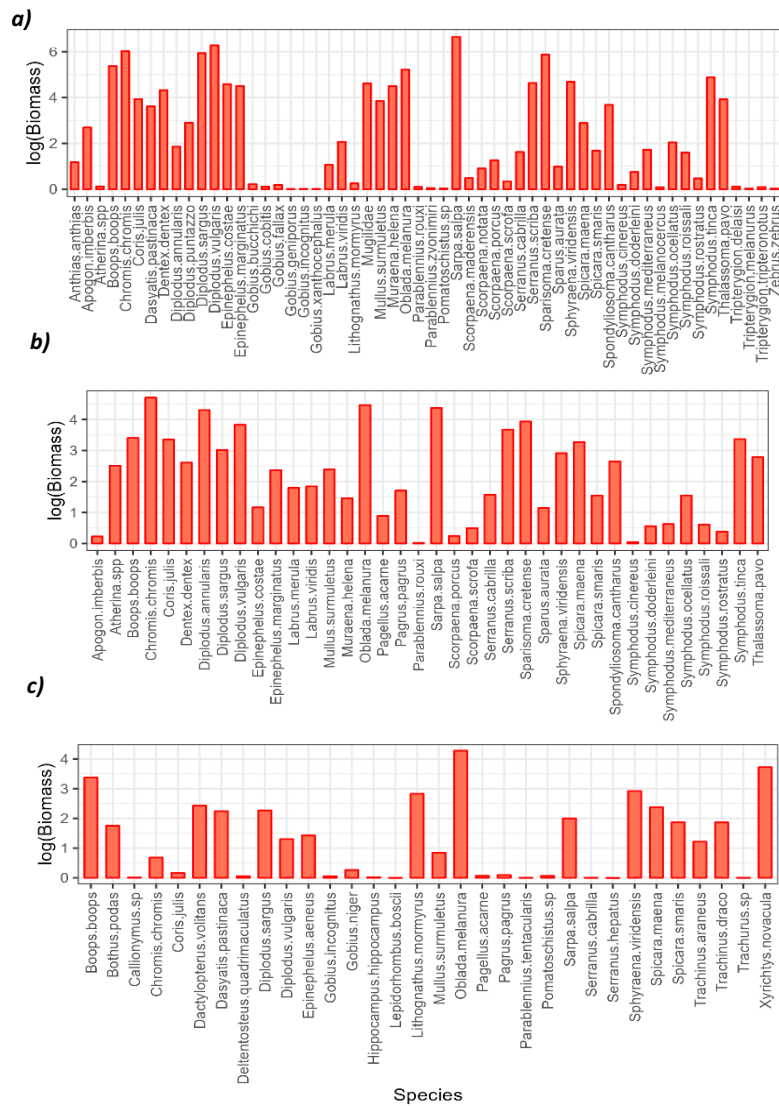


Figure 5.3. Mean biomass for each species in rocky (a), and sandy *Posidonia* (b), and sandy (c) habitats.

### 3.1.3. Species co-occurrence

To further understand the patterns of occurrence of the species and better explore the dataset, a ranked cross-correlation output was compiled (Figure 3.4). Among the five highest correlated couples of species, we can find the Family *Mugilidae* and *Scorpaena notata* (0.59), *Trachinus araneus* and *T. draco* (0.50), *Diplodus puntazzo* and *D. sargus* (0.43), *Parablennius zvonimiri*

and *Symphodus doderleini* (0.43), *Diplodus sargus* and *Sparisoma cretense* (0.42). Those are just the highest correlated examples of significant correlations ( $p < 0.05$ ), that can inform about the “probability” of observing the two species considered at the same time (i.e. in the same replicate).

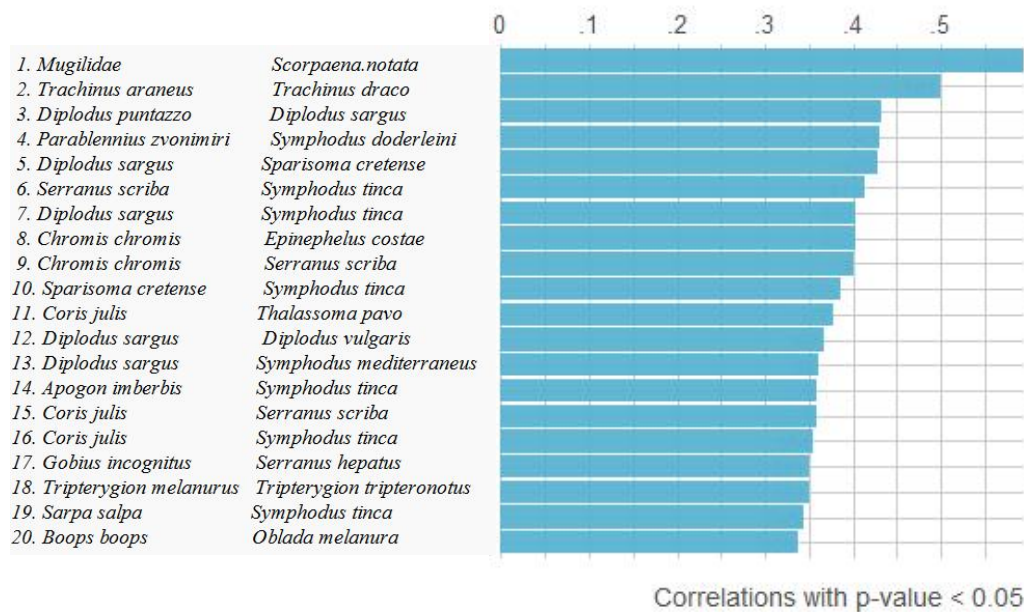


Figure 3.4. Ranked cross-correlations for the abundance matrix of the species found. The plot shows the 20 most correlated species pairs.

## 3.2. The habitats

### 3.2.1. Species richness per habitat

In terms of species richness (figure 3.5a), this had a mean value of 6.96 (SE  $\pm$  0.2) species/125 m<sup>2</sup> in *Posidonia* meadows, mean number of 10.22 ( $\pm$  0.19) species/125 m<sup>2</sup> was instead observed in rocky bottoms, while an average of just 1.26 ( $\pm$  0.08) species/125 m<sup>2</sup> was found on sandy bottoms. Variability among

the groups was statistically significant (df: 6, F: 360.2,  $p < 0.05$ , ANOVA). The following pairwise comparisons for all the habitat pairs resulted significant as well. The addition of the nested and random factors (locations nested in habitat, and sites nested in the locations) gave better results (in terms of AIC values), and so it has been kept with the consideration of all the factors in the final model.

### ***3.2.2. Diversity indices***

The diversity indices provided a complementary piece of information for the diversity estimates of the habitat. The Shannon index ( $H'$ ), representing the evenness component of a community along with the simple specific diversity, has given the highest values in rocky bottoms, specifically with a mean value of 1.43 ( $\pm 0.04$ ), followed by *Posidonia* meadows, where the mean value of  $H'$  is 1.14 ( $\pm 0.04$ ). Sandy bottoms showed instead very low values of the Shannon Index, stopping at 0.23 ( $\pm 0.03$ ). The differences resulted statistically significant (df: 6, F: 166.9,  $p < 0.05$ , ANOVA) and the pairwise differences for the habitats assessed that each habitat was significantly different from each other. Shannon index showed a significative improvement in the ANOVA output when considering the nested random factors (localities and sites).

The results regarding the Simpson's Index showed similar trend, as the obtained results were 0.62 ( $\pm 0.015$ ) for rocky bottoms, 0.5 ( $\pm 0.016$ ) for

*Posidonia* meadows, and  $0.37 (\pm 0.03)$  for sandy substrates. The differences between the groups were statistically significant (df: 6, F:11.6,  $p < 0.05$ , ANOVA) but in this case, the difference in the mean values between the rocky and *Posidonia* meadows were not statistically significant (assessed through pairwise comparisons). The inclusion of the nested and random factors (locations nested in habitat, and sites nested in the locations) improved the model also in this case.

