

# **Morphological structure and biodiversity in fish assemblages**

*Estructura morfològica i biodiversitat en comunitats de peixos*

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*Mahatma Gandhi*

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# 1

## **General Introduction**





### **1.1 Importance of morphology measurement in biological studies: towards the concept of ecomorphology**

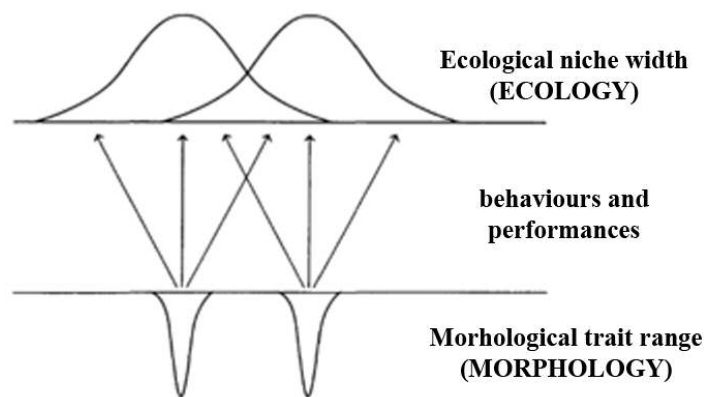
One of the essential principles provided by the Darwin's theory of natural selection is that the evolution of organisms and their phenotypic features should be assessed by analyzing the interaction between the anatomical structures of organisms with the external environmental conditions acting on them (Darwin, 1859; Allen, 1907; Thompson, 1917; Bock and von Wahlert 1965). Basing on this premise, since then the study of morphology of organisms attracted high attention within the scientific community, in order to describe and understanding the evolution, adaptations and behaviors of organisms from their morphological and anatomical differences. From its early times, the study of morphology of organisms was focused in descriptive and comparative anatomical analyses used with taxonomical and phylogenetic purposes (Bock, 1990). The first references manifesting the relation between the morphology of species with their surrounding environment appeared at the beginning of the 20<sup>th</sup> century, suggesting the existence of direct correlations between the phenotype (morphology) and the physic external factors (Allen, 1907), and that this association was the main driver of the evolution of species. This hypothesis was accepted, maintained and incorporated to studies of many scientific branches. In its studies of comparative anatomy from natural observations in the wild, Böker (1935) defined the term "ecological anatomy", which linked again the morphological features of organisms with the environmental conditions. Other disciplines, such as systematic and genetics, also began to consider these statements in its competences (Dobzhansky, 1937; Mayr, 1942).

However, at half 20<sup>th</sup> century (1950s-1960s), the field experienced significant changes that allowed to expand their research competences, which represented essential steps for the subsequent progress in the study of the morphology of organisms. Although the morphology-environment relationship prevailed, the morphology of organisms began to be linked with their ecological and functional habits within ecosystems. Among biologists increased the hypothesis that many aspects of the ecological and functional proprieties of species could be inferred from the analysis of their morphological features. Bock and von Walhert (1965) suggested that any component of the life history of organisms (ecology, biology, behaviour, etc.) can be considered as a "form and function" complex which is the result of a biological

adaptation determined by the interactions of organism with the environmental conditions. Studies began to focus on the functional proprieties of the anatomical structures, catalogued as the main responsible of the shape design of the morphological features. Thereby, at half century a growing trend that directly related the morphology, function and ecology of species began to be established.

According to this new scientific current, ecologists, traditionally interested in the exploitation of the available resources within communities and competition and coexistence relationships between organisms, promptly perceived that morphology of species were also essential to analyze many ecological questions. Thus, several studies focusing on important ecological topics such as resource partitioning, concept of niche, habitat differentiation, competition or adaptations within communities (Hutchinson, 1959; Keast and Webb, 1966; MacArthur, 1968; Schoener, 1974) incorporated the measurement of morphological traits of species for their analyses, concluding that morphological differences between species could help to elucidate the ecological structure of communities. Their assumptions were based on that morphological features of species were related with food acquisition, locomotion strategies and other environmental demands, and therefore they were essential to determine the position of species in the resource dimension and understand the niche differentiation within communities. Since then, most of studies supported the hypothesis defending that the ecological habits of species was closely related to its morphology, both being key aspects to define the biological and functional role of species within ecosystems, and both shaped by the environmental factors (physical and biotic) acting on organisms. In this context, the emergence of this new approach highlighting the importance of morphology and its relationship with the ecology of species (Fig. 1) was called *ecomorphology* (Karr and James, 1975). Ecomorphology was defined as the study of the interactions between the morphology of organisms and its environment in an ecological and evolutionary context (Bock, 1990; Motta and Kotrschal, 1992; Motta et al., 1995a; Douglas and Matthews, 1992; Ricklefs and Miles, 1994). For instance, it had been demonstrated that in birds, morphological traits of the body, beak, wings, tarsus and toes were essential defining ecological habits such as foraging behaviors, flight maneuverability or habitat use among species (Cody and Mooney, 1978; Leilser and Winkler, 1985; Ricklefs and Travis, 1980; Miles et al., 1987). In lizards, some studies demonstrated that the measurement of body shape, tail shape or forelimbs and

hindlimbs lengths determined the running and jumping efficiency, key in many behaviors such as foraging, predator evasion and substrate choice (Moermond, 1979; Losos, 1990). Or in fishes, where morphology of mouth, jaws, head, body shape and fins had been widely studied in order to explain feeding habits, trophic position, locomotion and defensive strategies (Gatz, 1979; Webb, 1984; Wainwright, 1988; Winemiller, 1991; Norton et al., 1995; Wainwright and Richard, 1995). Besides, these interactions can be assessed in multiple levels: among individuals of a species, among different species or taxa and even among communities. Thus, this approach allowed linking morphological variance with ecological performance until community level. Then, among other competences, ecomorphology began to be applied in studies of organization and structure of biological communities (Gatz, 1979; Winemiller, 1991; Ricklefs and Miles, 1994; Wainwright and Reilly, 1994; Winemiller et al., 1995; Foote, 1997).



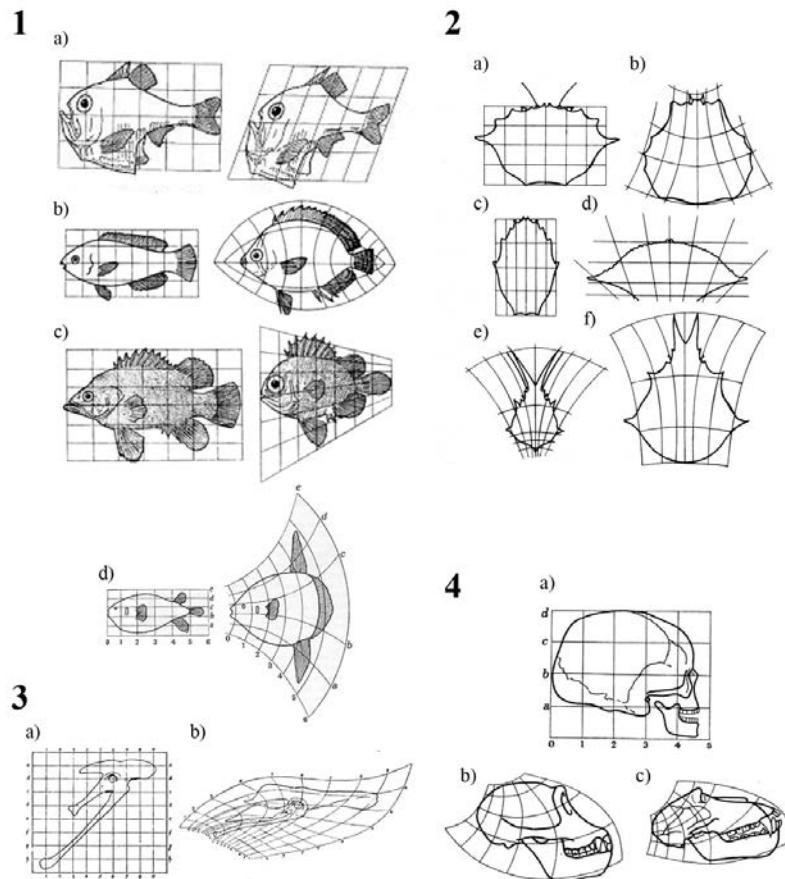
**Figure 1.** Graphic explaining the relationship between ecology and morphology. The bell-shape curves represent the width of an arbitrary ecological niche (above), and the phenotypic range of an arbitrary morphological trait (below). The arrows represent the acting mechanisms (behaviours) and their efficiency (performance) that connects the morphology with ecology. Obtained from Ricklefs and Miles, 1994.

One of the main advantages of ecomorphological studies was their predictive ability, based on the hypothesis that if environmental factors constrain morphology and ecology of species, we should be able to predict the ecological patterns of individuals, assemblages or communities from their morphological traits (Karr and James, 1975; Motta and Kotrschal, 1992; Ricklefs and Miles, 1994). When environment factors affect to species and interspecific competition predominates within communities, species develop morphological adaptations allowing them to specialize in exploiting determined resources of the total ecological niche. Thereby, the ecological niche, which can be seen

as a multidimensional space where species locate based on their ecological habits, is partially constrained by morphological traits of species (Keast and Webb, 1966; MacArthur, 1968; Gatz, 1979). Thus, species distribute along a *morphospace*, where species locate based on their morphological characteristics indicating the structural complexity of the community, forming different guilds (subsets of species that present similarities in particular ecological features, Simberloff and Dayan, 1991). The assessment of the distribution and occupancy patterns of this morphological space, using combination of statistical analytical methods (i.e., packing of species, average distances between species) or multivariate spatial methods (i.e., principal components analysis), allow inferring and speculating about the ecological functioning and structure of communities (Gatz, 1979; Ricklefs and Travis, 1980; Ricklefs and Miles, 1994). Therefore, given the continuous growing of the scientific field and the constant theoretical and methodological progresses, biologists and ecologists became to be strongly interested in the morphological diversity because it contributed to better understand certain key aspects of organization of communities within ecosystems, such as the relationships between morphological traits and environmental factors, community structure (distribution and abundance of species, coexistence and dominance processes within communities), habitat and resource partitioning, competitive interactions or diversity (Schoener, 1974; Karr and James, 1975; Gatz, 1979; Ricklefs and Miles, 1994; Wainwright and Reilly, 1994; Foote, 1997).

### **1.2 Techniques for measuring morphological variability: from traditional methods to geometric morphometrics**

Since its origin as a scientific discipline, the study of morphology of organisms has constantly evolved through different measurement methods and analytical processes. In the early 20<sup>th</sup> century, the research discipline experienced a transition from a traditionally descriptive field to a measurable and quantitative science (Bookstein, 1998). Studies began to set quantitative data from measurable anatomical structures in order to compare among organisms. D'Arcy Thompson (1915, 1917) was one of the pioneers investigating on the form and shape differences between morphological structures of different animal taxa (Fig. 2), predicting that the study of morphology and shape would become a widely treated scientific field during the remaining century.



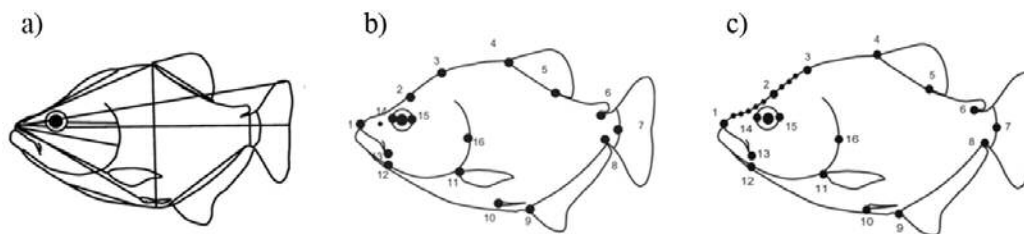
**Figure 2.** Examples of differences in morphology and shape in several groups of organisms proposed by Thompson (1917). Method of Cartesian transformations in (1) fishes (body of a) *Argyropelecus olfersi* to *Sternoptyx diaphana*, b) *Scarus* sp. to *Pomacanthus* sp., c) *Polyprion* sp. to *Pseudopriacanthus* sp., and d) *Diodon* sp. to *Orthogoriscus* sp.), (2) brachyuran crabs (crustaceans) (carapaces of a) *Geryon* sp., b) *Paralomis* sp., c) *Corystes* sp., d) *Lupa* sp., e) *Scyramathia* sp., and f) *Chorinus* sp.), (3) birds (pelvis of a) *Archaeopteryx* sp. and b) *Apatornis* sp.) and (4) hominids (skulls of a) human, b) chimpanzee and c) baboon).

Over the years, the development of rigorous associated multivariate statistical methods allowed improving the description and analysis of shape variation between structures, as well as testing its mathematical significance (Marcus, 1990; Rohlf and Marcus, 1993). The measurement and analysis of shape variation and its relation with other variables was called *morphometrics* (Bookstein, 1991; Dryden and Mardia, 1998; Adams et al., 2004; Mitteroecker and Gunz, 2009) (Fig. 3). Initially, most traditional morphometric studies assessed the morphological variation among groups from linear measurements and applying complex multivariate statistical analyses (Strauss and Bookstein, 1982; Marcus, 1990; Winemiller, 1991; Winemiller et al., 1995; Klingenberg and Ekau, 1996). Although these methods provided valuable advances and

## 1. General Introduction

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contributed to the evolution of the scientific field, over the years researchers detected several lacks and drawbacks in their application: i) linear measurements usually depend on the size of structures and allometry, and both effects should be removed (Leonart et al., 2000; Adams et al., 2004); ii) the lack of homologous points defining the distances to measure caused that some of the linear measurements were difficult to standardize (Adams et al., 2004); iii) they can be insufficient to discriminate between closely similar entities, and is more time-consuming compared with more evolved morphometric methods (Zelditch et al., 2004; Smith and Hendricks, 2013). However, the most highlighted problem lied in that these methods are sometimes unable to define the exact geometrical structure of an object, impeding to graphically represent the shape variation since some proprieties of the shape variables are not preserved (Adams et al., 2004). Looking for alternative methods to solve these setbacks, during late 1980s and early 1990s morphometrics manifested important advances in the methods for obtaining and analyzing morphological data that were considered as a 'revolution' in the field (Rohlf and Marcus, 1993). The geometry of morphological structures became from special interest analyzing the shape variation, since more complex anatomical structures (such as general body shape) should be described in more detail to compute their overall morphological information. Additionally, rigorous and more robust statistical methods including multivariate analysis that conserved the geometrical information of structures through the analyses were developed. This revolutionary new approach was called *geometric morphometrics* (GM) (Bookstein, 1991; Corti, 1993; Rohlf and Marcus, 1993; Adams et al., 2004), consisting in the analysis of Cartesian geometric coordinates between morphological structures rather than linear, outline or volumetric variables.



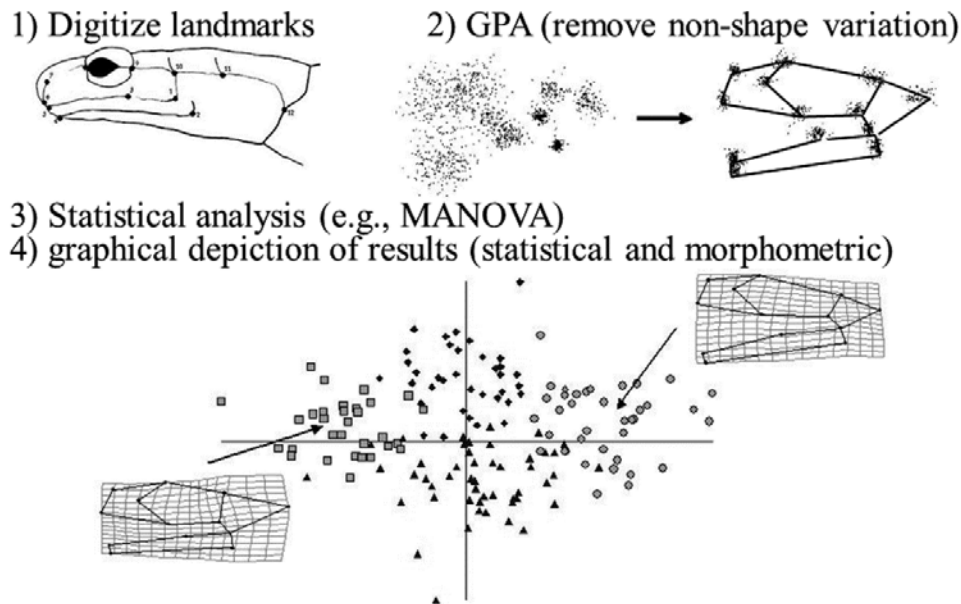
**Figure 3.** Evolution of methods of morphometric measurements: (a) traditional linear measurements of the external morphology of a teleost, (b) landmark-based GM measurements (homologous coordinate points in anatomical structures of interest, defining the geometric shape of the object) of the external morphology of a teleost, (c) addition of sliding semilandmarks (individually not homologous points) on the head profile to capture additional and more accurate information of its curvature. Obtained from Zelditch et al., 2012.

From its origin, given the fast and continuous advances in the methods analyzing the shape variation, GM data was collected using different mechanisms, including outlines curves, surfaces or coordinate points. Two main methodologies were developed to capture the shape information. The first used techniques were the outline methods, based on the decomposition of the outline of structures in multiple points, fit them with mathematical functions (such as Fourier analysis, curvature scales or wavelets) and compare their coefficients using it as shape variables. These methods were adequate in cases of rigid structures with few homologous points (Parisi-Baradad et al., 2005); however they presented a lack of consensus on the optimal statistical procedure to analyze the results (Adams et al., 2004). The second method were the landmark-based techniques, which have been consolidated over the years as one of the most useful and appropriate methodology quantifying the shape variation between structures since they possess more powerful statistical support related to the definition and analysis of the shape variation (Kendall, 1984, 1985; Adams et al., 2004, 2013). These methods consist in the definition and selection of homologous coordinate points (*landmarks*) in anatomical structures of interest. Before analyzing immediately the landmarks configuration between structures, landmarks data should be previously processed to make them comparable using superimposition methods, which remove the non-shape components associated to differences in scale, orientation and position of structures (Rohlf and Slice, 1990; Adams, 1999). Although several superimposition techniques have been described, the general Procrustes analysis (GPA, or also GLS along the thesis) has been considered the most complete method. This technique translates the center of each configuration to a common centroid point, scaling them to a unit centroid size and rotating them to minimize the distances between corresponding landmarks (Rohlf and Slice, 1990). In addition, GPA procedure also provides the uniform components of the shape variation for each analyzed object (*partial or relative warps*) applying the thin-plate spline approach, which creates a consensus configuration by averaging the coordinates of the landmarks that allows mapping the deformation in shape between structures (Bookstein, 1991; Kassam et al., 2002; Langerhans et al., 2007). These parameters (*warps*) can be used as shape variables in multivariate statistical analyses to investigate changes in shape within and between structures, since the differences between them can be interpreted as variation in their shapes (Rohlf and Marcus, 1993; Kassam et al., 2002; Zelditch et al., 2003). Finally, the results of all these statistical treatments can be plotted in space (the morphospace), providing a graphical

## 1. General Introduction

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representation that allows to better visualizing and interpreting the variation patterns in shape. This combination of strict and rigorous statistical procedure with graphical representations that facilitate the interpretation of the changes in shape, as well as the conservation of the geometric traits of objects along all the analyses, make that, in landmark-based methods, GPA was considered as one of the most complete and powerful procedures analyzing the shape variation between objects (Fig. 4).



**Figure 4.** Explanatory diagram of the different steps during a landmark-based geometric morphometric procedure. 1) Selection and digitization of the landmarks on the anatomical points of interest (in this case, head of *Plethodon salamander*), 2) Representation before and after the application of the general Procrustes analysis (GPA) (in this case, landmarks of 154 specimens), 3) Statistical analysis performed (i.e., MANOVA, PCA, etc.), 4) graphical depiction of results (representation of the distribution of specimens based on their shape, with thin-plate spline deformation grids of mean specimens of two of the different groups). Obtained from Adams et al., 2013.

However, landmark methods also present some limitations: i) a determined set of established landmarks could not be sufficient to represent the overall geometric shape of an object; or ii) the shape of objects that lack of obvious fixed points to define (such as curves or not fixed structures) but that can provide important biological information during the analysis cannot be defined with landmarks (Adams et al., 2004). In this context, advances in the GM methods during the 1990's allowed defining an additional type of coordinate points, called *semilandmarks* (Bookstein, 1991, 1997), able to slide along the outlines and surfaces of structures and thus defining the shape of boundary curves or not fixed structures. In addition, they could be statistically treated in the same



way than traditional landmarks because they support GPA analyses. Thus, semilandmarks can be included in analyses of traditional landmarks, extending the landmark-based analyses to curves or not fixed structures and therefore helping to provide a richer and more accurate description of shape of objects (Bookstein, 1997; Bookstein et al., 1999; Adams et al., 2004).

Given its interest, utility and applicability in many scientific disciplines, the field of GM has been and is in constant evolution producing new developments and applications until nowadays. And future expectations seem to predict that advances will continue in many research ways. During the 1990's and early 21<sup>st</sup> century many progresses and applications has been discovered (Adams et al., 2013), such as the concept of missing landmarks for absent or not preserved structures, the use of landmarks in three-dimensional studies, the use in studies of symmetry and allometry of structures, or even applications in other scientific fields such as genetics, phylogeny, integration and modularity or biomechanics. For more information about the GM advances in the recent years, see the complete reviews Mitteroecker and Gunz (2009) and Adams et al. (2013).

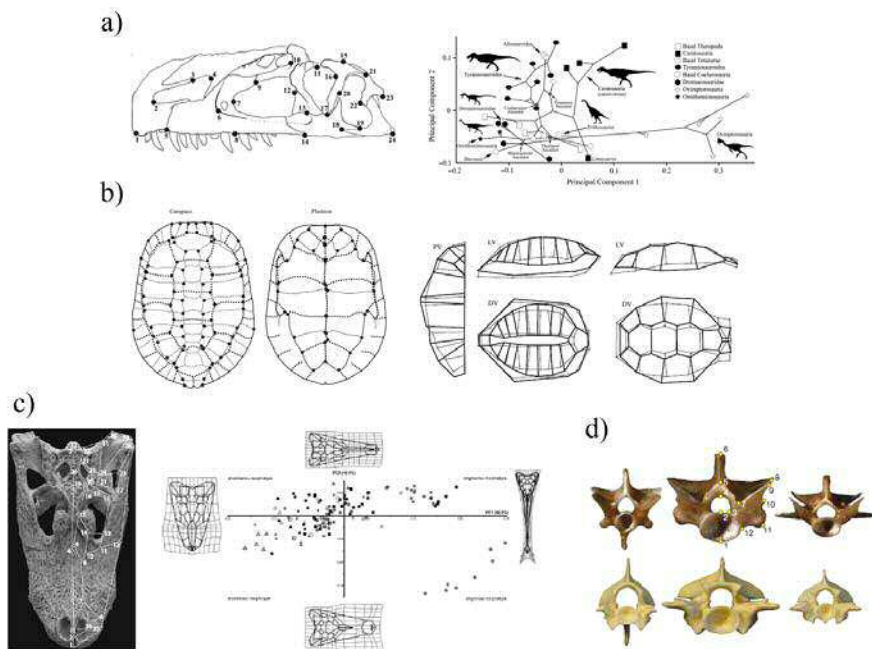
### **1.3 Current applications of landmark-based GM methods**

The constant progress of their measuring methods, their conservative ability to retain the shape properties along all the analytical process, as well as the improving of their associated statistical analysis, caused that the advantages of GM rapidly attracted the attention of the scientific community. During the 1990s, the importance of GM methods strongly increased, demonstrated by the increasing number of studies using these methods in their publications from this decade until today (see Adams et al., 2004). The methodological approach became to be more known and accepted through the years, and biologists attempted to integrate it and expand their use to other research fields. Since then, the application of GM methods has been used in any scientific branches that required performing comparative morphology (Zelditch et al., 2004).

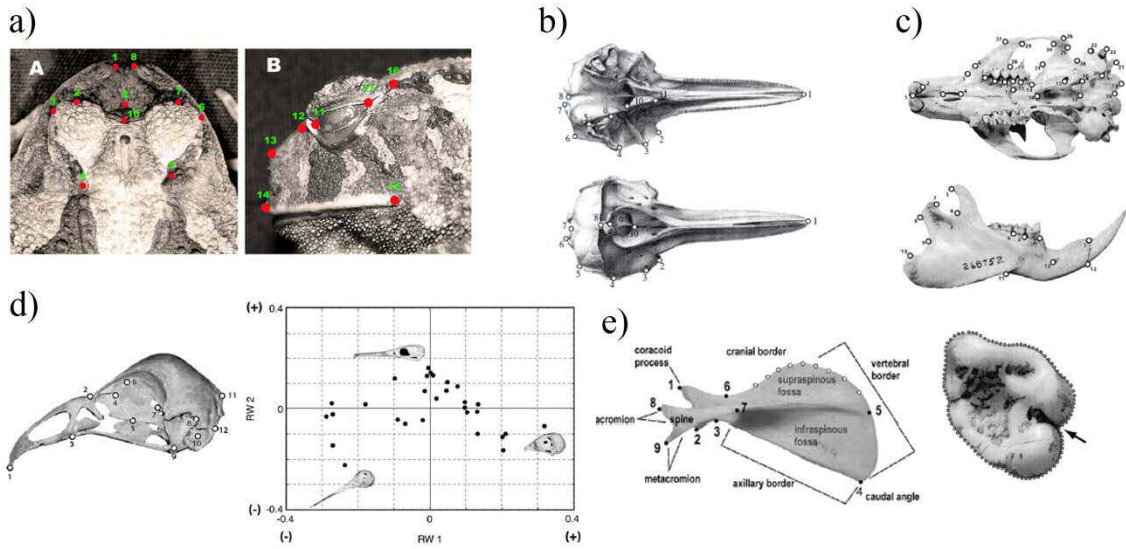
Some of the main research fields that usually have used GM methods are systematics, phylogeny, paleontology, taxonomy and evolutionary biology. However, one of the disciplines where it has been more expanded is in ecology of communities. Analyses testing the differences in bony structures (cranial structures and skulls,

## 1. General Introduction

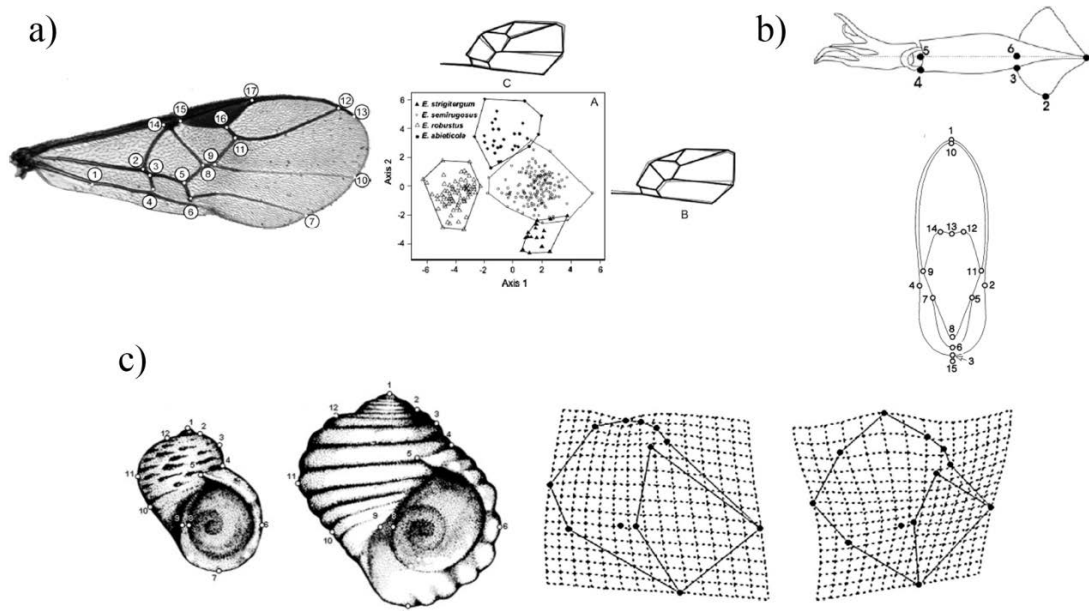
mandibles and jaws, dentition, vertebrae, structural bones, otholits, etc.) or overall body shape for evolutionary, taxonomical, ecological or biological purposes have been widely applied in many different orders, such as dinosaurs (Young and Larvan, 2010; Brusatte et al., 2012), reptiles (Claude et al., 2003; Stayton, 2005; Pierce et al., 2008; Kaliontzopoulou, 2011; Head and Polly, 2015), amphibians (Stayton and Ruta, 2006; Vieira et al., 2008), birds (Magurán-Lobón and Buscalioni, 2006; Degrange and Picasso, 2010; Klingenberg and Magurán-Lobón, 2013), several groups of mammals (Marcus et al., 2000; Cardini and O’Higgins, 2004; Caumul and Polly, 2005; Evin et al., 2008; Amaral et al., 2009), or even in invertebrates, such as studies of the wings variability and asymmetry in insects (Klingenberg and McIntyre, 1998; Klingenberg et al., 2001; Villemant et al., 2007; Johansson et al., 2009), variation in shell shapes in mollusks (Carvajal-Rodríguez et al., 2005; Rufino et al., 2006; Serb et al., 2011) or variation of hard structures in cephalopods (Lombarte et al., 2006; Neige, 2003, 2006; Crespi-Abril et al., 2009), among others (Figs. 5, 6 and 7). GM has also been used in studies of developmental biology and ontogeny among many animal groups (Rohlf, 1998; Monteiro, 2000; Zelditch et al., 2000; 2004; Bastir and Rosas, 2004; Crespi-Abril et al., 2009).



**Figure 5.** Examples of application of landmark-based GM methods in different research fields and on different vertebrate groups: (a) evolution of the cranial structure of theropod dinosaurs (from Brusatte et al., 2012); (b) effects of environment in the evolution of turtle shells (from Claude et al., 2003); (c) morphospace occupation and mechanical performance of extant crocodilian skulls (from Pierce et al., 2008); (d) morphological variation in the pre-cloacal vertebrae in lizards (*Pogona vitticeps*) and snakes (*Pantherophis guttatus*) (from Head and Polly, 2015).



**Figure 6.** Examples of application of landmark-based GM methods in different research fields and on different vertebrate groups: (a) variations in head shape of neotropical toad populations (*Proceratophrys cristiceps*) (from Vieira et al., 2008); (b) cranial shape differentiation between different cetacean species (from Amaral et al., 2009); (c) skull, mandible and molar shape variation in marmots (*Marmota* sp.) for phylogenetic purposes (from Caumul and Polly, 2005); (d) morphological evolution in avian skulls (from Marugán-Lobón and Buscalioni 2006); (e) form, function and phylogeny from the scapula of South American rodents (Rodentia: Hystricognathi) (from Morgan, 2009).