### **3.2.3. Biomass per habitat**

Biomass values (figure 3.5b) reflected the richness trends, with rocky bottoms showing the highest biomass ( $3949.8 \pm 344.2$  g/125 m<sup>2</sup>), followed by *Posidonia* meadows ( $738.7 \pm 72.2$  g/125 m<sup>2</sup>) and Sandy bottoms ( $244.3 \pm 105.2$  g/125 m<sup>2</sup>). The differences among the habitats were statistically significant (df: 6, F: 22.8,  $p < 0.05$ , ANOVA), but in this case, only rocky bottoms significantly differed from the other habitats (assessed through pairwise comparisons), while Sandy and *Posidonia* meadows did not show significant differences. The outcome of the ANOVA regarding the two random factors nested in the “habitat” improved the model also in this case.

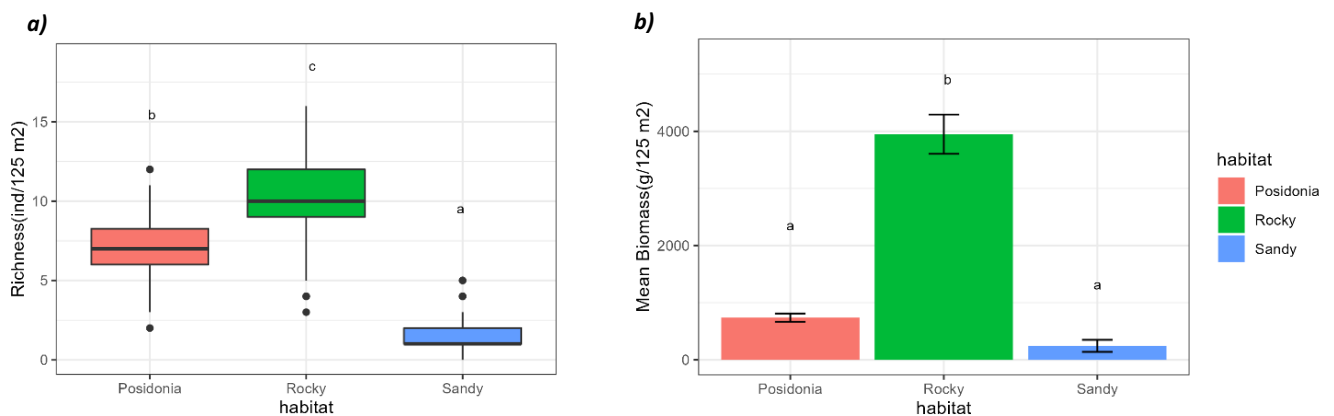


Figure 3.5. Mean richness (a) and biomass (b) for each habitat.

### 3.2.4. Similarities and differences in species composition between the habitats

In rocky bottoms, the number of unique species found was 16, followed by 14 unique species in sandy bottoms. *Posidonia* meadows did not record any unique species, which is quite an interesting outcome. Even more interesting was the percentage of unique species in relation to the total number of species recorded in each habitat. In fact, in sandy bottoms almost half (43.8%) of the total species are unique for this habitat, “outscore” this value calculated for rocky habitats (28.6%).

On the other hand, the similarity between the assemblages in the different habitats was calculated (Figure 3.6). These values are in accordance with the previous results. In fact, the two habitat types sharing more species are rocky and *Posidonia* (24 species), while sandy habitats share not so many species

with the other two (4 species with rocky habitats and 2 with *Posidonia* ones).

Furthermore, 12 species are shared between all the three considered habitats, such as *C. chromis*, *S. salpa* and *M. surmuletus*, possibly underlining their generalist habits.

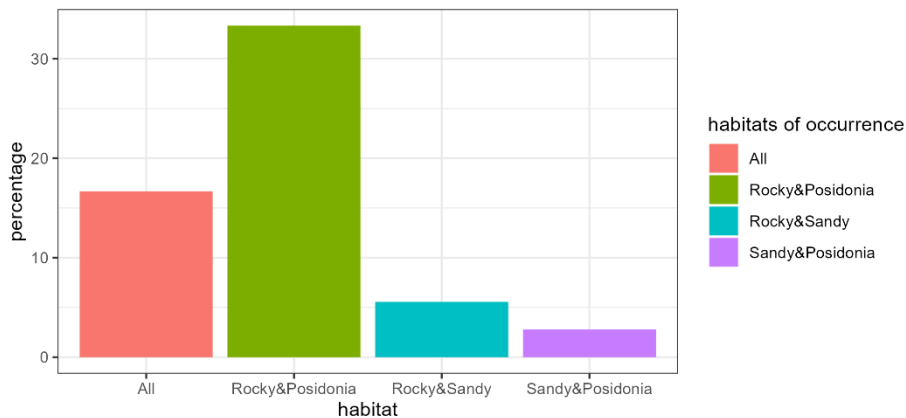


Figure 3.6. percentage of species found in common between the habitats.

### 3.2.5. The $\beta$ -diversity

$\beta$ -diversity estimates have been divided in our case in the Local Contribution to Beta Diversity (LCBD) and Species Contribution to Beta Diversity (SCBD).

The results regarding LCBD gave emphasis to the significance of the previous results, as they highlight a marked difference between sandy sites, being by far the habitat with the highest mean contribution to the LCBD ( $0.0025 \pm 7.45 \times 10^5$ ), as we can see in figure 3.7, meaning that the fish assemblages inhabiting this kind of habitat are confirmed to be the most “unique”, while *Posidonia* and rocky bottoms have been showing lower mean values,

respectively  $0.0019 \pm 3.54 \times 10^{-5}$  and  $0.0016 \pm 2 \times 10^{-5}$ .

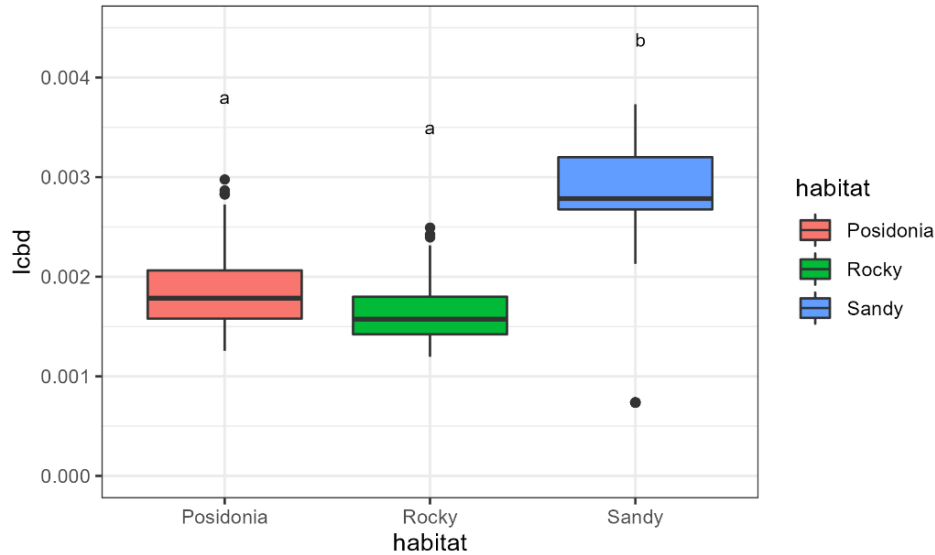


Figure 3.7. Local Contribution to Beta Diversity per habitat.