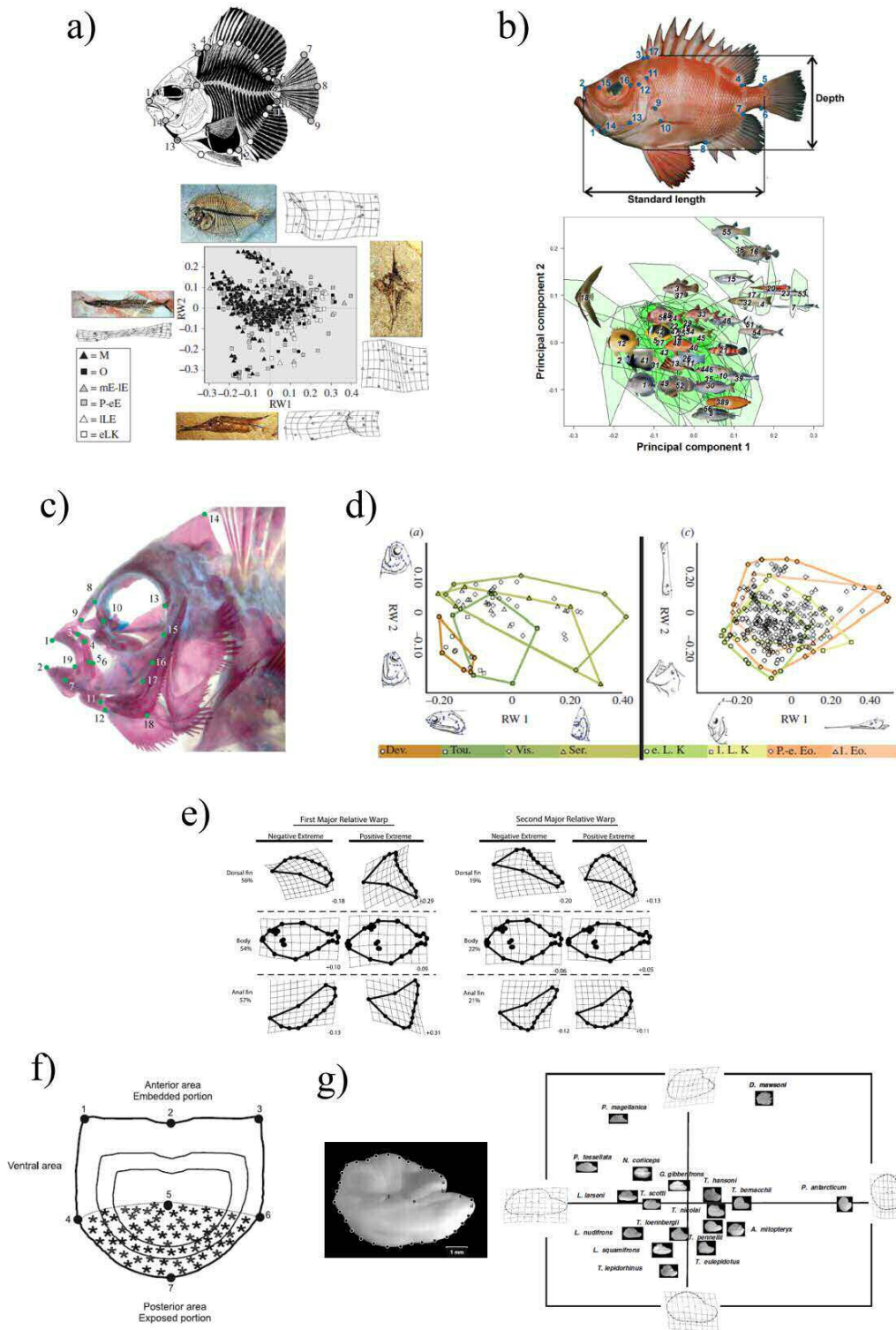
**Figure 7.** Examples of application of landmark-based GM methods in different research fields and on different invertebrate groups: (a) morphological differentiation of wing venation in species of hymenopters (*Eubazus* sp.) (from Villemant et al., 2007); (b) Ontogenetic variation on body shape of *Illex argentinus* (from Crespi-Abril et al., 2010) and morphological diversity of cephalopod cuttlebones (from Neige, 2003); (c) shell form differences within a marine gastropod specie (*Littorina saxatilis*) (from Carvajal-Rodríguez et al., 2005).

However, fishes have been one of the zoological groups more traditionally explored in studies applying GM methods (Fig. 8). Its high morphological plasticity and variability in forms and structures has attracted the attention of researchers of many scientific disciplines. The analyses of morphological features of fishes cover from the overall body shape (Loy et al., 1999, 2001; Valentin et al., 2002; Chakrabarty, 2005; Clabaut et al., 2007; Costa and Cataudella, 2007; Antonucci et al., 2009; Young et al., 2009; Claverie and Wainwright, 2014), until more specific anatomical structures such as skulls and pieces from maxillas and mandibles (Wainwright et al., 2002, 2004; Albertson and Kocher, 2005; Postl et al., 2008; Cooper and Westneat, 2009; Cooper et al., 2010), fins (Wainwright et al., 2002; Dornburg et al., 2011; Vergara-Solana et al., 2014), scales (Ibañez et al., 2007a) or otoliths (Monteiro et al., 2005; Ponton, 2006; Lombarte et al., 2010, Tuset et al., 2016), among others. Similarly than in other animal groups, GM methods in fishes have been widely applied in several research disciplines and for many purposes: from studies of taxonomic differentiation between species (Loy et al., 2001; Valentin et al., 2002; Langerhans et al., 2003) to more complex studies analyzing phylogenetic relationships, evolution processes or paleontological assessments (Rüber and Adams, 2001; Kassam et al., 2003; Clabaut et al., 2007; Cooper and Westneat, 2009; Young et al., 2009; Friedman et al., 2010); also in phylogenetic studies as a tool supporting the hypothesis obtained from the molecular results (Vergara-Solana et al., 2014); as proxy to evaluate ontogenetic shape trends associated to symmetric and allometric changes (Loy et al., 1998; Monterio et al., 2005; Frederich et al., 2008); in aquaculture-related studies investigating the effects of environmental conditions on the species or deformation processes (Verhaegen et al., 2007; Ambrosio et al., 2008); or even for fishery stocks assessments (Cadrin and Friedland, 1999; Cadrin, 2000). Scientific fields that have also extensively resorted to GM techniques are ecology and biodiversity of communities: determination of the morphological diversity within species or communities (Chakrabarty, 2005; Angeles et al., 2014), use of morphology to differentiate the ecological habits and behaviors of species within communities, such as locomotion performance, feeding strategies, habitat use or resource partitioning (Wainwright et al., 2002, 2004; Costa and Cataudella, 2007; Pulcini et al., 2008; Antonucci et al., 2009); as a method describing the internal structure and organization of communities (Recasens et al., 2006); or even as a tool helping to understand the effects of external phenomena on fish assemblages, such as

natural or antropogenetic perturbations (Lombarte et al., 2012) or biological invasions (Azzurro et al., 2014).

Other scientific branch where GM has been strongly introduced is anthropology and human biology (O'Higgins, 2000; Richtsmeier et al., 2002; Mitteroecker and Gunz, 2009; Mitteroecker et al., 2013). A great variability of related studies has been tested employing GM methods, since evolutionary development patterns of many structural bones from apes to earlier hominids and humans (Bookstein et al., 1999; Frost et al., 2003; Pérez et al., 2006), ontogenic changes and allometry in body structures in humans or earlier hominids (Ponce de León and Zollikofer, 2001; Bastir and Rosas, 2004; Gayzik et al., 2008) or even sexual or age-related dimorphisms and identification processes in forensic analyses (Franklin et al., 2007; Kimmerle et al., 2008). Besides, GM methods are not exclusive from the animal kingdom. In plants, for instance, they are also very common in order to investigate similar topics than in zoological studies: morphological plasticity and allometry of leafs or flowers (van der Niet et al., 2010; Viscosi, 2015), differentiation and taxonomical classification of similar species (Magrini and Scoppola, 2010; Viscosi and Cardini, 2011) or even to understand the strategies of plants such as polinitization and flowering (Gómez et al., 2008).

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**Figure 8.** Examples of application of landmark-based GM methods on fishes in different research fields: landmark and semilandmark scheme and morphospace representation from (a) spiny-finned teleosts after the end-Cretaceous extinction (from Friedman, 2010) and from (b) 2939 Indo-Pacific reef fishes (from Claverie and Wainwright, 2014); (c) morphological diversity and function of damselfish (Pomacentridae) skulls (from Cooper and Westneat, 2010); (d) morphospace representation of the cranial variability of early actinopterygians of Devonian-Cretaceous (from Sallan and Friedman, 2012); (e) shape variability of dorsal and anal fins in the study of the locomotor strategy of triggerfishes (Balistidae) (from Dornburg et al., 2011); (f) interspecific differentiation in scales within the family Mugilidae (from Ibañez et al., 2007a); (g) landmark scheme and morphospace representation of otoliths sagittae in Nototheniidae (from Lombarte et al., 2010).



#### **1.4 Relationship of morphology with the biodiversity determination of communities**

Biodiversity is an extremely wide multidimensional concept that encloses genetic and phenotypic variability, specific richness, functional proprieties of species and phylogenetic relationships between them. Consequently, its meaning and computation require of multiple mathematical indices impossible to be measured as a single measure (Purvis and Hector, 2000; Pavoine and Bonsall, 2011; Magurran, 2013; Loiseau and Gaertner, 2015). Recent studies have organized biodiversity as a three-dimensional concept formed by a combination of structural (ecological), taxonomical, phylogenetic and functional measures (Caddotte et al., 2010; Lyashevskaya and Farnsworth, 2012). Traditionally, in biological systems the most commonly used biodiversity measures by scientists and policy makers have been ecological or structural diversity indices, mainly based on richness and abundance of species within communities, since they are good descriptors of the variability of communities and are easily and rapidly computable (Magurran, 1988). However, these measures have begun to be questioned as appropriate biodiversity descriptors because they present some limitations: i) they are simple  $\alpha$ -numerical values that ignore the ecological, taxonomical, life history and functional traits of species within ecosystems; ii) they depend on the standardization of the used sampling methods, which can provide different representations of the biodiversity of communities, as well as on the sampling effort, that could be really hard to obtain a real representation of assemblages; iii) they are unable to detect disturbances caused by external factors (including anthropogenic impacts) affecting the diversity parameters of communities; and iv) they are not indicative of structure of communities (Gaston, 1996; Purvis and Hector, 2000; Mouillot et al., 2005; de Juan et al., 2009; Muntadas et al., 2016). Therefore, these metrics have been criticized to provide an incomplete viewpoint of biodiversity. Taxonomical indices, that consider the taxonomical and phylogenetic relationships between species, are also frequently used in diversity analyses of biological communities. They avoid problems related with sampling methods and effort, they are unbiased by the sampling effort (sample size) and allow analyzing qualitative and historical data (Warwick and Clarke, 1995; Clarke and Warwick, 1998, 2001). However, sometimes they are incapable to explain phenomena of adaptive radiation within communities, as well as disturbances that can affect the structure of

communities, such as environmental gradients or anthropogenic effects (Sommerfield et al., 1997; Mouillot et al., 2005).

Nowadays, functional diversity indices have spread in studies of biological communities because it considers the role that species play within communities, which helps to evaluate the organization and functioning of ecosystems as well as the consequences of the natural or anthropogenic disturbances on the structure of their communities (Petchey and Gaston, 2002; de Juan et al., 2007, 2009; Somerfield et al., 2008; Flynn et al., 2009; Villéger et al., 2010; Mouillot et al., 2014; Muntadas et al., 2015, 2016). Usually, measuring functional diversity consist in a compilation of biological characters of species that affect directly to their habits and fitness (such as body shape, diet, foraging methods, size, activity, mode of locomotion, reproduction, resilience or habitat) or directly a mixture of morphological measures with ecological meaning and functional role, that allow to investigate the structure and organization of communities. The main drawback of these most specific indices lies on the lack of information of some functional traits of species (especially those of inaccessible ecosystems) that usually requires expert knowledge to quantify the indices. Likewise, there exist a lack of standardization and consensus in the selection of the functional characteristics to consider, causing certain degree of subjectivity and a higher difficulty to compare different functional indices (Petchey and Gaston, 2002, 2006; Villéger et al., 2008).

Concurrently, in the last decades, a new scientific approach has arisen in the studies of diversity of communities, based on the premise that shape, form and morphological traits of species are directly linked to their ecological and biological strategies within communities (Karr and James, 1975; Gatz, 1979; Winemiller et al., 1991; Motta et al., 1995b; Foote, 1997). The assessment of morphological diversity within communities can help to understand and explain its structure and dynamics (Ricklefs and Miles, 1994; Wainwright and Reilly, 1994; Langerhans et al., 2003; Willis et al., 2005; Montaña and Winemiller, 2010). In fact, most of traits employed in functional diversity measures are morphological characters (Mason et al., 2007; Villéger et al., 2010; Mouillot et al., 2014). In addition, the computation of morphological variability and the analysis of morphospace occupation also allow obtaining numerical measures of biodiversity able to capture more ecological properties than a simple enumeration of species (Foote, 1997; Ciampaglio et al., 2001). Among the previously explained



competences, GM has been also used with these biodiversity purposes. For instance, in fish assemblages several biodiversity descriptors have been successfully generated both for qualitative and quantitative data (Recasens et al., 2006; Lombarte et al., 2012). Besides quantifying the morphological variability of systems, these indices provide essential morpho-functional information helping to understand the internal structure of communities.

Therefore, the incorporation of this new approach considering the morphological information of species to biodiversity studies that only use ecological parameters has allowed inferring in ecological habits of species complementing the results of functional diversity studies, which has been essential to improve the knowledge and understanding about the dynamics, structure and organization of communities (Karr and James, 1975; Bock, 1990; Ricklefs and Miles, 1994; Foote, 1997). Therefore, these findings seem to suggest that natural directions in ecological and biodiversity studies of communities should assimilate the topic of measurement and analysis of the morphology of species in order to progress in the current knowledge of these research fields.



# 2

## **Objectives and structure of the thesis**



The overall objective of this thesis was to determine and describe the morphological variability of several fish assemblages from landmark-based morphometric methods, in order to highlight the importance of the study of the morphology of species (morphological diversity) as an alternative and complementary useful tool in biodiversity studies, as well as its ability to infer in internal dynamics of ecosystems that helps improving the knowledge and understanding of structure of biological communities. To test these hypotheses, several fish assemblages with different geographical, environmental, ecological and hydrological conditions were used, from the NW Mediterranean Sea (Catalan coast, Balearic Basin and Balearic Islands) and from the NE Atlantic Ocean (Canary Islands). In order to achieve the general objectives, more specific aims were also addressed:

- 1.** To apply a specific methodology for the computation of the morphological diversity in fishes based on geometric morphometrics methods, including the overall body shape and the shape and position of fins and sensory organs, and demonstrate and support its validity and utility in studies of biodiversity and structure of communities.
- 2.** To develop and test new morphological diversity measures from geometric morphometric methods and describe their correlations and trends with other existent biodiversity components (ecological, taxonomical and functional diversity) in order to provide an additional complementary approach that helps improving the knowledge in biodiversity studies of fish assemblages.
- 3.** To characterize and determine the diversity of several fish assemblages with different ecological, hydrological and geographical characteristics using the computed ecological, taxonomical, morphological and functional indices: from mesopelagic fish assemblages from the Canary Islands, to coastal fish communities along the Catalan coast or demersal fish assemblages along a wide bathymetric range along the continental shelf and slope of the Balearic Basin and around the Balearic Islands.
- 4.** To perform a comparative of the different analyzed fish assemblages based on their morphospace configurations, and thus assess and discuss the relationship of the morphological approach applied in the present thesis, including the biodiversity

## **2. Objectives and structure of the thesis**

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indices and morphospace configurations, with the description of the composition, distribution, structure and organization of fish assemblages.

- 5.** To demonstrate the ability of the morphological outcomes as a descriptive tool inferring in ecological dynamics that shapes the structure, organization and functioning of fish communities, such as effects of external environmental factors, the resource partitioning, trophic relationships, the habitat use, or interspecific relationships such as coexistence, dominance and competition.

The structure of this thesis is presented as a collection of scientific articles prepared to be published in peer-reviewed specialized journals. Following the General Introduction (**Chapter 1**), the Objectives and Structure of the thesis section (**Chapter 2**) and the Report of the Supervisors (**Chapter 3**), the Results of the thesis are provided. They are divided in two main sections.

*Section 1* represents the methodological part of the thesis, where the landmark-based methodologies of quantification of the morphological variation are presented and tested in order to demonstrate its validity as a tool to in biodiversity studies and analyzing the structure of fish communities. This section is divided in two different chapters:

**Chapter 4** compares different landmark-based methods commonly used in the bibliography, including this one considered during the entire thesis, in order to identify the landmark selection scheme that includes the maximum amount of morphological information of species. In addition, the internal structure and organization of morphospaces provided by the different procedures is analyzed using different analytical methods.

**Chapter 5** describes a new morphological diversity metric computed using geometric morphometric methods and analyzes their relationship with other morphological, ecological, taxonomical and functional diversity indices. The computation and comparison of indices is performed using both qualitative and quantitative data.

*Section 2* represents the applicative approach of the thesis, where the GM methods used in the methodological section are applied and tested in fish assemblages from different environmental, ecological and hydrological characteristics in order to demonstrate the ability of the morphological variability methods to provide useful information in the analysis of the structure and organization of fish communities. This section is divided in three different chapters:

**Chapter 6** characterizes the morphological variability of mesopelagic fish assemblages around the Canary Islands (NE Atlantic Ocean) and analyzes the differences in their morphospaces occupation using two different spatial methods: convex hull and patterning.

**Chapter 7** describes the ecological and morphological diversity of several coastal fish assemblages from different locations of the Catalan coast (NW Mediterranean Sea). The morphological approach is performed using the GM procedure used during the entire thesis. In addition, the environmental factors affecting to the structure of fish communities are identified.

**Chapter 8** analyzes the changes in the morphological and functional structure and diversity of demersal fish communities along a wide depth range, including the continental shelf and slope (40-2200 m), from the Balearic Basin and around Mallorca and Menorca Islands (NW Mediterranean Sea). The morpho-functional approach is tested as a tool addressing key ecological factors affecting the structure of communities, such as the resource partitioning, habitat use and interespecific relationships such as dominance, competition and coexistence.

**Chapter 9** contains the General Discussion of the obtained results in the present thesis.

**Chapter 10** enumerates the main Conclusions of the present thesis.

**Chapter 11** includes the list of all the References used in the present thesis.

**Chapter 12** includes a Summary of the thesis in Catalan language.

**Chapter 13** represents the Appendix 1 section with the Supplementary Material of the different Results chapters.

**Chapter 14** is the Appendix 2 section that incorporates a PDF copy of the already published chapters in form of scientific articles.

**Chapter 15** includes a Glossary with the definition of all the acronyms and abbreviations present along the entire thesis.



# 3

## **Report of the supervisors**



Dr. Víctor Manuel Tuset Andújar and Dr. Antoni Lombarte Carrera, director and co-director of the present thesis titled “*Morphological structure and biodiversity in fish assemblages*” presented by Marc Farré Foix, certify that the research studies included in this thesis have been submitted to peer-review specialized international journals. The entire thesis is composed by a total of five studies: three of them have already been published, one has recently been accepted (February 2016) and is already available online, and one is currently under revision. The details of each publication and the Impact Factors of each journal (ISI Journal Citation Reports) are detailed below:

**Chapter 4: Farré, M.**, Tuset, V.M., Maynou, F., Recasens, L., Lombarte, A. (accepted on February 2016). *Selection of landmarks and semilandmarks in fishes for geometric morphometric analyses: a comparative study based on analytical methods*. *Scientia Marina* 80(2), 175-186. DOI: <http://dx.doi.org/10.3989/scimar.04280.15A>.

Impact factor (2016): **1.144**.

ISI Journal Citation Reports, Ranking: 63/103 (Marine and Freshwater Biology), **Q3**.

The PhD candidate has actively participated in the conception of hypotheses, in the experimental design (bibliographic research, selection of the different landmark-based schemes and selection of the analytical methods to apply), has performed all the GM, statistical and morphospace occupation analyses and has participated in the interpretation of results, discussion and redaction of the manuscript.

**Chapter 5: Farré, M.**, Tuset, V.M., Maynou, F., Recasens, L., Lombarte, A. (2013). *Geometric morphology as an alternative for measuring the diversity of fish assemblages*. *Ecological Indicators* 29: 159-166. DOI: <http://dx.doi.org/10.1016/j.ecolind.2012.12.005>.

Impact factor (2013): **3.23**.

ISI Journal of Report Citations, Ranking: 37/216 (Environmental Sciences), **Q1**.

The PhD candidate has actively participated in the experimental design and has performed all the analyses and methods (GM procedure including the creation of morphospaces, computation of all the diversity indices, correlation analyses between indices, etc.). In addition, he also has strongly contributed in the interpretation of results, discussion and redaction of manuscript.

### 3. Report of the supervisors

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**Chapter 6:** Tuset, V.M., **Farré, M.**, Lombarte, A., Bordes, F., Wienerroither, R., Olivar, P. (2014). *A comparative study of morphospace occupation of mesopelagic fish assemblages from the Canary Islands (North-eastern Atlantic)*. *Ichthyological Research* 61, 152-158. DOI: 10.1007/s10228-014-0390-2.

Impact factor (2014): **0.810**.

ISI Journal of Report Citations, Ranking: 104/154 (Zoology), **Q3**.

The PhD candidate has contributed in the development of the performed analyses (GM procedure, patterning and convex hull analyses) and has participated in the interpretation of results and discussion.

**Chapter 7:** **Farré, M.**, Lombarte, A., Maynou, F., Recasens, L., Tuset, V.M. (2015). *Habitat influence in the morphological diversity of coastal fish assemblages*. *Journal of Sea Research* 99: 107-117. DOI: <http://dx.doi.org/10.1016/j.seares.2015.03.002>.

Impact factor (2015): **1.990**.

ISI Journal of Report Citations, Ranking: 29/103 (Marine and Freshwater Biology), **Q2**; 22/61 (Oceanography), **Q2**.

The PhD candidate has actively participated in organization and treatment of overall dataset, has performed all the analyses (GM procedure, building of morphospaces, ecological and morphological description and comparison between communities, CCA analysis to assess the effects of environmental factors, etc.) and has participated in the interpretation of results, discussion and redaction of manuscript.

**Chapter 8:** **Farré, M.**, Tuset, V.M., Cartes, J.E., Massu, E., Lombarte, A. (under revision). *Depth-related trends in morphological and functional diversity of demersal fish assemblages in the western Mediterranean Sea*. *Progress in Oceanography*.

Impact factor (2016): **3.025**.

ISI Journal of Report Citations, Ranking: 5/61 (Oceanography), **Q1**.

The PhD candidate has actively participated in the organization and treatment of data and in the definition of the fish assemblages. He has performed all the analyses (GM procedure, building of morphological and functional space and Voronoi tessellations, computation of all the diversity indices and all the statistical analyses, etc.) and has

strongly participated in the interpretation of results, discussion and redaction of the manuscript.

The director and co-director also assure that all the coauthors of the different scientific articles included in the present thesis have not used, implicitly or explicitly, these articles for the elaboration of other doctoral thesis.

Barcelona, May 2016.

**Dr. Víctor Manuel Tuset Andújar**

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## **Section 1**

# **Methodological Part**





# 4

## **Selection of landmarks and semilandmarks in fishes for geometric morphometric analyses: a comparative study based on analytical methods**



**Selection of landmarks and semilandmarks in fishes for geometric  
morphometric analyses: a comparative study based on analytical  
methods**

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##### **Abstract**

We applied and compared three different sets of landmarks and semilandmarks commonly used in studies of fish assemblages to identify a standardized method of landmark selection that includes the maximum amount of morphological information of species. The different landmark-based methods used produced differences regarding the distribution of case-study species within the morphospace. We suggest that adding landmarks and semilandmarks that provide more specific information about anatomical structures with important roles in the biology of species, such as transformed fins or sensory organs, contributes to a clearer differentiation of species within the morphospace and a better interpretation of its occupancy. In addition, three types of method were used to establish how species are distributed within morphospace. The results demonstrated that aggregation points methods, including analyses based on quadrants or distances, are more appropriate for this purpose than indices of morphological disparity. The results also confirmed that although numerical methods are needed to test the statistical significance of outcomes, graphical methods provide a more intuitive interpretation of morphospace occupancy. The kernel density and Gabriel graph were useful to infer the morphospace zone where species are more densely grouped, improving the knowledge of space occupancy and structural complexity of fish assemblages.

**Keywords:** Morphological traits; Landmarks; Geometric morphometrics; Diversity; Point pattern; Morphospace; Marine fishes.

## Resum

El present estudi pretén comparar la estructura d'una comunitat de peixos mitjançant l'anàlisi morfològic de punts homòlegs (*landmarks*) y equidistants (*semilandmarks*) sobre les espècies de la comunitat. Per tal d'assolir aquest objectiu, es van utilitzar tres metodologies diferents descrites en la literatura a l'hora de definir aquests punts per tal d'identificar quina d'elles incloïa la màxima quantitat d'informació morfològica possible sobre les espècies. Les tres opcions van proporcionar resultats diferents en relació a la distribució de les espècies dins el morfoespai. Els resultats van suggerir que la incorporació de punts que aportin informació més específica sobre estructures anatòmiques amb funcions importants en la biologia de les espècies, com ara aletes modificades o òrgans sensorials, contribueix a una diferenciació més clara de les espècies i a una millor interpretació de la ocupació del morfoespai. Addicionalment, es van utilitzar varis mètodes numèrics i gràfics per tal d'establir el patró de distribució de les espècies dins el morfoespai. Els resultats van demostrar que el mètodes d'agregació de punts, incloent anàlisis basats en quadrants o distàncies, son més apropiats per aquest propòsit que els índexs de disparitat morfològica. Els resultats també van confirmar que encara que els mètodes numèrics son necessaris per avaluar la significança estadística dels mateixos, els mètodes gràfics proporcionen una interpretació més intuïtiva i clara de la distribució de les espècies dins el morfoespai. La densitat de kernel i els gràfics de Gabriel van demostrar ser molt útils a l'hora de deduir la zona del morfoespai on les espècies estaven més densament agrupades, fet que ajuda a millorar el coneixement sobre la ocupació de l'espai i la complexitat estructural en comunitats de peixos.

##### 4.1 Introduction

The use of the morphology emerged as a scientific discipline in the early 20th century based on the ‘form, shape, and function’ of species morphologies (Thompson, 1915; Russell, 1916). From then until now, this approach has been applied in many studies and has been suggested as a useful tool to better understand the mechanisms promoting species coexistence, for inferring the ecological strategies of species (e.g., Gatz, 1979; Bellwood et al., 2006) and for investigating fluctuations within a community due to natural or anthropogenic perturbations (Villéger et al., 2010; Korn et al. 2013). Initially, changes in shape of species were assessed from linear measurements (Strauss and Bookstein 1982; Winemiller, 1991; Klingenberg and Ekau, 1996). In the 1990s, a new approach, called geometric morphometrics, allowed analyzing shape variation and its covariation (Bookstein, 1991; Rohlf and Marcus, 1993; Adams et al., 2013). These methods quantify the shape variation of objects from the Cartesian coordinates of anatomical landmarks, unifying a rigorous statistical theory with analytical procedures for superimposing landmark configurations of all specimens in a common coordinate system. Therefore, in addition to dealing with issues related with allometry and isometry, the power of this method lies in the ability to detect and visualize shape differences more clearly than classical approaches (Clabaut et al., 2007; Adams et al., 2013).

In landmark-based studies, a common “conflict” arises in the definition of the number and position of the homologous landmarks between organisms (Cadrin, 2000; Klingenberg, 2010; Smith and Hendricks, 2013). This is an important setback because the use of different criteria to define landmarks can influence results (Klingenberg, 2010; Van Bocxlaer and Schultheiß, 2010; Adams et al., 2013). In fishes, most landmark sets have mainly focused on feeding and locomotion apparatus, which are considered the primary drivers of co-existence and specific richness (e.g., Winemiller, 1991; Wainwright et al., 2002; Cooper and Westneat, 2009), and on body shape, which is a multitasking factor contributing to multiple traits, such as swimming, food capture, evading predators, courtship, defending territories or spawning (e.g., Valentin et al., 2002; Costa and Cataudella, 2007; Walker, 2010). Other anatomical parts, such as pelvic and pectoral fins or sensorial organs (barbels or illicia), are not usually included

because they are not rigid structures and are difficult to preserve intact, and it is often difficult to define homologous positions of these structures between species (Bookstein, 1991; Chakrabarty, 2005). Nevertheless, it has been demonstrated that these structures are key factors in many fish behaviours (Yamanoue et al., 2010), such as movement and body position (Zuanon et al. 2006), prey capture (Laurenson et al., 2004) and receiving chemical stimuli (Kasumyan, 2011), so they are important in the functional and ecological role of species within communities. Although many researchers currently question their use in landmark methods, claiming that they are not solid structures, that they have highly variable positions that are difficult to standardize, or even that some of them are absent (Chakrabarty 2005), fins have been applied in evolutionary (Friedman, 2010; Dornburg et al., 2011), phylogenetic (Vergara-Solana et al., 2014), ecological (Wainwright et al., 2002; Lombarte et al., 2012; Farré et al., 2015) and biodiversity studies (Farré et al., 2013).

Morphological variations between organisms can be plotted in a morphospace where the species distribution and occupied space provide useful information on the structural complexity of the community (McClain et al., 2004; Clabaut et al., 2007). There are three main approaches for exploring the distribution of points within space: indices of morphological disparity, quadrant analyses (based on density of points), and nearest-neighbour analyses (based on distance between points and their association), which can be represented in numerical measurements or graphical analysis (Ciampaglio et al., 2001; Zelditch et al., 2004; Werdelin and Lewis, 2013). Numerical methods such as the morphological disparity (e.g. sum of range, sum of variance or position of centroid), the average link length of a minimum spanning tree, the average distance between any species and its nearest neighbour or participation ratio, do not provide the relative position of points in morphospace (Foote, 1997; Ciampaglio et al., 2001; Zelditch et al., 2004). Nevertheless, it is possible to infer whether data follow random, uniform, or clustered spatial patterns (Pie and Traniello, 2007).

By contrast, graphical approaches are alternative ways for improving the knowledge of the distribution of points. The convex hull is useful to detect species contributing at a greater extent to the diversity of morphospace (Cornwell et al., 2006; Werdelin and Lewis, 2013). However, this approach is unable to assess the internal structure of morphospace (Shen et al., 2008; Tuset et al., 2014). The analysis of the distribution of points within morphospace is usually performed using the Euclidean minimum

spanning tree, relative neighbourhood graph, nearest-neighbour graph, Gabriel graph or kernel density, which display the main groupings of species and gaps where species are absent (Gabriel and Sokal, 1969; Worton, 1989; Dale and Fortin, 2010). Similarly, Ripley's function infers on the spatial distribution pattern (random, uniform, or clustered) (Ripley, 1979; Perry et al., 2006; Werdelin and Lewis, 2013).

Our hypothesis was that the selection scheme of landmarks and semilandmarks can affect the morphospace configuration of fish assemblages. Therefore, the aims of the present study were (i) to apply, assess and compare different landmark and semilandmark schemes used in previous fish studies to discern the differences between the criteria and determine how the selection of landmarks influences the distribution patterns of fishes within the morphospace, and (ii) to analyse the occupation of morphospaces using different analytical methods and identify those that provide most complete information in order to explain the and organization of fish assemblages.

## 4.2 Materials and Methods

### 4.2.1 Fish collection

A fish database of a coastal assemblage of the Catalan Coast, northwestern Mediterranean (40.5° - 42.5°N, 0.30° - 3.25°E) was used for this study. In particular, an artificial reef-sandy assemblage of the central coast (41°10.52'N; 1°35.16'E) was selected due to its high species richness, morphological richness and functional and taxonomical diversity (Farré et al., 2013). This artificial reef consists of a group of modules that were installed between 1987 and 1998 to avoid illegal trawling (Recasens et al., 2006). Fishes were collected bi-monthly by small-scale vessels with trammel nets in 2000-2003. The characteristics of trammel net fisheries in the study area are described in the literature (Recasens et al., 2006; Farré et al., 2013). For each fishing operation, the entire fish catch (commercial plus discarded fraction) was retained. A total of 48 species were identified (Mercader et al., 2001; Nelson, 2006) (Table 1) and photographed (only one specimen per species).



**Table 1.** List of species of the artificial reef-sandy assemblage analysed in this study (Calafell, Catalan coast, NW Mediterranean), the taxonomical classification of the species (order and family) and the acronym used for each species.