Regarding  $\beta$ -diversity, the ANOVA assessed that the differences between the groups were statistically significant (df: 6, F:27.6,  $p < 0.05$ ), but the pairwise comparisons revealed that *Posidonia* and rocky habitats did not significantly differ. The best model for the LCBD component was again the “complete” one, that included both nested random factors.

To go deeper into the characterization of the  $\beta$ -diversity component of the Calabrian coastline, the SCBD was calculated (figure 3.8), to better understand which are specifically the species most responsible for the differentiation patterns identified for the habitats. The most influential species, with a very high SCBD value (0.18), is *X. novacula*, which has been already mentioned

before as one of the species inhabiting exclusively sandy bottoms, followed by *C. chromis* (0.12), *C. julis* (0.052), *O. melanura* (0.049), and *B. podas* (0.048).

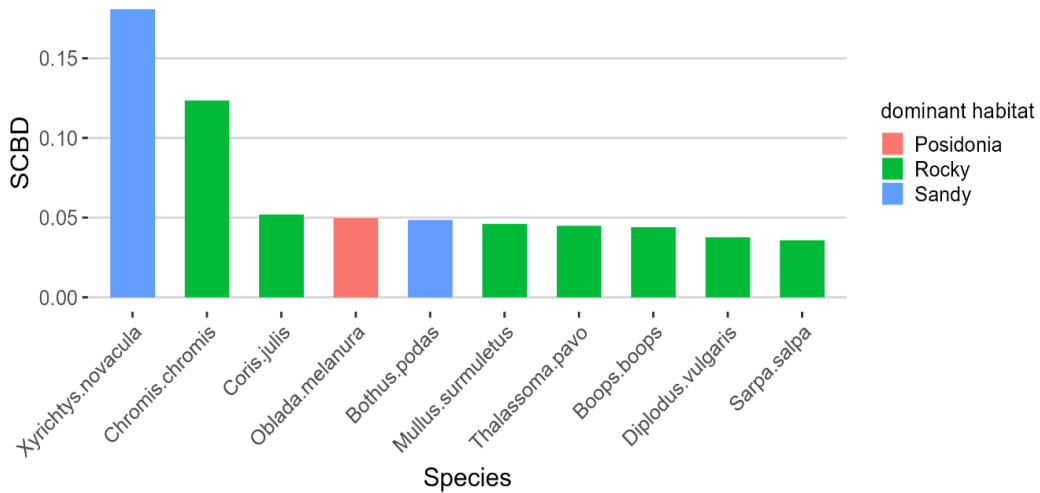


Figure 3.6. Species Contribution to Beta Diversity. The colors of the column represent the dominant (or preferred) habitat for each selected species.

### 3.2.6. Assemblage composition in the three habitats

The graphical results of the NMDS (Figure 3.9), also completed by the calculation of clusters to highlight the habitat types, provided a good summary of the differences in assemblage composition between the sites, and their link with the species.

First of all, the calculation made by choosing a 2-dimensional output (NMDS1 and NMDS2), generated a stress value of 0.17, which states a good representation of the simplified community. The stress represents the difference between the data point position in the two-dimensional plot and the “real”



distance calculations in the multidimensional space. Moreover, the sites belonging to rocky bottoms did not show so much variability and even represented a sort of subset of *Posidonia meadows*, despite actually being the most diverse habitat if considering the diversity metrics. *Posidonia* sites shows a slightly higher variability, overlapping in few cases with the cluster of the sandy sites. Sandy bottoms are instead completely separated from the other two clusters, and the differences in the rank-based distances between the sites are more evident than in the other cases, forming a very wide cluster. The rank-based positions of the species, indicating how the species are distributed in the plot and how they link with the sites, are in accordance with the previous results, especially looking at the highlighted species, which are the ones with the highest values of SCBD, with *X. novacula* and *B. podas* being the most “distant” species from the rocky and *Posidonia* meadows, and on the opposite side *C. chromis* and *O. melanura*. More in general terms, we can say that the position of species in the plot overlapped quite well with their previously obtained preferred (or dominant) habitat.

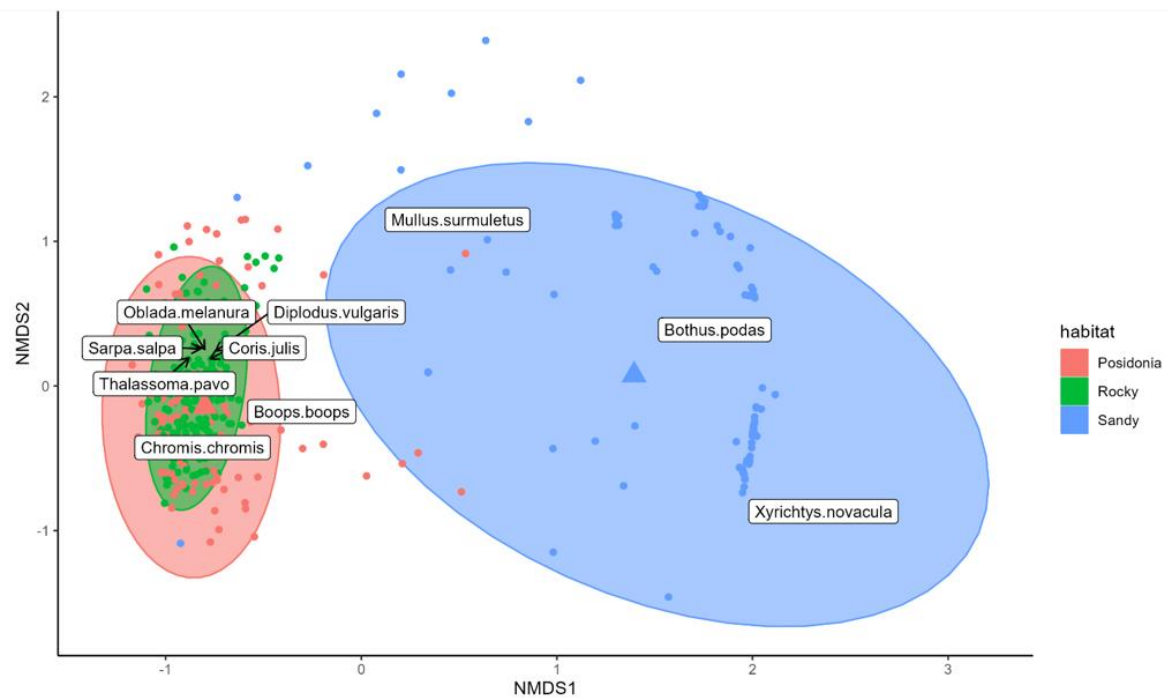


Figure 3.9. Nonmetric Multidimensional Scaling for the sites (points) aggregated per habitat type (colors). The groupwise centroids (triangles) have been calculated to allow the clusterization and highlight the distinctions between the habitats. The species displayed in the labels (10) are the ones with the highest contribution to  $\beta$ -diversity.

The PERMANOVA (Table 3.2) on the abundance data matrix was useful as a confirmation of the graphical hints given by the NMDS. Its results revealed that the differences between the habitats for the fish assemblages were significant. Both location (df: 10, pseudo-F: 2.4,  $p < 0.05$ ) and site (df: 49, pseudo-F: 4.5,  $p < 0.05$ ) factors were significant.

The pairwise tests performed for the habitat factor confirmed that each pair of habitat tested was significantly different from each other ( $p < 0.05$ ).