Order	Family	Specie	Acronym
Anguiliformes	Congridae	<i>Conger conger</i>	Ccon
Gadiformes	Merlucciidae	<i>Merluccius merluccius</i>	Mmer
Gadiformes	Phycidae	<i>Phycis phycis</i>	Pphy
Lophiiformes	Lophiidae	<i>Lophius piscatorius</i>	Lpis
Mugiliformes	Mugilidae	<i>Chelon labrosus</i>	Clab
Mugiliformes	Mugilidae	<i>Liza aurata</i>	Laur
Mugiliformes	Mugilidae	<i>Mugil cephalus</i>	Mcep
Mugiliformes	Mugilidae	<i>Liza ramada</i>	Lram
Perciformes	Moronidae	<i>Dicentrarchus labrax</i>	Dlab
Perciformes	Serranidae	<i>Serranus cabrilla</i>	Scab
Perciformes	Carangidae	<i>Seriola dumerili</i>	Sdum
Perciformes	Haemulidae	<i>Pomadasys incisus</i>	Pinc
Perciformes	Sparidae	<i>Boops boops</i>	Bboo
Perciformes	Sparidae	<i>Dentex dentex</i>	Dden
Perciformes	Sparidae	<i>Diplodus annularis</i>	Dann
Perciformes	Sparidae	<i>Diplodus cervinus</i>	Dcer
Perciformes	Sparidae	<i>Diplodus sargus</i>	Dsar
Perciformes	Sparidae	<i>Diplodus vulgaris</i>	Dvul
Perciformes	Sparidae	<i>Lithognathus mormyrus</i>	Lmor
Perciformes	Sparidae	<i>Pagellus acarne</i>	Paca
Perciformes	Sparidae	<i>Pagellus bogaraveo</i>	Pbog
Perciformes	Sparidae	<i>Pagellus erythrinus</i>	Pery
Perciformes	Sparidae	<i>Pagrus pagrus</i>	Ppag
Perciformes	Sparidae	<i>Sparus aurata</i>	Saur
Perciformes	Sparidae	<i>Spondyliosoma cantharus</i>	Scan
Perciformes	Sciaenidae	<i>Sciaena umbra</i>	Sumb
Perciformes	Sciaenidae	<i>Umbrina canariensis</i>	Ucan
Perciformes	Sciaenidae	<i>Umbrina cirrosa</i>	Ucir
Perciformes	Mullidae	<i>Mullus barbatus</i>	Mbar
Perciformes	Mullidae	<i>Mullus surmuletus</i>	Msur
Perciformes	Pomacentridae	<i>Chromis chromis</i>	Cchr
Perciformes	Labridae	<i>Coris julis</i>	Cjul
Perciformes	Labridae	<i>Labrus merula</i>	Lmer
Perciformes	Uranoscopidae	<i>Uranoscopus scaber</i>	Usca
Pleuronectiformes	Scophthalmidae	<i>Scophthalmus rhombus</i>	Srho
Pleuronectiformes	Scophthalmidae	<i>Psetta maxima</i>	Pmax
Pleuronectiformes	Bothidae	<i>Arnoglossus laterna</i>	Alat
Pleuronectiformes	Bothidae	<i>Bothus podas</i>	Bpod
Pleuronectiformes	Citharidae	<i>Citharus linguatula</i>	Clin
Pleuronectiformes	Soleidae	<i>Microchirus variegatus</i>	Mvar
Pleuronectiformes	Soleidae	<i>Solea lascaris</i>	Slas

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Pleuronectiformes	Soleidae	<i>Solea senegalensis</i>	Ssen
Pleuronectiformes	Soleidae	<i>Solea solea</i>	Ssol
Pleuronectiformes	Soleidae	<i>Synaptura lusitanica</i>	Slus
Scorpaeniformes	Scorpaenidae	<i>Scorpaena notata</i>	Snot
Scorpaeniformes	Scorpaenidae	<i>Scorpaena porcus</i>	Spor
Scorpaeniformes	Scorpaenidae	<i>Scorpaena scrofa</i>	Sscr
Scorpaeniformes	Triglidae	<i>Trigla lucerna</i>	Tluc

The photographic record of species was carried out using standardised and homologous body position for all species (facing left), including fins and sensorial organs position and size, in order to avoid differences in disposition of anatomical structures between species that allow the application and comparison of different landmark-based methods in the morphological analyses (see Fig. 1).

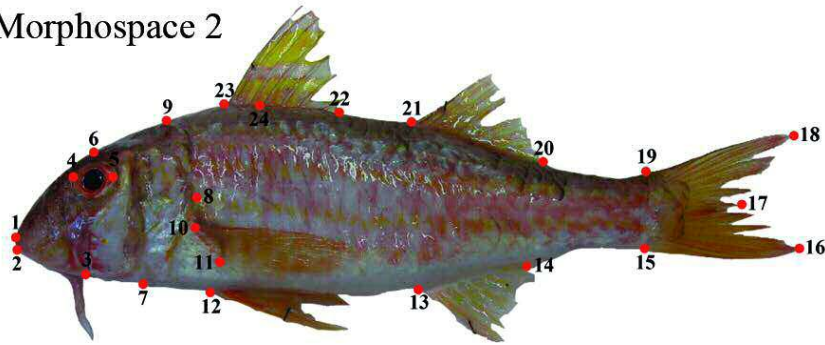
##### 4.2.2 Building morphospaces

Morphological diversity of fish shapes was quantified using geometric morphometric techniques (Bookstein, 1991; Rohlf and Marcus, 1993; Zelditch et al., 2004). The selection of landmarks and semilandmarks was performed based on commonly used choices in previous morphometric studies in fishes. Three different criteria considering all the recorded options in the bibliography were used (detailed description of the meaning of landmarks and semilandmarks for each method is provided in Table 2): first, defining basically the body and head shape, widely used and considered to best represent the external shape of the body morphology (Fig. 1A, morphospace 1) (Loy et al., 1999; Chakrabarty, 2005; Costa and Cataudella, 2007); second, adding the eye size and the position of fins and caudal fin shapes, traits often recorded in paleontological and evolutionary studies given their ecological and functional relevance (Fig. 1B, morphospace 2) (Young et al., 2009; Friedman, 2010); and third, a partial combination of the above-mentioned methods including the shape, size and position of all fins and sensorial organs (Fig. 1C, morphospace 3) (Recasens et al., 2006; Farré et al., 2013; Azzurro et al., 2014). We digitised the landmarks and semilandmarks in one standardised image of the left profile of species previously obtained as a consensus figure from different specimens using tpsDig v. 2.16 software (Rohlf, 2010a) for

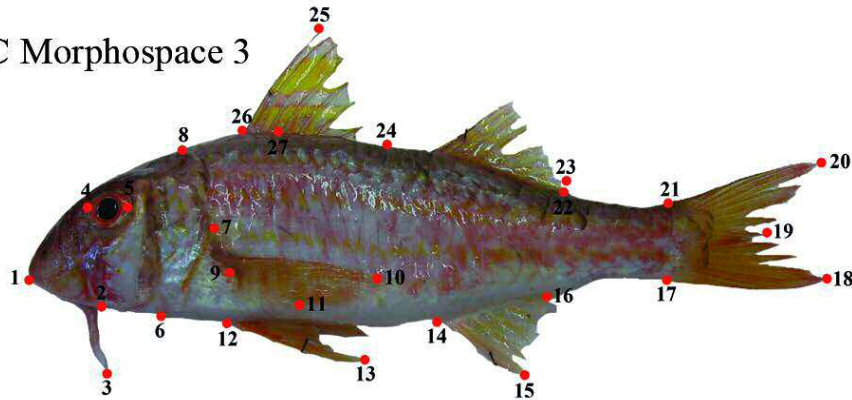
geometric morphometric analysis. However, direct analysis of landmark coordinates contains other components unrelated to shape, such as position, orientation and size (Angeles et al., 2014). To remove these distortions, a generalised least-squares superimposition procedure (GLS or GPA, generalised Procrustes) was applied, translating all specimens to a common centroid position in the coordinate system, scaling them to unit centroid size and rotating them to minimise the distances between corresponding landmarks (Kassam et al., 2003; Angeles et al., 2014). Thus, working on standardized consensus images, superimposition methods allow the analysis of morphology independently of size (Layman et al., 2005). However, GLS Procrustes coordinates are not expressed in Euclidean shape space. Therefore, these coordinates should be previously projected in a Euclidean tangent space in order to test if the shape variation is small enough to consider that this new tangent space is a good representation of the Procrustes data in a Euclidean space (Dryden and Mardia, 1998). Then, to check whether the variation between both spaces was minimum for our communities, we computed the correlations between the tangent and Procrustes distances using *tpsSmall* v. 1.28 (Rohlf, 2013). The results of correlations (Morphospace 1: uncentred correlation=0.999988, root mean square error=0.000419; Morphospace 2: uncentered correlation=0.999993, root mean square error=0.000404; Morphospace 3: uncentered correlation=0.999979, root mean square error=0.000639) confirmed that for the three methodologies both spaces were nearly identical.

We then conducted a relative warp analysis of superimposed images using *tpsRelw* v. 1.49 (Rohlf, 2010b). Each relative warp axis represents a set of specific morphological characteristics, allowing particular morphological attributes of species to be analyzed directly (e.g., Rohlf and Marcus, 1993; Zelditch et al., 2004; Layman et al., 2005). Morphospaces were built from relative warps 1, 2 and 3 in order to capture the maximum and most important information about shape variation (Recasens et al., 2006). These first three relative warps attained 84.7% (morphospace 1), 81.7% (morphospace 2) and 78.6% (morphospace 3) of total morphological variability, considered a sufficiently representative percentage of the total amount of explained morphological variation. Finally, we reduced the three axes to two by applying a non-metric multidimensional scaling technique (nMDS) (Shen et al., 2008) to obtain a multidimensional graphical representation of the distribution of fish assemblages based on their similarity.

## B Morphospace 2



## C Morphospace 3



**Figure 1.** Location of the selected landmarks and semilandmarks in the left side of standardised images for the three different used methods (morphospace 1, 2 and 3). The description of the meaning of landmarks for each method is detailed in Table 2. In method 1 (A, morphospace 1), landmark 15 is a semilandmark; in method 2 (B, morphospace 2), landmarks 16, 17, 18 and 24 are semilandmarks; and in method 3 (C, morphospace 3), landmarks 3, 10, 11, 13, 15, 18, 19, 20, 23, 24, 25 and 27 are semilandmarks. Species in the images is *Mullus surmuletus*.

**Table 2.** Description of the morphological meaning of the selected landmarks and semilandmarks for the 3 analysed methods. Landmark scheme of the morphospace 1 based from Loy et al., 1999; Chakrabarty, 2005 and Costa and Cataudella, 2007; morphospace 2 based from Young et al., 2009 and Friedman, 2010; and morphospace 3 based from Recasens et al., 2006; Farré et al., 2013 and Azzurro et al., 2014. In bold the exclusive landmarks of each morphospace; the remaining are homologous in all the morphospaces.

Landmarks	Morphospace 1	Morphospace 2	Morphospace 3
1	Anterior tip of the mouth	<b>Anterior tip of the snout bone</b>	Anterior tip of the mouth
2	Posterior tip of the mouth	Anterior tip of the mouth	Posterior tip of the mouth
3	<b>Central point in the midline through the eye</b>	Posterior tip of the mouth	<b>Distal tip of the barbel, placed at 80° of the body margin (or projection in the lower jaw inferior margin of the position of the hyomandibular insertion, when no barbels)</b>
4	Ventral margin in the end of the head	Anterior margin in the maximum eye width	Anterior margin in the maximum eye width
5	Dorsal margin in the end of the head	Posterior margin in the maximum eye width	Posterior margin in the maximum eye width
6	Dorsal insertion of the pectoral fin	<b>Dorsal margin of the head exactly above the centre of the eye</b>	Ventral margin in the end of the head
7	Insertion of the pelvic fin	Ventral margin in the end of the head	Posterior margin in the end of the head
8	Anterior insertion of the anal fin	Posterior margin in the end of the head	Dorsal margin in the end of the head
9	Posterior insertion of the anal fin	Dorsal margin in the end of the head	<b>Central point in the baseline of the pectoral fin</b>
10	Ventral insertion of the caudal fin	Dorsal insertion of the pectoral fin	<b>Posterior tip of the pectoral fin when the fin is in position of maximum extension</b>
11	<b>Posterior margin of the caudal peduncle</b>	<b>Ventral insertion of the pectoral fin</b>	<b>Ventral margin of the pectoral fin when the fin is in position of maximum extension</b>
12	Dorsal insertion of the caudal fin	Insertion of the pelvic fin	Insertion of the pelvic fin

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13	Posterior insertion of the dorsal fin (second dorsal fin if exists)	Anterior insertion of the anal fin	<b>Distal tip of the pelvic fin when the fin is in position of maximum extension</b>
14	Anterior insertion of the dorsal fin (first dorsal fin if second fin exists)	Posterior insertion of the anal fin	Anterior insertion of the anal fin
15	Point of maximum body height in the body margin	Ventral insertion of the caudal fin	<b>Distal tip from the anterior insertion of the anal fin when the fin is in position of maximum extension</b>
16	-	Distal tip of the ventral lobe of the caudal fin when the fin is in position of maximum extension	Posterior insertion of the anal fin
17	-	Posterior margin of the caudal fin between dorsal and ventral lobes	Ventral insertion of the caudal fin
18	-	Distal tip of the dorsal lobe of the caudal fin when the fin is in position of maximum extension	Distal tip of the ventral lobe of the caudal fin when the fin is in position of maximum extension
19	-	Dorsal insertion of the caudal fin	Posterior margin of the caudal fin between dorsal and ventral lobes
20	-	Posterior insertion of the dorsal fin (second dorsal fin if exists)	Distal tip of the dorsal lobe of the caudal fin when the fin is in position of maximum extension
21	-	<b>Anterior insertion of the second dorsal fin (if exists)</b>	Dorsal insertion of the caudal fin
22	-	<b>Posterior insertion of the first dorsal fin (if second dorsal fin exists)</b>	Posterior insertion of the dorsal fin (second dorsal fin if exists)
23	-	Anterior insertion of the dorsal fin (first dorsal fin if second fin exists)	<b>Posterior tip of the dorsal fin (second dorsal fin if exists) when the fin is in position of maximum extension</b>

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24	-	Point of maximum body height in the body margin		<b>Transi</b> <b>soft ra</b> <b>one do</b> <b>in the</b> <b>fins o</b> <b>body (</b>
25	-		-	<b>Distal</b> <b>dorsal</b> <b>fin exi</b> <b>of ma</b>
26	-		-	Anterie (first d
27	-		-	Point o body m

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##### 4.2.3 Point pattern analyses

Three types of descriptor were used to establish the spatial variability in the morphospaces: indices of morphological disparity, quadrant analyses and nearest neighbour analyses (a complete scheme of the different analyses performed is shown in Figure 2). The last two analyses included numerical and graphical methods.

Among the various disparity measures described in the literature (Ciampaglio et al., 2001; Wills, 2001; Korn et al., 2013), the following two indices of morphological disparity were used: a) *Sum of variance (SOV)*, which is the sum of the variances along all the morphospace axes; and b) *Sum of range of the middle two quartiles (QSOR)*, which defines the area that is occupied by the middle two quartiles of the data points along the x and y axes, providing information about the distribution pattern of points within the morphospace.

In the quadrant analyses, it was estimated the *variance-to-mean ratio*, a numerical method which is defined as the ratio of variance to the mean:

$$VMR = \frac{\sigma^2}{\mu},$$

when  $VMR > 1$ , it corresponds to a clustered distribution; when  $VMR < 1$ , it denotes an ordered distribution; and when  $VMR \approx 1$ , the distribution is uniform or more exactly follows a Poisson random distribution. A Kolmogorov-Smirnov (*K-S* test) test was applied to compare the observed and expected frequencies derived from the Poisson frequency distribution (Anderson et al., 1982). Graphically, the *kernel density* was determined for the localisation of clusters of species using a Gaussian function:

$$f(x, y) = \frac{1}{2\pi r^2} \sum_i e^{-\frac{d_i^2}{2r^2}}$$

where  $d_i = \sqrt{(x - x_i)^2 + (y - y_i)^2}$ ,  $x$  and  $y$  are the coordinates of points, and  $r$  is the radius (Worton, 1989; Fortin et al., 2005; Werdelin and Lewis, 2013).

For nearest-neighbour analyses, the numerical value of the *Clark-Evans nearest neighbour* was obtained to compare the average distance between nearest neighbours



with the expected distance in the case of random distribution using the following equation:

$$r = \frac{\text{mean distance}}{\frac{1}{2}\sqrt{\text{density}}}$$

when  $r < 1$ , points are clustered; when  $r = 1$  the points occur in a random distribution; and when  $r > 1$ , the points are evenly dispersed (Davis, 1986; Werdelin and Lewis, 2013). The expected (theoretical) distribution under the null hypothesis is plotted as a continuous curve together with the histogram of observed distances. The expected probability density function as a function of distance  $r$  is:

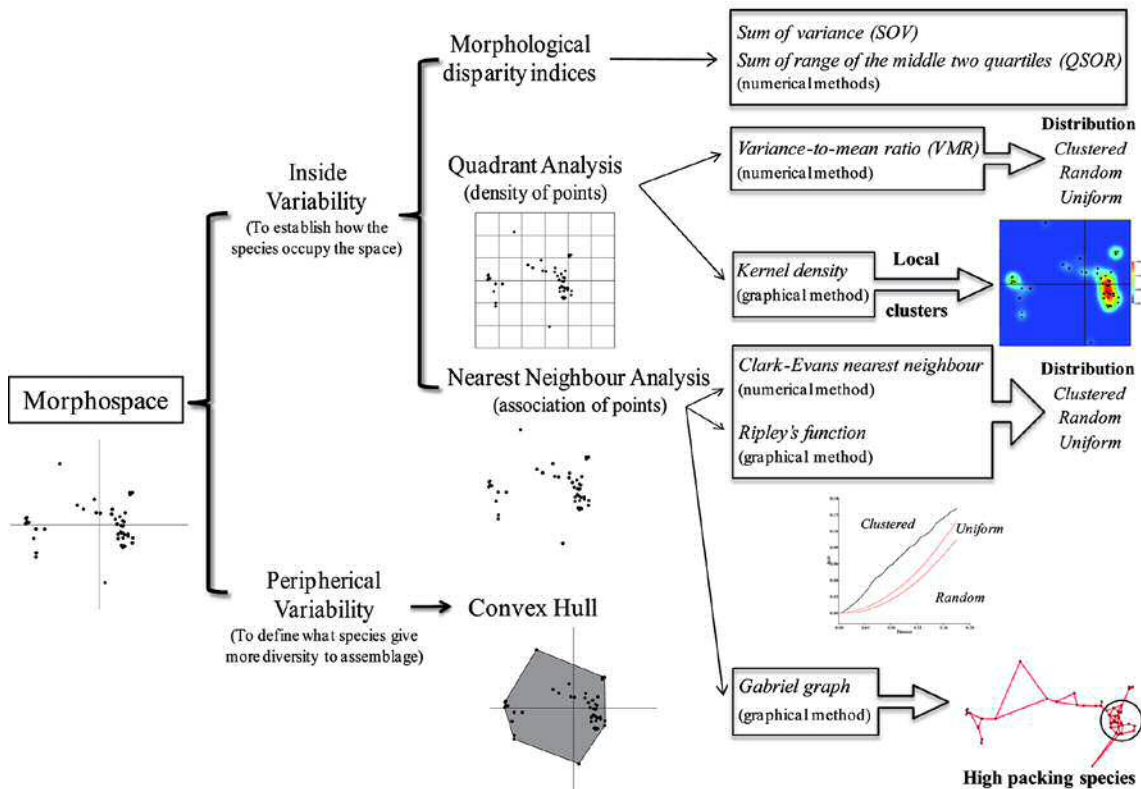
$$g(r) = 2\rho\pi r e^{-\rho\pi r^2}$$

where  $\rho = n/A$  is the density,  $n$  is number of points, and  $A$  is the estimation area from the convex hull (Clark and Evans, 1954; Cornwell et al., 2006). In addition, it was also estimated the *Ripley's function*, a graphical method that is also related to the nearest-neighbour distribution function and incorporates local variations, defined as:

$$\hat{K}(d) = \frac{1}{\lambda n} \sum_{i=1}^n \sum_{j \neq i} I(d_{ij} < d)$$

where  $d_{ij}$  is the Euclidean distance between the  $i^{\text{th}}$  and  $j^{\text{th}}$  points in a data set of  $n$  points, and  $\lambda$  is the average density of points (Ripley, 1979; Dixon, 2002; Perry et al., 2006). Finally, the localisation of species clusters was obtained from the *Gabriel graph*, an undirected graph or beta-skeleton expressing one notion of proximity or nearness among points allowing the localisation of packings. The graph consists of two sets: nodes or points, and edges or lines, which represent connections between pairs of nodes showing which points are clumped (Gabriel and Sokal, 1969; Dale and Fortin, 2010).

Finally, another graphical method, the *convex hull*, was used to define which species contribute most to the morphological diversity of morphospaces, allowing us to determine the peripheral shape of morphospaces.



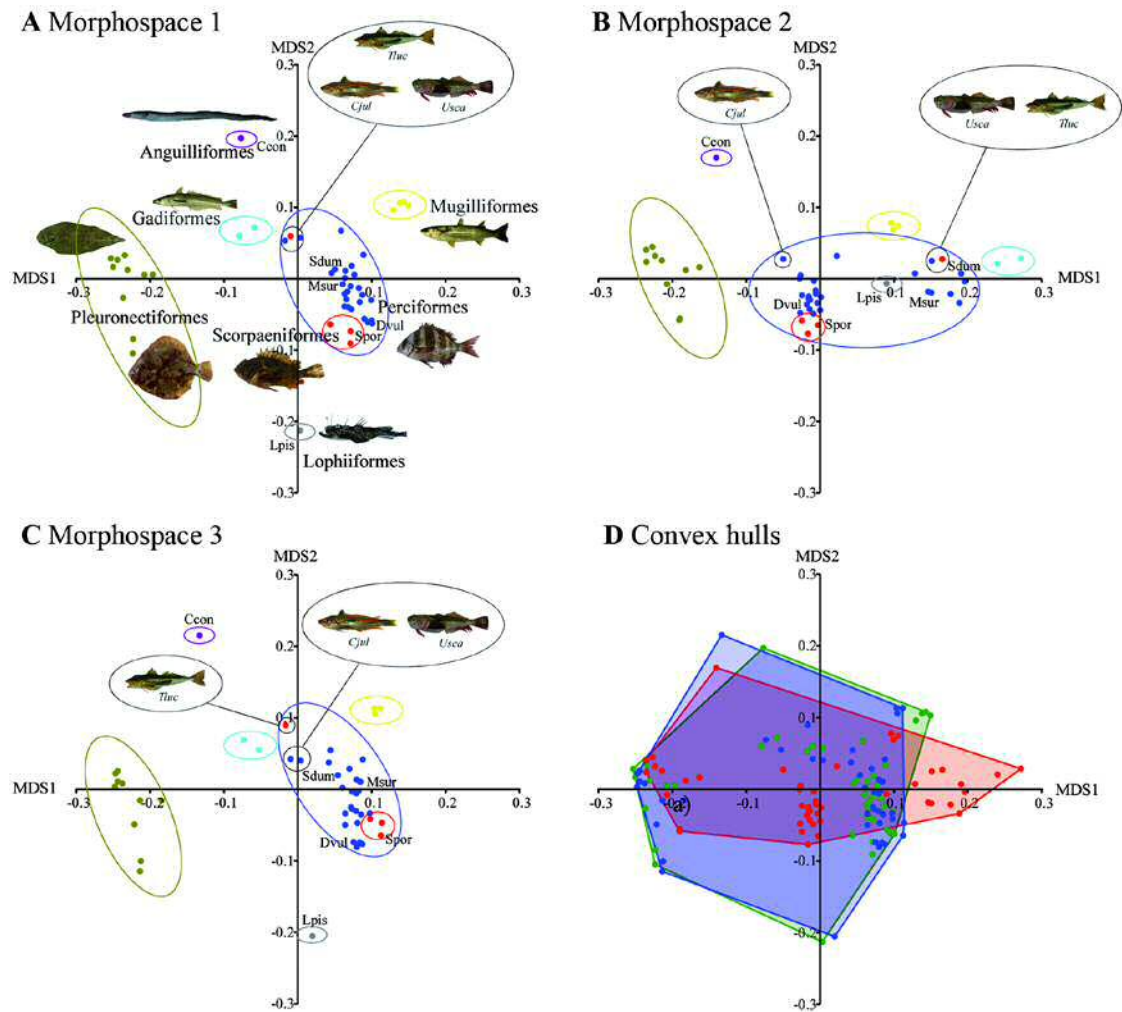
**Figure 2.** Explanatory scheme for the procedure of analysis of morphospaces, including all the used analyses and methods.

## 4.3 Results

### 4.3.1 Species distribution within the morphospace

All the morphospaces showed a similar spatial variability in the species distribution, with matched or very similar convex hulls configurations (Fig. 3D). Morphospaces 1 and 3 presented no species close to the morphospace core. However, two species packs formed by Perciformes-Scorpaeniformes and Pleuronectiformes were located to the right and left side, respectively, while other different groups, including Anguilliformes, Gadiformes, Lophiiformes and Mugiliformes, occupied their own isolated areas in the morphospace (Fig. 3A and 3C). Instead, morphospace 2 showed a different spatial organisation that was more extended in the first axis, separating the fishes in relation to

number and position of dorsal fins (Fig. 3B). Thus, negative values mainly corresponded to species with a continuous dorsal fin along the body located in the anterior position; the morphospace core was occupied by benthic species with one shorter dorsal fin originating at the end of the head, as in some Perciformes (Labridae, Serranidae and Sparidae) and Scorpaeniformes; and positive values were associated with species with two dorsal fins, including a high variety of fishes, such as Gadiformes, Mugiliformes and some Perciformes (Scianidae, Mullidae or Carangidae) (Fig. 3B).



**Figure 3.** Representation of the morphospace for the A) first, B) second and C) third method showing the main differentiated groups of species. Ccon = *Conger conger*; Cjul = *Coris julis*; Dvul = *Diplodus vulgaris*; Lpis = *Lophius piscatorius*; Msur = *Mullus surmuletus*; Sdum = *Seriola dumerili*; Spor = *Scorpaena porcus*; Thuc = *Trigla lucerna*; Usca = *Uranoscopus scaber*. Colour legend of dots: Perciformes in dark blue, Scorpaeniformes in red, Pleuronectiformes in brown, Gadiformes in light blue, Mugiliformes in yellow, Lophiiformes in grey and Anguilliformes in purple. D) Superimposed representation of the convex hull structure of the morphospaces for the three analysed methods. Morphospace 1 in green, morphospace 2 in red and morphospace 3 in blue, n=48.

The second axis mainly distinguished between elongated (positive values) or rounded (negative values) body shapes in all of the morphospaces (Figs. 3A and 3C), although in morphospace 2 this distinction was less evident because species were more compacted along the axis (Fig. 3B). However, the axis also separated species based on other morphological characteristics, such as the relation between head and body size (species with larger heads in relation to body size presenting negative values and species with smaller heads showing positive values) and the number and position of pelvic and dorsal fins. Morphospaces 1 and 3 were characterised by the isolation of the anglerfish (*Lophius piscatorius*, Lophiiformes), having a transformed first ray of the first dorsal. Moreover, nektonic (*Seriola dumerili*, Carangidae) and epibenthic (*Mullus surmuletus*, Mullidae) species with two dorsal fins were located slightly separated along the second axis compared with species with one dorsal fin (*Diplodus vulgaris*, Sparidae, or *Scorpaena porcus*, Scorpaenidae) (Fig. 3A and 3C). However, benthic species with specially adapted pectoral fins, such as *Trigla lucerna*, were isolated and clearly identified in morphospace 3 (Fig. 3C). Moreover, in morphospace 2 only *Conger conger* (Anguilliformes) showed an extreme distribution because of its specially elongated shape, as was also shown in all of the morphospaces, whereas all remaining species were concentrated between -0.1 and 0.1 values, confirming a greater compaction along the axis (Fig. 3B).

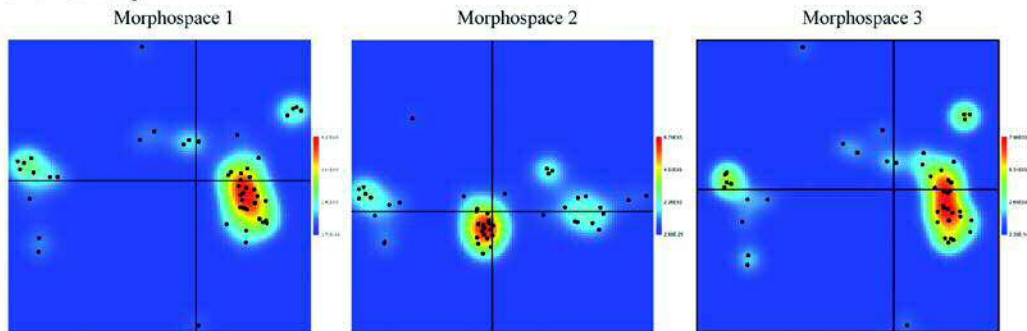
#### 4.3.2 Accounting for the observed morphological variation

The SOV showed no differences among morphospaces, reaching similar values of variance (0.021) in the three cases. By contrast, the QSOR revealed greater disparity, attaining the highest value (0.028) in morphospace 2, which demonstrated a more dispersed distribution of points compared with the remaining morphospaces. Although morphospaces 1 and 3 yielded similar values (0.011 and 0.015, respectively), the lowest filled area in morphospace 1 denoted a more compacted distribution of points located in the two middle quartiles than morphospace 3.

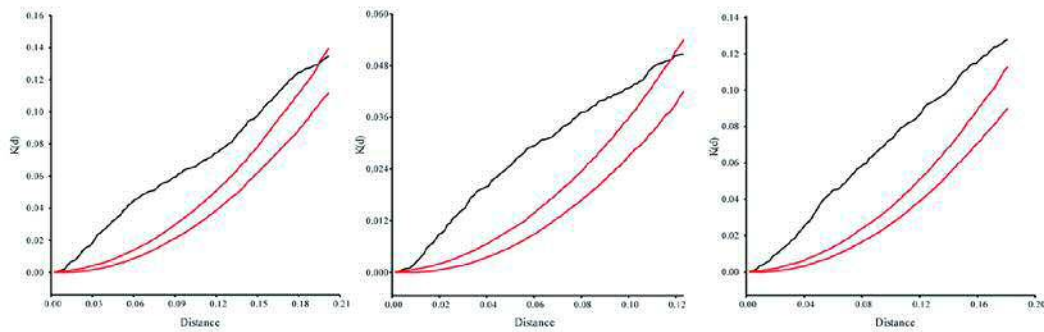
The VMR yielded values of 8.83, 6.64 and 7.8 for morphospace 1, 2 and 3, respectively, corresponding with clustered distributions in all cases ( $K-S$  test=0.4031,

$P=0.2267$ ;  $K-S$  test=0.4031,  $P=0.2267$ ;  $K-S$  test=0.4308,  $P=0.2267$ , respectively). The kernel analysis evidenced an area of high density in the three morphospaces (red-orange zone; Fig. 4A), which was formed by 12, 12 and 9 species in morphospaces 1, 2 and 3, respectively. Morphospace 2 displayed several medium-density zones separated from each other, whereas in morphospaces 1 and 3 the species were more closely distributed among them, especially near the centroid, forming a main core zone and favouring the connection between lesser densities (Fig. 4A).

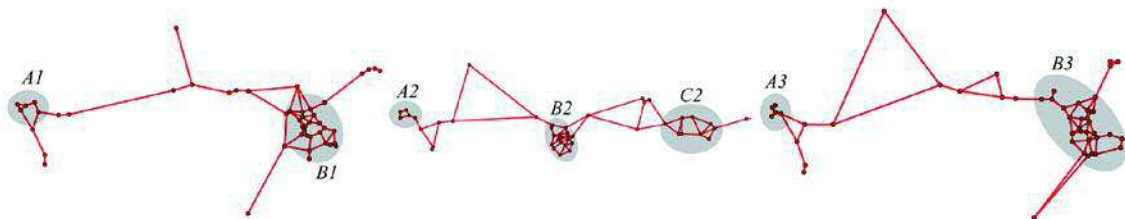
A Kernel density



B Ripley function



C Gabriels graphs



**Figure 4.** Representation of A) the Kernel density, B) the graphic of the Ripley's function and C) the Gabriel graphs for the three analysed methods. In the kernel graphics, colour legend indicates the degree of density of species (maximum density in red, minimum density in dark blue). In the graphic of the Ripley's function, the two red curves represent the 95% confidence envelopes of the function; and the black is the obtained curve. In the Gabriel graphs, grey shading circles represent the main species packings,  $n=48$ .

The Clark-Evans approach also denoted a clustered distribution of species in morphospace 1 ( $Z=-3.6158$ ,  $P<0.05$ ,  $r=0.7$ ), morphospace 2 ( $Z=-3.0809$ ,  $P<0.05$ ,  $r=0.743$ ) and morphospace 3 ( $Z=-3.6312$ ,  $P<0.05$ ,  $r=0.6996$ ). The Ripley's function values were higher than those corresponding to spatial randomness, thus confirming the presence of clusters in the three morphospaces (Fig. 4B). The Gabriel graphs displayed two similar clusters of species in the three morphospaces (Fig. 4C). First, a limited number of flatfishes formed  $A_i$  clusters. Second, a noticeable packing of similar species (sparids, serranids, pomacentrids, haemulids, mullids and scorpaenids) configured the  $B_i$  clusters, showing a lesser distance and triangulation of points in morphospace 2 than in the remaining morphospaces. Finally, in morphospace 2, a third species packing was observed ( $C_2$  cluster), formed exclusively by species similar to  $B_i$  clusters but with two dorsal fins, whereas morphospace 3 was similar to morphospace 1 and showed no  $C$  clusters.