Table 3.2. PERMANOVA output on the square root transformed data of the fish abundance. (Significance :  $p < 0.05$ )

<i>Source</i>	<i>df</i>	<i>SS</i>	<i>Pseudo-F</i>	<i>p (perm)</i>
<i>habitat</i>	2	$5.17 \times 10^5$	25.504	0.0001
<i>location(habitat)</i>	10	$1.14 \times 10^5$	2.4339	0.0001
<i>site(location(habitat))</i>	49	$2.31 \times 10^5$	4.4813	0.0001
<i>Residuals</i>	434	$4.56 \times 10^5$		
<i>Total</i>	495	$1.42 \times 10^6$		

### 3.2.7. Drivers of species richness and predicted patterns along Calabrian coasts

Among the three models' families tested at the beginning, the one with the best fit, based on the AIC results (table 3.3a), was the GAM-based model. The backward selection of the variables optimized the previously selected model with a lower AIC (1915.221), and finally allowed the composition of the final model, that is a GAM model with a Poisson error distribution composed of:

$$\text{Richness} \sim \text{factor}(\text{habitat}) + \text{s}(\text{SST}, \text{bs} = \text{"cs"}) + \text{s}(\text{SSS}, \text{bs} = \text{"cs"}) + \text{chl}$$

Where "habitat" is the main factor related to richness, "SST" and "SSS" are included in a smoothing term with a shrunk cubic regression spline, and "chl" is linearly correlated to the response variable.

The results of the ANOVA (table 3.3b) regarding the variables included in the model resulted significant for all the factors ( $p < 0.05$ ) apart from “chl” ( $p = 0.0594$ ), that was still included by the automatic computation of the model.

Table 3.3. (a) Results of the AIC, representing the model fit; (b) Results of the ANOVA on the terms of the chosen GAM model. The *df* values noted with “\*” are referred to “expected” degrees of freedom.

a)		b)			
Model	AIC	Factor	<i>df</i>	Chi squared	<i>p</i> -value
Linear	2038	habitat	2	882.610	< 2e-16
GLM	1943	chl	1	3.553	0.0594
GAM	1942	<i>s</i> (SST)	1.609*	7.452	0.00396
		<i>s</i> (SSS)	5.587*	62.163	< 2e-16

The model results showed that the habitat factor (figure 3.10a) appears highly significant in shaping richness values, producing evident differences in the results, with sandy bottoms being the less rich in species, the rocky bottoms being in the opposite side the richest habitats, and *Posidonia* meadows assemblages being slightly less rich than rocky, but more than sandy assemblages. In regard to the environmental variables, fish richness shows an evident decline as the SST (figure 3.10b) and SSS increase (figure 3.10c). In particular, richness values decrease steeply as the temperature exceeds 21.2 °C.

As for the chlorophyll-a concentration (figure 3.10d), this variable causes similar responses to SST and SSS, so its increase leads to a reduction of species richness, but the related plot turns out linear, because the term included in the model is linearly correlated to the response variable.

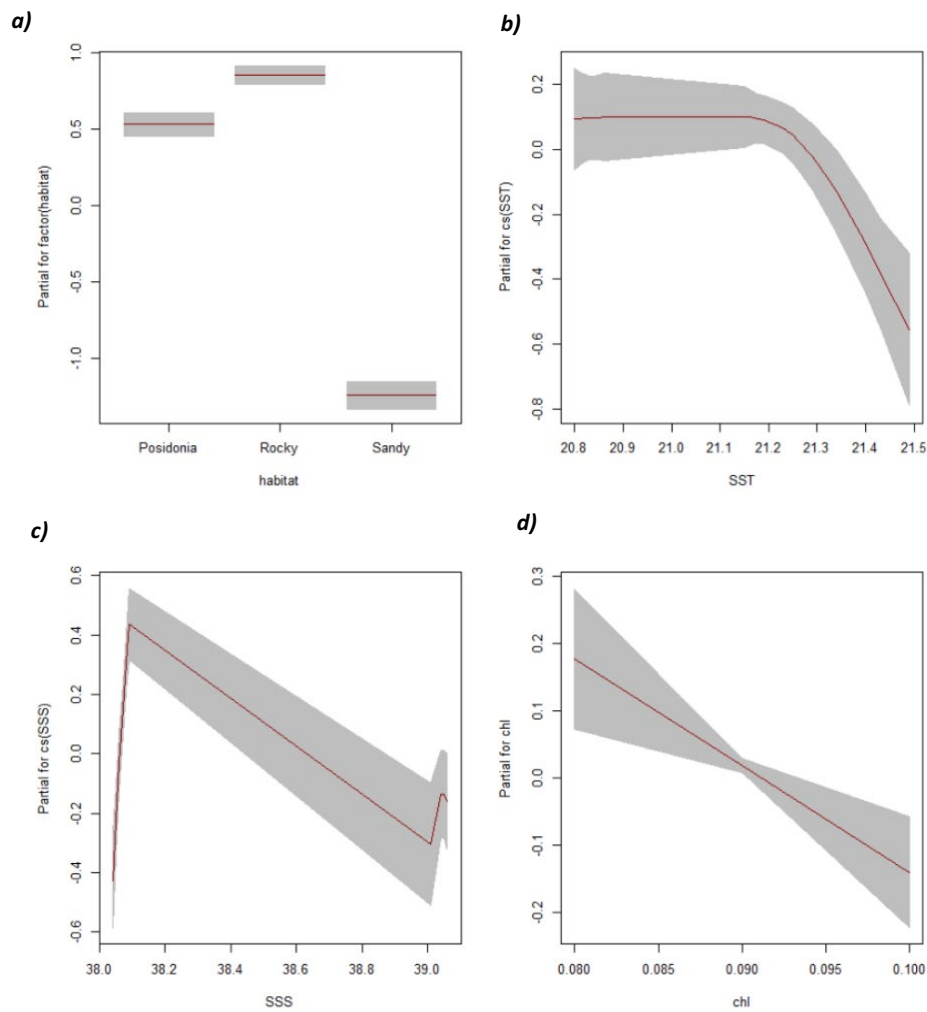


Figure 3.70. Results of the GAM model for the specific richness regarding each individual parameter. (a) habitat, (b) SST, (c) SSS, and (d) chl.

Finally, the results obtained have been used to predict the possible patterns of species richness along the entire Calabrian coastline (figure 3.11).

The general trend concerning most of the extension of coastal habitats (< 30 m) is of a low species richness, around 3-4 species for every spatial unit (125 m<sup>2</sup>). Nonetheless, there are some areas with a higher number of species predicted by the model, and, especially around Vibo Valentia, there are some spots in which the predicted species richness is around 13-14 species, that is a major increase with respect to the rest of the coast, and it can be further defined as an “hotspot” for the Calabrian coastlines.

Another zone in which there is higher richness than average is located on the opposite side of Calabria, in particular in correspondence to the Marine Protected Area of Capo Rizzuto and surroundings, on the Ionian coast. In this case, the species richness is less than in the previous case, around 7-8 species per spatial unit predicted, but there are some smaller patches in which richness reaches values of about 11-12 species. The last zone that revealed interesting outcomes regarding the response variables is located in the Messina strait, where richness goes up to 12-13 species.

The error distribution has been graphically represented as well, and in general terms, the error is quite low (around 1-2 species), so it is confident to assess that the predictions are accurate in most of the cases.