#### 4.4 Discussion

Landmark-based methods considering only overall body shape have often been used in studies analysing intraspecific or interspecific differences between taxonomically close species (Loy et al., 1999; Valentin et al., 2002; Costa and Cataudella, 2007), showing that such variability is related to their ecological features (Loy et al., 2001; Rüber and Adams, 2001). In local assemblages, the ecological relationships between species play a strong role in determining the morphological adaptations to many life habits (Clabaut et al., 2007; Ricklefs, 2012), suggesting that there is a strong link between ecology and morphology of fish species (Douglas and Matthews, 1992; Willis et al., 2005; Cooper and Westneat, 2009). Feeding preference is the main ecological factor influencing morphospace structuring, differentiating strict herbivores with small heads, omnivores with taller bodies and shorter caudal peduncles and predators with longer bodies adapted to swimming and larger heads and mouths (Cavalcanti et al., 1999; Kassam et al., 2003; Costa and Cataudella, 2007). Nevertheless, body shape is also affected by habitat: rounded-shaped species are adapted to low activity living in generalist habits, whereas elongated-shaped species swim in the water column (Clabaut et al., 2007; Farré et al., 2015). In fact, fishes with flattened or elongated shapes (eels or

flatfishes) are usually located at the periphery of morphospaces (Friedman, 2010; Tuset et al., 2014; present study).

Although more studies should be performed on other fish communities to confirm these statements at more general level, our results indicate that the use of specific landmarks and semilandmarks related to fins and external sensorial organs helps to clarify the differentiation between species because it provides more detailed and accurate morphological information on the species, which translates into differences in the species distribution within the morphospace structure. However, due to the lack of similar comparative studies of different landmarks schemes, it is necessary to test this methodology in communities with different ecological characteristics to confirm the results of the present study. The most noticeable difference between morphospace 1 and 3 was related to fishes with special morphological structures. The isolated location of *Trigla lucerna* in morphospace 3 reinforces this assertion, as it presents an extremely extended pectoral fin with the first three rays transformed involved in locomotion, substrate lodging or feeding strategies (Jamon et al., 2007). Moreover, fishes with presence of sensorial chin barbels used for stimuli reception and finding of food items (Lombarte and Aguirre, 1997; Hutchings and Griffiths, 2005), such as *Mullus* spp. and *Umbrina* spp., were also slightly separated from the main group of Perciformes in relation to the morphospace. It is important to highlight the use of fin shape and sensorial organs (morphospace 3) for analysing the morphological structure of fish assemblages because these anatomical characteristics are common for many species. For example, needlefishes use their characteristic compact set of fins to alter the flows created by body movement, a defining feature of their locomotion strategy (Liao, 2002); in burrowing eels, the caudal fin is intimately related to their digging ability (De Schepper et al., 2007), whereas in pelagic eels the presence of a continuous fin resulting from the confluence of dorsal, caudal and anal fins improves swimming performance (Tytell and Lauder, 2004); or flying fishes, which possess extremely long pectoral fins that enable gliding flights out of the water after self-propelled jumps to escape predators or to save locomotion costs (Davenport, 1994). In addition, benthic species in contact with the substratum, such as frogfishes or many scorpionfishes, use synchronised movements of pectoral and pelvic fins to move over the substrate or to maintain static positions in defensive, alert or rest behaviours (Gosline, 1994; Yamanoue et al., 2010), or transformations of pelvic fins into suction discs that help to the adherence on the

substrate appear in gobies (Schoenfuss and Blob, 2003). The reduction or modification of pelvic fins used during aggressive or courtships behaviours are also common in balistoids (Yamanoue et al., 2010), as well as the occurrence of spines in pelvic, dorsal and median fins for defence and propulsion purposes in gasterosteids and scorpionfishes (Gosline, 1994). By contrast, the identification of species by including the position of fins (morphospace 2) clearly influenced the morphospace distribution. In this case, although many species were located in a similar position in morphospaces 1 and 3, the variation in the number of dorsal fins conditioned the results. As this biological character is very relevant in taxonomy, phylogeny and evolution (Nelson, 2006), it suggests that species distribution within morphospace 2 is not sufficient for a full ecological understanding.

The combination of different methods is the best approach for analyzing species occupation within morphospace (Perry et al., 2006; Van Bocxlaer and Schultheiß, 2010). Depending on the aims of the study, all of the methods have advantages and drawbacks, as discussed above, so an ensemble of different analyses is necessary to corroborate and complement outcomes and obtain a better understanding of the point patterns, thus avoiding the bias that may result from a specific chosen analysis (Wiegand and Moloney, 2004; Perry et al., 2006). Although numerical methods are needed to test the statistical significance of outcomes, they are restricted to interactions between points at short scales and can omit relationships at larger distances. Graphical methods are recommended at larger scales because they provide a better and more intuitive visual interpretation of morphospace shape (e.g., Perry et al., 2006; Werdelin and Lewis, 2013; Tuset et al., 2014). In this study, the indices of morphological disparity did not provide enough information regarding the spatial distribution of species within morphospaces. The variance of the different axes changes among morphospaces, but their cumulative contribution can express similar total variability even if the morphospaces possess different configurations, as shown in our results (Foote, 1997; Ciampaglio et al., 2001; Korn et al., 2013). Although calculating the areas occupied by points helps to analyse the distribution pattern of points, the measure does not permit the establishment of the specific location and occupation of these points within the morphospace. Therefore, these measurements fail in terms of estimating the distribution and occupation of morphospaces; it is better to use quadrant and nearest-



neighbour analyses for these purposes (Shen et al., 2008; Ricklefs, 2012; Tuset et al., 2014).

Kernel density graphics represented a visual image of species distribution within morphospace and species density in a fixed area, which was a useful tool for delimiting the range of species and quantifying their occurrence probability in space (Silverman, 1986; Worton, 1989; Fortin et al., 2005). The results showed slight differences between morphospaces, especially between 1 and 3, focusing mainly on the area shape of higher density (red colour in Fig. 4a). However, in morphospace 3, this area was arranged in a more elongated and straightened way than in morphospaces 1 and 2 due to species disaggregation favoured by the presence of landmarks defining the presence of chin barbels and a better differentiation of swimming species. However, this graphical representation is unable to establish the connections between close species and organize them in local clusters (Shen et al., 2008; Werdelin and Lewis, 2013). The variance-to-mean ratio and Ripley's function determined a clustered distribution in the three morphospaces, but it cannot display the location of local clusters, thus limiting the perception of morphospace structure. In this context, the Gabriel graph allowed to identify the packing species based on the distances and connections between them. The Gabriel method likely provides a more complex graphical representation to be considered as an extension of the Euclidean minimum spanning tree, the relative neighbourhood graph, and the nearest-neighbour graph (Gabriel and Sokal, 1969). Evidently, the selection of the clusters of species within the graph is partially subjective, but ecologically it is very interesting because graphs are able to describe important ecological characteristics of communities, such as structural complexity or relationships between species (Strogatz, 2001; Dale and Fortin, 2010), where species that are close together interact in the same environment and exploit similar resources. Thus, the packing of species can provide useful information about the internal dynamics within communities. Hence, we propose that natural directions for future research should include this topic in order to test the usefulness and abilities of this graphical method in the study structural complexity of communities.

In conclusion, the results of this study suggest that depending on the purposes, several methods of landmark selection are able to display the distribution of species within morphospace (Adams et al., 2013). However, including the maximum of anatomical traits of species, especially those with special morphological adaptations,

such as Stomiiformes, Lophiiformes, Ipnopidae (Aulopiformes), etc. (Tuset et al., 2014; Farré et al., 2015), can be important in order to better differentiate the species and characterise them ecologically, as our results demonstrate. Therefore, in analysis of fish communities where species of special morphologies can be present, the method considering fin shape and sensorial organs in the landmark configuration provides an appropriate and accurate description of the spatial occupancy of species that helps to better understand the structural complexity and ecological processes of fish assemblages. Moreover, although graphical methods are in general more intuitive and interpretable, a combination of different analytical methods, including numerical and graphical, is the better and more complete option to assess the internal occupation of morphospaces.

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# 5

## **Geometric morphology as an alternative for measuring the diversity of fish assemblages**



**Geometric morphology as an alternative for measuring  
the diversity of fish assemblages**

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### **Abstract**

Biological diversity can be measured using ecological, taxonomic and functional indices, although numerous studies have concluded that organism morphology can be also a source for computing diversity indices. In the present study, we characterised fish morphology using geometric morphology, which included body shape landmarks as well as the morphology of fins, and we computed the correlation among ecological, taxonomic, functional and morphological indices (including a new index defined here called “morphological richness”). Morphological indices were calculated both from abundance data and presence/absence data. To carry out this study, thirteen fish assemblages of two different areas of the Catalan coast (north-western Mediterranean) were analysed. The data was sampled by commercial fishing vessels using trammel nets. The results clearly indicated that each type of morphological index is related to one dimension of the biodiversity space. Furthermore, we demonstrated that presence/absence data provided the similar results as abundance data when using morphological indices, opening the possibility to analyse the evolution of fish assemblages over time from species checklists collected in experimental surveys from the late XIX century to the present.

**Keywords:** Biodiversity; Morphological diversity; Geometrical morphology; Fish assemblages.

### Resum

La diversitat biològica es pot mesurar mitjançant nombrosos índexs, com ara de caràcter ecològic, taxonòmic o funcional. No obstant, varis estudis han conclòs que els caràcters morfològics dels organismes també poden ser utilitzats com a font per a la mesura d'índexs de diversitat. En el present estudi, es va caracteritzar la morfologia d'espècies de peixos utilitzant mètodes de morfometria geomètrica. Es van seleccionar punts homòlegs (*landmarks*) per definir la forma general del cos així com també la morfologia de les aletes. Les diferents mesures obtingudes a partir d'aquests anàlisis (incloent un nou índex definit per primer cop en aquest estudi, anomenat "riquesa morfològica") es van comparar amb altres índexs ecològics, taxonòmics i funcionals, i també es van calcular les correlacions entre tots els índexs computats. Els índexs morfològics van ser calculats per duplicat, emprant dades d'abundància de les espècies així com dades de presència/absència. Per realitzar l'estudi, es van analitzar tretze comunitats de peixos provinents de diferents zones de la costa catalana (nord-est del mar Mediterrani). El mostreig va ser realitzat per vaixells de pesca comercial mitjançant arts de tresmall. Els resultats van indicar que cadascun dels diferents tipus d'índexs morfològics calculats estan relacionats amb una dimensió de la biodiversitat diferent. Addicionalment, l'estudi va demostrar que els índexs morfològics calculats amb dades qualitatives (presència/absència) proporcionen resultats semblants als obtinguts quan els mateixos índexs es calculen amb dades quantitatives (abundància), obrint la possibilitat d'analitzar dades històriques obtingudes en mostrejos experimentals al llarg del temps fins a la actualitat disposant únicament del llistat d'espècies presents, i així poder avaluar la evolució històrica de la diversitat en comunitats de peixos.

### 5.1 Introduction

A recent study organized biodiversity in a three-dimensional space formed by one dimension of structural complexity, and two different mixtures of taxonomic and functional diversity (Lyashevskaya and Farnsworth, 2012). Functional diversity is considered as the main key in biodiversity studies because it explains the roles that organisms play within ecosystems. Measuring functional diversity is usually approached by pooling functional traits which can be any biological feature that affects species (i.e. prey capture efficiency, diet, foraging methods, size, mode of locomotion, reproduction or habitat) or which are a combination of morphological measures with ecological meaning and functional role (Mouillot et al., 2005; Somerfield et al., 2008; Villéger et al., 2010; Albouy et al., 2011).

In the study of fish assemblages, the most used morpho-functional characters are mainly focused on food acquisition and locomotion (Webb, 1984; Fulton et al., 2001; Dumay et al., 2004; Bellwood et al., 2006; Villéger et al., 2011; Albouy et al., 2011). However, there are some other morphological characteristics that are not usually considered and give relevant information about fish adaptations to environment. For example, tripodfishes (*Bathypterois* spp.) have elongate pelvic and caudal fin rays that hold the body above the sediment, resulting in so-called 'bathypterioform' movement, which describes the functional role of the fins associated with landing (Davis and Chakrabarty, 2011); in some scorpaeniform fishes the paired fins (pelvic and pectoral fins) have other functions associated with a life style on the sea, such as "walking", perching or probing for food items (Gosline, 1994); suckerfishes (Echinidae) are commensals of sharks and rays who attach to their hosts by means of a powerful suction disc that is a transformation of the dorsal fin (Muss and Nielsen, 1999); some goatfishes (Mullidae), haddock or cods (Gadidae) have sensorial barbels on the chin, which allows them to discriminate and locate sources of sensory stimuli (food sources or predators) (Lombarte et al., 2003); ophidiids have pelvic fins modified as sensory barbels (Helfman et al., 1997); and in Tetraodontiforms four different locomotion patterns are described, related to differentiated position and shape of dorsal, anal and pectoral fins (Colgate and Lynch, 2004). In addition, the eye diameter is a key factor in food acquisition, although in complex habitats (such as coral reefs) or with high



turbidity the visual field decreases favouring the development of other sensorial organs (Lombarte and Aguirre, 1997; Willis et al., 2005).

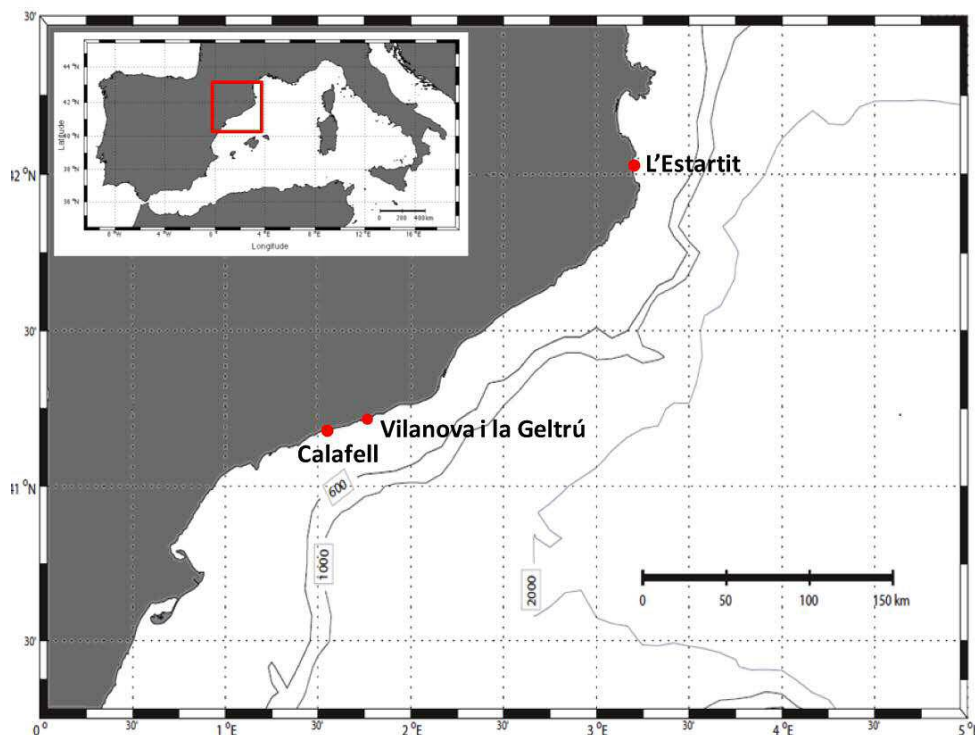
The shape and position of morphological characters can also be described using geometric morphometry based on landmarks analyses (Bookstein, 1991; Rohlf and Marcus, 1993). Initially, this was used to test for significant correlations between body shape and ecological traits (Langerhans et al., 2004; Clabaut et al., 2007; Lombarte et al., 2010). Later, this technique was used to measure the variation of biodiversity in time or space (Neige, 2003; McClain et al., 2004). In addition, the spatial distribution of fishes, called morphospace, allows discerning the structural complexity of communities (Willis et al., 2005). Although there are numerous metrics in the literature, morphological disparity is a measure of the amount of morphological variation in a group of samples, taking into account the volume of the hyperdimensional morphospace occupied, the relative distances between samples, and the number of samples (Clabaut et al., 2007); and it is often used for quantifying the species distribution within morphospace (Foote, 1993; Ciampaglio et al., 2001). Thus, morphological disparity is an invaluable source of information enriching the knowledge of dynamic processes of ecological systems (Roy et al., 2001; McClain et al., 2004; Gerber et al., 2008). Even more, the organism shape is strongly related to taxonomy, and the taxonomy can be used as a proxy for the phylogenetic affiliations (Zelditch et al., 2003; Price et al., 2011). In fishes, the position and number of body fins is a taxonomical criterion (Nelson, 2006), and its identification with landmarks is very easy. Thus, Recasens et al. (2006) developed a geometric morphological index for fishes including the general characterization of body shape, head, eye, mouth and position and length of fins to provide a comprehensive picture of the structure of fish assemblages, including ecological and evolutionary processes. The goal was to create an index easily acquired providing information on diversity and structure fish assemblages at the same time.