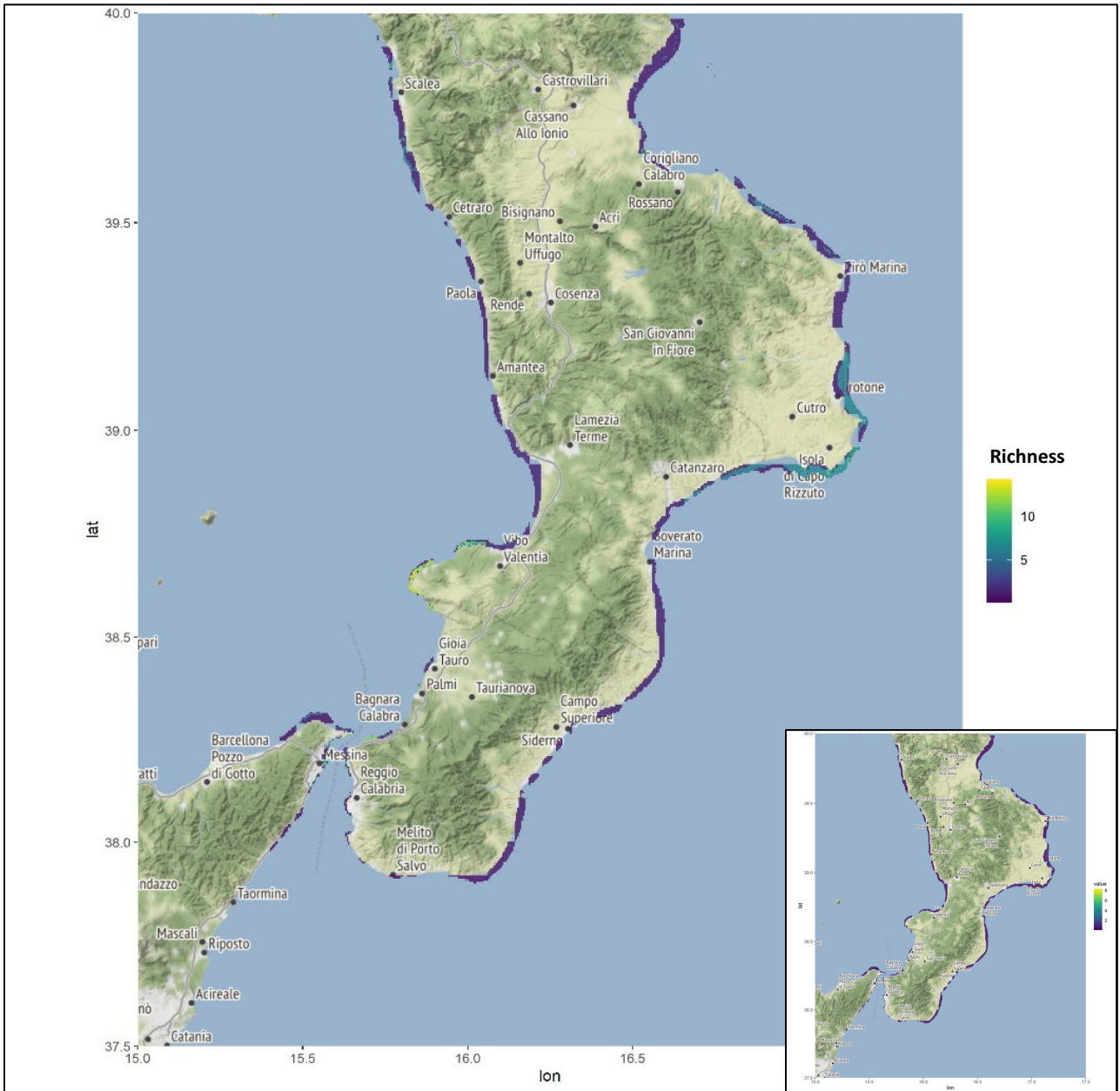


Figure 3.11. Species Richness in the Calabrian coasts, based on the prediction of the Spatial Distribution Model. The smaller panel indicates the error distribution for the model.

## **4. DISCUSSION**

The characterization of coastal fish diversity along Calabrian coasts resulted in a total of 72 species belonging to 25 families observed. This result is consistent and even slightly higher than other studies performed in the Mediterranean Sea using the same methodologies (UVC) and considering similar heterogeneity regarding the habitat-types sampled (Guidetti, 2000, Franco et al., 2006, La Mesa et al., 2011). Moreover, the results may represent a baseline for future comparisons, given the scarcity of such kind of studies (Guidetti, 2000, La Mesa et al., 2011), considering multiple habitats in coastal ecosystems (i.e. rocky bottoms, seagrasses meadows, and sandy bottoms), and the rapid changes the Mediterranean basin is experiencing. In fact, other investigations only focused on rocky fish assemblages (De Girolamo and Mazzoldi, 2001, Piazzini et al., 2012, Carminatto et al., 2020, Bevilacqua et al., 2021), or seagrasses meadows (Bell and Harmelin-Vivien, 1982, Moranta et al., 2006, Deudero et al., 2008), but the addition of sandy bottoms resulted in an increase of the species encountered, due to their contribution to the total pool. In fact, a maximum of 65 species were recorded in the other studies (Piazzini et al., 2012, focused on rocky reefs assemblages). This number results even higher than ours if we just consider rocky bottoms, but the consideration of a complete landscape composed by more than just one specific habitat, as in our case, increases the



total number of species. Moreover, the habitat factor was never considered in other studies (Lazzari et al., 2020).

#### ***4.1. Overall species abundance and biomass of the Calabrian coasts***

To go more in details on the taxa found, the families that were represented by more species are Labridae (13 species), Sparidae (12 species), Gobiidae (10 species), and Serranidae (7 species). These families are generally well represented in Mediterranean coastal systems, as they include very heterogeneous species, capable of inhabiting all the habitat-types present in the shallow layers. For example, fish belonging to the *Labridae* observed during this study include species such as *Coris julis*, known to be widely spread all over the rocky habitats and in *Posidonia* meadows of the Mediterranean Sea (Fruciano et al., 2011), and others being more specialist regarding the habitat use. For example *Symphodus rostratus* is known to be commonly found in *Posidonia* meadows (Deudero et al., 2008), as also confirmed by our results, while others almost exclusively inhabit sandy bottoms, as in the case of *Xyrichtys novacula* (Alós et al., 2012).

Similarly, *Sparidae* family includes species from the genus *Diplodus*, commonly found in infralittoral rocky habitats (Sala and Ballesteros, 1997), and *Posidonia* meadows (i.e. *Diplodus annularis*, Francour, 1997) and other

species like *Lithognathus mormyrus* that occur predominantly over unvegetated sandy habitats (Guidetti, 2000, Matic-Skoko et al., 2007).

So, the wide-spectrum habitat-use for the organisms belonging to the mentioned families could be one of the reasons favoring their presence with high specific diversity over the study.

At species level, *Chromis chromis*, *Boops boops*, and *Oblada melanura*, are the most abundant species, usually occurring in large schools (Allam, 2003, Gkafas et al., 2013, Pinnegar, 2018). Their presence in the habitats sampled is quite consistent. Another abundant species was *Xyrichtys novacula* although this has been observed only in sandy habitats, in accordance with literature on its life habits (Alós et al., 2012).

Biomass measurements (intended as community biomass), that represent instead the fish net weight and could provide an indication about the stability of the community (Cardinale et al., 2013), highlighted a slightly different picture for the principal contributors to the biomass in the transects. This is the case of *Sarpa salpa* and *Diplodus vulgaris* for rocky substrates, that were recorded not only with multiple specimens for most of their observations, but can also reach quite large body-sizes (Gordoa et al., 1997, Buñuel et al., 2020), so they can easily be dominant in terms of biomass. For similar reasons, *Posidonia* meadows recorded highest biomasses values for *Oblada melanura*,

that show comparable characteristics, but holds higher affinity with this habitat (Kalogirou et al., 2010), and for *Chromis chromis*, probably due to the very high densities recorded in this habitat. In sandy bottoms, the species showing the highest biomass values is *Xyrichtys novacula*, in accordance with the previous considerations about the abundance. In this case, this result could be due to its diffused presence in most of sandy replicates, but also, in some cases, because of the lack of other organisms. In fact, the dominant species recorded both for *Posidonia* and sandy habitats have a mean biomass one order of magnitude lower than the ones in rocky bottoms, and this difference is relevant and should be mentioned as we are considering the relative dominance of fish species for each habitat.

#### ***4.1.1. The Species Contribution to Beta Diversity (SCBD)***

Here we follow the approach to  $\beta$ -diversity estimations suggested by Legendre and de Cáceres (2013), so both the species contribution (SCBD) and the contribution of the habitat (LCBD) to  $\beta$ -diversity were considered crucial to combine the fish assemblages with the habitat in which they are hosted.

In fact, the first contributor to  $\beta$ -diversity among the species found is *X. novacula*, which is one of the species uniquely inhabiting sandy bottoms. This species inhabits the sandy and muddy substrates of almost all the western Mediterranean Sea (Castriota et al., 2005). It is reported that *X. novacula*

mainly feeds on small organisms, mostly mollusks, but also on crabs, shrimps, polychaetes and other inhabitants of soft bottoms (Cardinale et al., 1997). The species spends its whole life in such substrates with an harem social organization (Candi et al., 2004), which is typical of protogynous species (Plant and Zeleznik, 2014) like *X. novacula*. Despite of its quite generalist habits, this species seems to not compete with other species of sandy habitats, likely because of its high capacity to survive in open sandy environment, by burying itself under the sand in presence of possible threats (Alós et al., 2012).

*Chromis chromis*, which is the second contributing species to  $\beta$ -diversity, is numerically the most abundant in the whole study area, partially explaining this high SCBD value (Carlucci et al., 2018). In fact, this species is very common in the coastal Mediterranean basin (Pinnegar, 2018), mainly feeding on plankton, and so not strictly associated to the benthic compartment as most of the other species considered. So, it is not easy to discriminate if its presence in one habitat is just transient or due to the exploitation of the resources provided by the habitat itself. We need also to consider the high patchy distribution of the habitats in the sampling locations, although the abundance of the species recorded in sandy habitats is considerably lower (one order of magnitude) than that recorded in the other two habitats.

Similar considerations could be made for *O. melanura*, that has quite similar

life habits to *C. chromis*, showing prevalent schooling behavior and a relevant motility among different habitats (Gkafas et al., 2013). The species prefers *Posidonia* meadows although with similar abundances to rocky substrates, and even in sandy substrates it showed quite high density compared to the other species.

*Coris julis* is another generalist species, but it is more strictly associated to the benthic compartment than the previous ones, being more sedentary (Fasulo et al., 2010) and defined as omnivorous, with preference for animal material (Karachle and Stergiou, 2008). This labrid has been observed predominantly in rocky substrates, but also in *Posidonia* meadows, while just rarely found in sandy habitats, even if its possible relationship with soft substrates has been already documented in past studies (Tortonese, 1970).

*Bothus podas* is uniquely found in sandy habitats, in agreement with literature data (Abid et al. 2013), although it has also been found on seagrasses of the Mediterranean Sea (Schintu et al., 1994). The diet is similar to *X. novacula*, being mainly constituted by crustaceans, mollusks, bryozoans, annelids, and other invertebrates (Abid et al., 2013). Also its social strategy is almost identical, as it forms harems as well (Carvalho et al., 2003), but in this case the species is gonochoric. The similarities in the feeding and even more in the social-reproductive strategies, could be defined as some of the factors for their

“success” in driving  $\beta$ -diversity patterns, but many others should be investigated (Heino and Grönroos, 2017). Moreover, the density of *B. podas* is not as high as the other species that contribute the most to  $\beta$ -diversity, even if considering just the sandy habitats, so its SCBD value becomes even more relevant, especially in validating the result obtained.

Another interesting species contributing to  $\beta$ -diversity is *M. surmuletus*, also in relation to its interesting position in the nMDS output. In fact, despite the dominant habitat in which it has been observed is rocky bottoms, it seems its position is “in the middle” between the clusters of rocky/*Posidonia* and the sandy one, being even included in the latter. This species can be found both in hard and soft substrates, especially due to its foraging behavior (Tserpes et al., 2002; Uiblein, 2007), based on small benthic invertebrates (Labropoulou et al., 1997), thus leading to a marked potential for mobility across different habitats (Ajemian et al., 2016).

These results were quite informative in connecting the observations regarding the species and the overall contribution of the habitats in creating diversity patterns.

#### ***4.2. Fish diversity in the different habitats of Calabrian coasts***

One of the main goals of this investigation was to assess the specific diversity

of each habitat.

Species richness statistically differ between habitats, and the highest values belong to rocky bottoms, followed by *Posidonia*, and lastly by sandy habitats. First of all, there is no extended information about how richness could variate in a landscape composed by all the habitats hereabove and considered in its completeness, at least when habitat is treated as the main factor of the analysis. In fact, proofs about the role of habitat complexity are most of the times limited to just one type of habitat, mainly rocky bottoms or seagrasses meadows (Staveley et al., 2017; Di Franco et al., 2021) or focused on tropical reef systems (Jenkins and Wheatley, 1998; Gratwicke and Speight, 2005; Ford et al., 2017), and few of them (Jenkins and Wheatley, 1998; Harper et al., 2022) covered a habitat variety large enough to give space to comparisons. In comparable investigations (Jenkins and Wheatley, 1998; Guidetti, 2000; Harper et al., 2022), more complex habitats, such as rocky bottoms (or reefs in the tropical environment) were richer in fish species, while *Posidonia* meadows, and even more sandy bottoms, showed lower complexity, highlighted as the first driver influencing fish assemblages (Hall and Kingsford, 2021). These results fit well with the ones obtained by our investigation.

The Shannon ( $H'$ ) and Simpson's ( $D$ ) indices were useful to have an additional comparison with the richness values, giving their power to describe different

properties of the community regarding fish diversity. The results confirmed that rocky bottoms are generally more diverse, showing higher values for rocky habitats both for  $H'$  and  $D$ , in both cases followed by *Posidonia* meadows and lastly by sandy bottoms. Despite of this, *Posidonia* and sandy habitats were not significantly different regarding the Simpson's index ( $p < 0.05$ ). Rocky bottoms not only show higher richness, but they probably highlight a more uniform distribution of the inhabiting species, meaning that all the species found are generally more evenly distributed in rocky bottoms, while the distribution of the species in sandy habitats is less uniform. Moreover, the values regarding the Simpson index could be a proxy that some species (the dominant ones) play a greater role in shaping the diversity of rocky bottoms than in the other habitats but, in this case, the difference between *Posidonia* and sandy habitats is less evident.

Studies carried out in the Mediterranean basin about fish biomass did not find a clear relationship of it with habitat complexity (Di Franco et al., 2021), although the results were limited to rocky assemblages and other drivers in that case may be influential, like the protection level (Guidetti et al., 2014; McClure et al., 2020). Our results proved a marked difference based on the habitat type, with rocky bottoms clearly outscoring the values of biomass with respect to *Posidonia* meadows and sandy bottoms, being not significantly different from



each other ( $p < 0.05$ ). Thus, habitat complexity likely contributes to the difference in biomass found in each habitat, together with food availability (Anderson and Sabado, 1995) and many other factors (McClanahan et al., 2019).

An interesting property of biomass measurements is its power to estimate both the quantity of organisms, and partially avoid a too simplistic consideration of all the species and individuals as “equal entities”. The difference between richness in rocky habitats and *Posidonia* meadows is less evident than the difference in their biomass. This difference could be due to the lower mean size of specimens from *Posidonia* meadows, acting as nursery areas and hosting the early life stages of many fish species, or because of small differences in the fish assemblages from the two habitats, as also suggested by the PERMANOVA results.

A different picture is outlined when looking at the fish communities in terms of unique species. The number of unique species, i.e., species recorded in just one habitat, provide information on how much each habitat contributes to the overall diversity (Hall and Kingsford, 2021). In this case, the pattern described so far is different, as rocky bottoms maintain the highest value in absolute terms (16 species), but followed by sandy habitats (14 species), with *Posidonia* meadows showing any unique species. The significance of this result is even

more relevant if put in terms of relative number of unique species compared to the total species in the community. In this case, sandy habitats recorded 43.8 % unique species, while rocky habitats just 28.6 %. So, sandy assemblages already appear to show a more marked difference in species composition compared to the other habitats. The dissimilarity of *Posidonia* meadows and rocky bottoms with sandy ones is confirmed also by the number of common species: just four species with rocky habitats and two species with *Posidonia* meadows.

Looking at the graphical output of the nMDS, replicates belonging to *Posidonia* meadows and rocky bottoms show high similarity in their associated diversity, with the clusters formed by them being almost overlapped. In particular, rocky bottom seems to be a sort of sub-sample of *Posidonia*, and so the distinction in the species present in this two habitat is not so evident. This is instead the case of sandy bottoms, that segregated in the nMDS from the other two habitats. Furthermore, also the distance within the sandy replicates seems to be greater in the nMDS graph, likely due to higher heterogeneity of the composition of sandy bottoms' replicates. These results confirm the expected contribution of each habitat to the overall diversity of the area, which was one of the expected goals of the investigation.

#### ***4.2.1. The Local Contribution to Beta Diversity (LCBD)***

An important step toward the process of estimating the contribution of each habitat to the overall diversity was the evaluation of  $\beta$ -diversity, as the division proposed by Legendre and de Cáceres (2013), i.e. LCBD and SCBD, that is the contribution of each habitat to the diversity (LCBD), and the identification of the species that contribute the most to dissimilarity among habitats (SCBD).

To our best knowledge, this approach has been rarely applied in the Mediterranean (Carlucci et al., 2018), and never as a tool coupled to the visual census sampling approach, as most of the times  $\beta$ -diversity is divided into “turnover” and “nestedness” components, meaning respectively the “replacement” of species and the “loss” of species between assemblages (Baselga, 2010). However, the potential and range of application of the proposed division of  $\beta$ -diversity is quite high (Harper et al., 2022).

In this specific case, the mean contribution of sandy habitats has been surprisingly pointed out as the most relevant, notwithstanding their underestimated importance as habitats contributing to the diversity of a seascape (Henseler et al., 2019). At the opposite end, rocky bottoms are the less relevant in terms of habitat contribution to  $\beta$ -diversity when considering this approach. This of course does not mean that sandy habitats are “more important” in providing diversity than the other two. As we know, also from

the diversity metrics hereabove, the contribution of rocky habitats and, to a lesser extent of *Posidonia* meadows, is not neglectable, but it appears important to consider a seascape in its integrity, as also the “less diverse” sandy habitats are here proven to be an enrichment to the total diversity, probably because of the almost completely different species that can be found there.

In addition, when analyzing the species contributing the most to  $\beta$ -diversity (SCBD), among the six most contributing ones, two are uniquely present in sandy bottoms (*X. novacula* and *B. podas*), and the other four (*C. chromis*, *O. melanura*, *C. julis*, and *M. surmuletus*) are generalist species, found during the study in all three habitat types, with differences in their relative densities on a case-by-case basis.

#### **4.2.2. Common species among the habitats and connectivity**

The number of common species between the habitats should be considered as well, especially when evaluating a complex seascape as the one under analysis. In this case, the high number of species in common between rocky and *Posidonia* assemblages (24) could be a proxy of the organisms moving between the two habitats, possibly bringing the overall system to higher abundances and biomass (Vega Fernández et al., 2008). The connectivity between seagrasses and hard bottoms is generally acknowledged in coastal seascapes (Jaxion-Harm et al., 2012), as fish species exploit these habitats in different life-stages and

can transit between them (Hyndes et al., 2018; Díaz et al., 2019; French et al., 2021). Of course, every habitat still holds a certain degree of differentiation in the fish assemblages composition, especially regarding the quantitative measures (abundances) of the species, as also suggested by the results of the PERMANOVA, but *Posidonia* meadows did not show any “unique” species, and this could be a good indication of the connectivity between the two habitats. Sandy bottoms instead show a low number of species in common with the other two habitats, with a very typical fish assemblages, that probably are a major driver for the patterns of  $\beta$ -diversity. To go further in the investigation of the connectivity between the habitats, other methodologies should be applied, such as the tagging of some key fish species in marine assemblages that show a good degree of distribution in the coastal habitats (Di Lorenzo et al., 2016) in order to assess the real connection between the different habitats.

#### ***4.3. Drivers of species richness and predicted patterns along Calabrian coasts***

The habitat-type was the main driver here investigated, although other variables were identified as possibly influencing the patterns related to species richness in the Calabrian coasts. The Species Distribution Model (SDM) gave us the possibility to simultaneously underline how biotic and abiotic drivers could be related to the richness values, and all the relationships found were similar in

their behavior. The significant variables obtained for the model into account (SST, SSS, chl-a; see Methods section, paragraph 2.5.6. for extended information) are among the most important ones in influencing the biotic component of marine ecosystems. In particular, as the Sea Surface Temperature (SST) and Sea Surface Salinity (SSS) increased, the specific richness decreased. This can suggest inferences when considering the trends of these variables, especially SST, in the last decades for the Mediterranean Sea (Sakalli 2017), and the concerning projections for the ones to come (Shaltout and Omstedt, 2014), that can be influential factors in predicting how richness in this area could be shaped in the near future.

Furthermore, the increasing SST could lead to tropicalization events (Ben Rais Lasram et al., 2008), changing the dynamics of the ecosystems because of the appearance of Non-Indigenous Species (NIS), that already increased steeply in the last decades in the Mediterranean Sea (Azzurro, 2008). So, while temperature trends could positively affect the abundance of some species found in the area (e.g. *Sparisoma cretense*, Astruch et al., 2016), most of them could be affected in the opposite way. It is worth noting that, during the Visual Census activities, no NIS has been encountered by the operators in the study area.

The salinity (SSS) had negative effects on species richness as well, but evidence of this on a larger scale are not so investigated as in the previous case.

Nonetheless, it is known that the trend of salinity is constantly increasing in the last decades, similarly to temperature (Jordà et al., 2017). The effects of salinity changes include a modification of the water masses circulation (Astraldi et al., 2002), with influences on the provision of food, nutrients and on the larval dispersion for fish species (Reiss et al., 2000; Williams and Follows, 2003; Tiedemann et al., 2018). In addition, salinity increase could be a factor (along with temperature) favoring the spread of NIS, especially the ones coming from the Red Sea (i.e. Lessepsian species), that will find suitable conditions for their settlement (Raitsos et al., 2010).

The relation found with chlorophyll levels is interesting as well, showing a linear reduction of species richness as the values increase. The effects of this factor are not always the same on an ecosystem and can be both related to an increase in richness values (Shah Esmaeili et al., 2022), but also be indicators of eutrophication phenomena after a certain threshold, bringing negative consequences to the ecosystem (Bell et al., 2014). So, while the effects in the range analyzed are negatively correlated with richness values, there are interesting results about how the increasing concentration of chlorophyll-a could be inversely related with the SST increase (Kotta and Kitsiou, 2019), leaving a high space for uncertainty regarding the relative importance of these drivers and their possible synergistic effects in shaping the fish assemblages of

this area.

Biomass has not been directly related to the drivers in our case, but there is evidence of a possible influence of them to it (Duffy et al., 2016).

The second scope for the development of a Distribution Model for Species richness was a projection of the richness values on the entire Calabrian coastal waters. The results of the model confirmed the trend of the sampled locations, with a low specific richness spread throughout the majority of the coastline, probably due to the prevalence of long stretches of sandy bottoms in the coastlines, that were proven to be less rich than the more complex habitats of the coastal system of this area. Moreover, two areas have been highlighted as more diverse: (1) the Marine Protected Area (MPA) of Capo Rizzuto (and surroundings) and (2) the area around Vibo Valentia. Separate consideration must be made on the two cases. The first one is the only MPA of the Calabrian coastline, and the higher richness values predicted could have been among the criteria for the establishment of this protected area, as it is one of the most heterogeneous spot in the Ionian coastline, with many habitats such as rocky bottoms and *Posidonia* ecosystems within a relatively small area, and thus hosting higher specific richness.

In the second case instead, there are no measures applied at the moment in the area, and the touristic pressure is quite high compared to other locations.



Despite of this, fish biodiversity values showed a marked positive difference from the rest of the coastal waters, and this should push to consider this area as a possible candidate to be protected, also giving the requirements brought by the global 30 x 30 initiative, that aims at protecting 30% of the world's total lands and waters by 2030, with 10% strictly protected. Of course, a deeper comprehension of the potential of this area should be obtained by sound assessments that focus on multiple aspects of biodiversity (Mouillot et al., 2011), but this could be a good starting point to discuss about its future protection.

#### ***4.4. Biases and strengths of the study and other possible approaches***

Looking at the depth range considered, the visual technique adopted, Underwater Visual Census (UVC), fits perfectly and complements other methods that could possibly be used for future assessments of the area, and already performed by other team members during the sampling campaign, but not analyzed in this particular investigation. Such methods are for example Baited Underwater Videos (BUVs), which could expand the operative range for the analyses at lower depths thanks to the absence of a diving operator, even if also still holding some limitations in their applicability, like the need to choose a priori a fixed spot where to deploy the instrument, without the flexible

approach typical of human-based methods (UVC in this specific case), and the limited visual field, that can be partially solved by using stereo/360° cameras (Mallet et al., 2021).

Other possible methodologies involve molecular techniques, like the environmental DNA (eDNA), which represents the cumulative genetic material that can be obtained from natural releases in an environmental medium like water. This tool has been revealed very useful in ecological studies (Fraija-Fernández et al., 2020), thanks to its ability to capture a wide but somehow different spectrum of species, often just partially overlapping with the biodiversity resulting from the traditional survey methodologies (Kelly et al., 2017). DNA is then processed with PCR and next-generation sequencing methodologies to build “libraries” of the collected material.

Finally, new approaches to be considered rely on “new” technologies that are reducing the limitations related to “classical” diving techniques, such as the use of Closed Circuit Rebreathers (CCR). This technique not only allows a partial overcoming of the limits related to depth thanks to their efficiency, and a stretch in the dive times with shortened decompressions, but also determines a less impacting presence of the operator, thanks to the avoidance of air bubbles production (Sieber and Pyle, 2010; Shepherd et al., 2021).

All these considerations led our investigation toward this methodological

direction.

Of course, the UVC holds some limitations as well, like the biases related to the experience of the observer and some possible behavioral changes in response to the diver presence (Kulbicki, 1998; Dickens et al., 2011), but it returns fast and quite accurate estimates while containing the costs. Furthermore, in deeper waters, SCUBA diving using classical “recreative” gears become challenging and so does diving for scientific purposes (i.e. UVC), because of the limited time that could be safely spent at such depths and the eventual need to perform complex diving profiles, requiring highly trained operators and specific equipment, and resulting in low replicability potential and long sampling times. To accomplish sampling at these depths, the use of video tools (i.e. BUVs) or other mentioned techniques could represent valuable alternatives as a visual approach.

Another portion of the study that could possibly be implemented is the lack of a temporal replication, for example in relation to seasonal variability. As widely known, seasonal patterns show high influence on the composition of fish assemblages (Claudet et al., 2006; Henriques et al., 2013), especially in temperate basins like the Mediterranean Sea, where oscillations in the abiotic, and consequently biotic factors (Duarte et al., 1999; Trabelsi and Rassoulzadegan, 2011) could play a relevant role in the marine ecosystems,

worth to be analyzed more in detail.

It is also important to mention that the methods used during the sampling procedures do not rely on catch-dependent data and so, while they still have all the above-mentioned limitations, they avoid all biases concerning the specific gears used for sampling in catch-dependent approaches (i.e. nets, vessels, etc.), which could lead to a possible misleading community composition due to a reduced range of taxa, trophic levels and size classes considered (Caldwell et al., 2016). So, while sampling did not just focus on fishery-targeted organisms but on all the species detected, allowing a more complete understanding of the overall ecological effects, also in relation to the habitat under the study lens, the results have the potential to improve many sectors, fisheries included, that could benefit from an enhancement of the accessible information, proceeding towards a more responsible approach to the sustainable resource management. The key to increase the possibilities of a reliable and robust assessment is to increase the amount of available data for the area, to allow the adoption of multiple approaches using all those mentioned techniques in the most efficient way possible, avoiding an excessive data overlap but having the possibility to obtain a complete assessment on the topic. Moreover, no method is more correct than others, and the most important features that must be considered are complementarity and intercomparability (Aglieri et al., 2021), achievable only

with the use of standardized procedures during the sampling design (Caldwell et al., 2016). This in the scope of a possible creation of timely and spatially extensive datasets and increase the knowledge about the fish diversity, to increase the reliability of the estimates and provide a baseline for any future actions aiming at protecting the biodiversity of the area. This planning should also consider how the different habitats can contribute to create a diverse seascape, with the inclusion of the often underestimated sandy habitats, that were proven to enhance the overall regional diversity thanks to unique fish assemblages they host and their unexpected contribution to  $\beta$ -diversity.

#### ***4.5. Conclusions***

The overall aim of this study was the assessment of coastal fish diversity and its drivers in the different coastal habitats. Following the three main goals, it is possible to conclude that:

1. The assessment of the **fish diversity of each habitat** under consideration resulted in a higher diversity of rocky habitats in terms of species richness, supported by the results regarding the biomass, and the diversity indices ( $H'$  and  $D$ ). Sandy bottoms were instead the less diverse habitat in relation to all these metrics, while *Posidonia*

meadows held an intermediate position, although some metrics, especially regarding biomass, were really low as well.

2. The **contribution of each habitat** to the overall diversity, achieved through the analysis of  $\beta$ -diversity, highlighted instead a high contribution of sandy bottoms to the degree of difference between the habitat-specific assemblages, determining the high importance of sandy assemblages in the creation of separated fish assemblages. In this case, the trends of  $\alpha$ -diversity were reverted, with rocky bottoms showing the lowest values of the two components in which  $\beta$ -diversity was divided (LCBD and SCBD). *Posidonia* assemblages were again in an intermediate situation, but other results such as the lack of unique species allows to infer about their hypothetical connectivity with rocky habitats and explain their low contribution to  $\beta$ -diversity. These results could be useful in future assessments, also in relation to the inclusion of a wider spectrum of habitats in marine spatial planning initiatives.
3. The **Upscaling of the biodiversity assessment**, accomplished with the use of a Species Distribution Model focused on species richness, provided interesting results on the decrease of the richness values with the increase of the variables considered (SST, SSS, and Chl-a),

indicating a possible relation with the present and future trajectories of climate change. Moreover, the predictions on the whole Calabrian coasts highlighted two areas with higher richness values: the area around the MPA of Capo Rizzuto (on the Ionian side), which is already protected to preserve its biodiversity, and the area around Vibo Valentia, that shows even higher richness values, that could be a priority area for protection in the future, towards the accomplishment of the 30x30 goal by 2030 (European commission, 2020; Mammola et al., 2020; Hermoso et al. 2022)

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