Herein, i) we establish a new geometric morphological index called morphological richness (*MR*), ii) we compare morphological richness and other geometric morphological indices among them, and iii) we evaluate the usefulness of the geometric morphological indices in studies of fish assemblages analysing their correlation to ecological, taxonomical and functional diversity indices.

### 5.2 Materials and methods

#### 5.2.1 Sampling

This study used data from shallow-water fish assemblages off the Catalan coast, western Mediterranean Sea (Fig. 1), collected with commercial fishing gear during different research projects. A total of 51 samples were obtained by small-scale vessels using trammel nets between February 2000-April 2001, December 2002-September 2003, and May 2009-April 2010 in the central study area (Vilanova i la Geltrú-Calafell). Additionally, 35 fishing operations by seven trammel netters in the northern study area (L'Estartit) were analysed between March and December 2003-2005. The characteristics of trammel net fisheries in the study areas are described elsewhere (Recasens et al., 2006; Stelzenmüller et al., 2009; Maynou et al., 2011; Martín et al., 2012).



**Figure 1.** Geographical localization of sampling.

For each fishing operation the entire fish catch (commercial plus discarded fraction) was retained. Species were identified (Mercader et al., 2001) and placed within a

taxonomic hierarchy according to Nelson's Fishes of the World (Nelson, 2006). Specimens were photographed using standardized body position (Recasens et al., 2006).

In each locality, the habitat of each fishing operation was classified according to the characteristics of the sea bottom. Seven types were established in the north of the Catalan coast: a) Sandy, <10 m depth; b) Sandy, 10-20 m; c) Sandy-Rocky, >20 m; d) Sandy-Muddy, 26-50 m; e) Muddy, 30-33 m; f) Rocky-Sandy, 10-22 m; g) Gravel-Sandy, 25-32 m. Six types of bottom were recognized in the central Catalan coast: a) Sandy, <10 m of depth; b) Sandy, >20 m; c) Sandy-Rocky, 15-19 m; d) Rocky-Sandy, 15-19 m; e) Artificial reef-Sandy, 15-19 m; f) Rocky-Seagrasses, 10-14 m.

### 5.2.2 Structural, taxonomical and functional indices

Several structural or ecological indices were calculated in order to characterize the species assemblages in each habitat type for the north and central locations: number of species or species richness ( $S$ ), Margalef's richness index ( $d$ ) (Margalef, 1958), Shannon's diversity index ( $H'$ ) (Shannon and Weaver, 1949), Simpson index ( $S'$ ) (Simpson, 1949), and Pielou's evenness index ( $J'$ ) (Pielou, 1975). Four taxonomic diversity indices were also considered (Warwick and Clarke, 1995; Clarke and Warwick, 1998, 2001): taxonomic diversity  $DELTA$  ( $\Delta$ ), taxonomic distinctness  $DSTR$  ( $\Delta^*$ ), average taxonomic distinctness  $AvTD$  ( $\Delta^+$ ) and variation in taxonomic distinctness  $VarTD$  ( $\Delta^+$ ).

Functional diversity ( $FD$ ) was calculated using the following functional traits (Table 1) (Colgate and Lynch, 2004; Somerfield et al., 2008; Villéger et al., 2010). It was calculated using the following protocol: i) construction of a species-trait matrix; ii) conversion of species-trait matrix into a distance matrix; iii) clustering distance matrix into a dendrogram using UPGMA; and iv) calculating functional diversity by summing dendrogram branch lengths of community species (Petchey and Gaston, 2006; Pavoine et al., 2009). Since the number of categories assigned to a trait may influence the specific weight of this category in the subsequent analysis (e.g., body shape has up to eight categories, while others have only two), the procedure was offset by including functional variables that had the same or similar weight (trophic level, resilience or growth rate) (Somerfield et al., 2008). Biological data to define these functional traits

## 5. Geometric morphology for measuring biodiversity

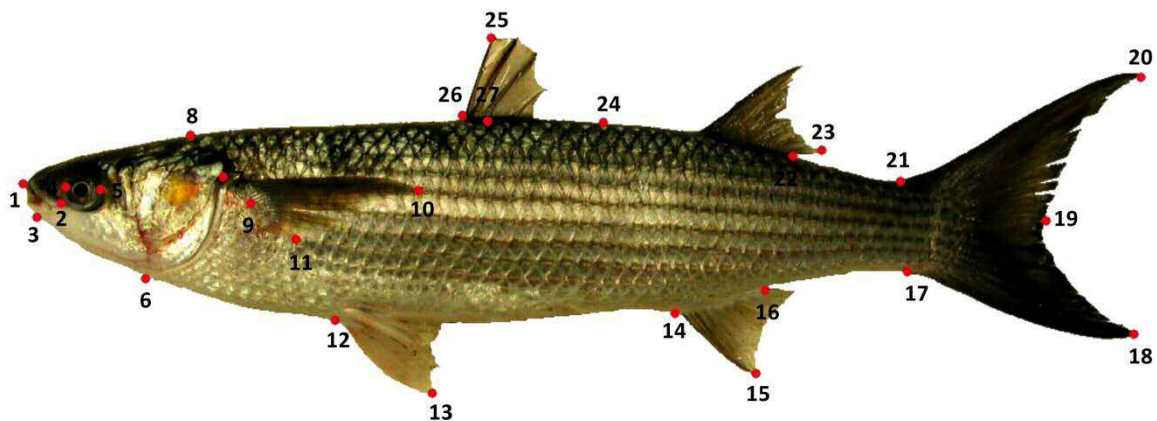
were obtained from published studies and *Fishbase* (Froese and Pauly, 2011).

**Table 1.** Functional traits used to characterize the functional diversity of each fish assemblage (Colgate and Lynch, 2004; Somerfield et al., 2008; Froese and Pauly, 2011).

Traits	Categories	Trait	Categories	
<b>Body shape</b>	Anguilliform	<b>Habitat</b>	Demersal	
	Fusiform		Pelagic	
	Elongated	<b>Environment</b>	Exclusively marine	
	Oblong		Other environments	
	Oval		<b>Life span</b>	Very low (minimum 14 years)
	Symmetrical flatfish			Low (4.5-14 years)
	Asymmetrical flatfish			Medium (1.4-4.5 years)
	High (maximum 1.5 years)			
<b>Special fins</b>	Presence			
	Absence			
<b>Sensorial barbels</b>	Presence	<b>Maximum length</b>	>10 cm	
	Absence		>20 cm	
<b>Burying ability</b>	Yes		>40 cm	
	No		>80 cm	
			<b>Growth rate</b>	>0.1 year <sup>-1</sup>
<b>Motility</b>	Sedentary		>0.2 year <sup>-1</sup>	
	Mobile		>0.3 year <sup>-1</sup>	
			>0.4 year <sup>-1</sup>	
<b>Locomotion</b>	Anguilliform		>0.5 year <sup>-1</sup>	
	Subcarangiform		>0.7 year <sup>-1</sup>	
	Carangiform	<b>Trophic level</b>	<2.5	
	Thunniform		2.6-3.0	
	Amiiform		3.1-3.4	
	Balistiform		3.5-4.0	
	Tetraodontiform		4.1-4.5	
	Bathypteroiform		>4.5	
<b>Spawning period</b>	Short (<3 months)			
	Large (≥ 3 months)			

## 5.2.3 Geometric morphological indices

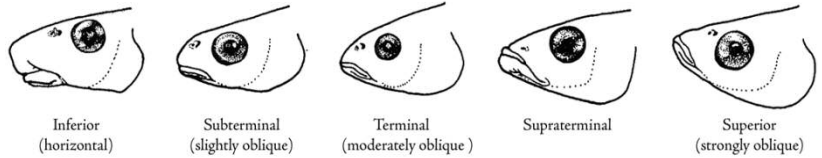
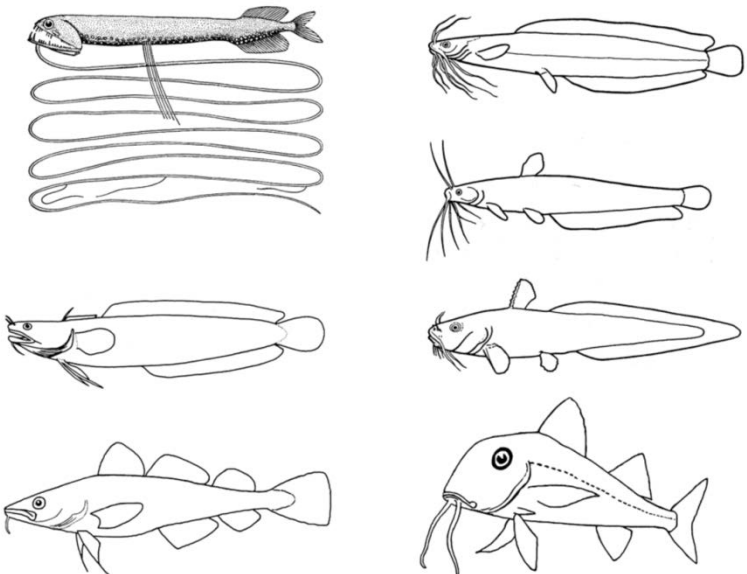
A total of 27 landmarks and semilandmarks (Fig. 2) with anatomical, ecological and taxonomical meaning were used (Recasens et al., 2006; Tables 2 and 3) for a specimen of each species from standardised images of the left side (using tpsDig, 2.16; Rohlf, 2010a). After digitalising the metric maps of each species, they were rotated, scaled (to unit centroid size) and translated using a generalised least-square superimposition procedure (GLS, generalised Procrustes) to remove scale and orientation distortions (using tpsRelw 1.49; Rohlf, 2010b). A thin-plate spline representation was used to fit an interpolated function to an average map (consensus configuration) of the profile shape and derive the uniform (relative warp) components of the shape variation. Changes in shape were visualised using relative warp analysis (Rohlf and Marcus, 1993). The first eight relative warp scores were selected to describe each species as they explained more than 98% of the total morphological variability (Recasens et al., 2006; Lombarte et al., 2012). The morphospace of each fish assemblage was defined using the area inside the convex hull (Cornwell et al., 2006) enclosing all the species among warps 1, 2 and 3.



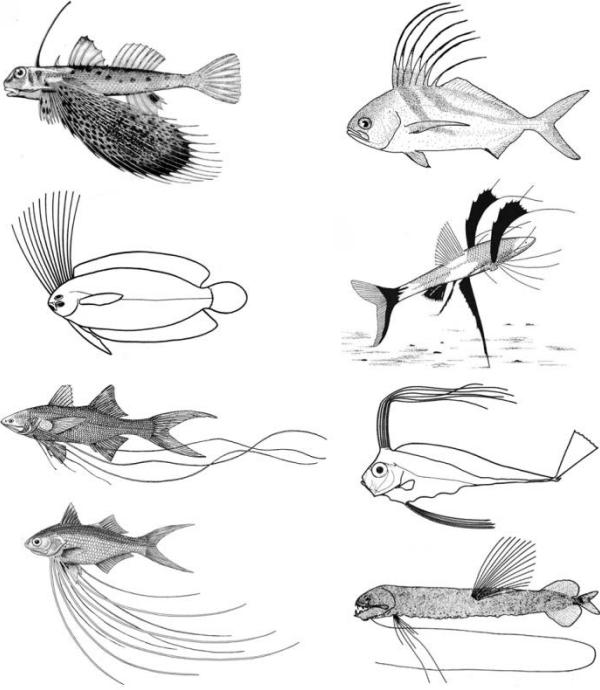
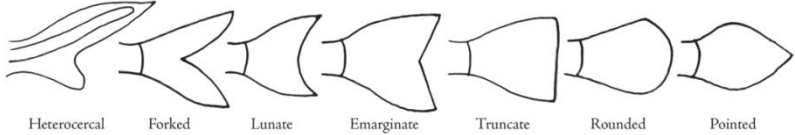
**Figure 2.** Identification of 27 landmarks and semilandmarks used in the geometric morphological analysis.

## 5. Geometric morphology for measuring biodiversity

**Table 2.** List of the 27 landmarks and semilandmarks used for explaining morphology of the body shape.

Points	Morphological meaning	Importance
1-2	Position and relative size of the mouth length respect to head and body size (from Jenkins and Burkhead, 1993)	<i>Ecological meaning:</i> related to food acquisition
 <p style="text-align: center;">           Inferior (horizontal)      Subterminal (slightly oblique)      Terminal (moderately oblique)      Supraterminal      Superior (strongly oblique)         </p>		
3	Differentiates among fishes with or without sensorial barbels on chin, and position and relative size of barbels (from Kasumyan, 2011)	<i>Ecological meaning:</i> extremely diverse, related to mode of life, behaviour and feeding strategies. <i>Taxonomic value</i>
		
4-5	Position and relative size of eye and its position respect to head and body size	<i>Ecological meaning:</i> related to food acquisition and life strategies
6-8	Indicates the relative height and width of head respect to the body size	<i>Ecological meaning:</i> related to food acquisition and life strategies
24	Indicates the presence/absence of one or two dorsal fins	<i>Taxonomic value</i>
27	Defines the point of maximum height of the body shape	<i>Ecological meaning:</i> related to locomotion and life strategies

**Table 3.** List of the 27 landmarks and semilandmarks used for explaining the fish morphology of fins.

Points	Morphological meaning	Importance
9-11	Indicates pectoral fin shape and its relative position (from Kasumyan, 2011)	<i>Ecological meaning:</i> related to swimming or walking over bottom, feeding and defensive strategies. <i>Taxonomic value</i>
		
12-13	Indicates pelvic fin shape and its relative position (see scheme before)	<i>Ecological meaning:</i> related to stability while swimming, crawling, walking over bottom or transformed in a suction cup type structure maintaining position in fast moving current
14-16	Indicates anal fin shape and its relative position (see scheme before)	<i>Ecological meaning:</i> related to stability while swimming, walking over bottom and primary propulsion in some species. <i>Taxonomic value</i>
22-23	Defines where second dorsal fin finishes and its relative position (see scheme before)	<i>Ecological meaning:</i> related to stability while swimming and life strategies. <i>Taxonomic value</i>
25-26	Defines where first dorsal fin starts and its relative position (see scheme before)	<i>Ecological meaning:</i> related to stability while swimming, primary propulsion in some species, large fins as structures for the detection food or attracting preys or transformed in a suction cup type structure maintaining position. <i>Taxonomic value</i>
17-21	Defines shape of peduncle and caudal fin (from Bugas et al., 2009)	<i>Ecological meaning:</i> related to locomotion
		

Relative warps were used to calculate morphological disparity,  $MD = \frac{\sum_j RW_j^2}{(N-1)}$ , where  $RW_j$  are the relative warps of species  $j$  and  $N$  is the total number of species (Zelditch et al., 2003; Antonucci et al., 2009). Furthermore, two indices were obtained with a similar protocol to that used to compute functional diversity (Petchey and Gaston, 2006): i) construction of a species-trait matrix; ii) conversion of species-trait matrix into an Euclidean distance matrix; iii) clustering distance matrix into a dendrogram using UPGMA; and iv) summing dendrogram branch lengths of community species. From these data we calculated the new morphological richness index,  $MR = \sum_j CC$ , where  $CC$  is the cluster coefficient and  $j$  is the species, and the morpho-geometric diversity index,  $EMI = \frac{\sum_j CC}{(N-1)}$ , where  $CC$  is the cluster coefficient,  $j$  is the species and  $N$  is the total number of species (Lombarte et al., 2012). The trees were subject to 1000 nonparametric bootstrap replicates to assess branch support. Finally, each morphological index was calculated from abundance data ( $MD$ ,  $MR$  and  $EMI$ ) and presence/absence data ( $MD2$ ,  $MR2$  and  $EMI2$ ). In the first case, the number of images analysed per species was equivalent to the relative abundance in the samples. The species with abundance equal to or less than 1% were analysed as one image, so as to include the largest possible number of species in the analyses. Independently of analysis type, in the presence/absence case, each species was represented by only one image (Recasens et al., 2006; Lombarte et al., 2012).

We selected two fish assemblages, sandy <10 m (north coast) and rocky-seagrasses (central coast), as example to explain the correlation among the morphological indices and the structure of assemblages. The criteria for the selection of these fish assemblages were based on dissimilarity in the morphological disparity, specific richness and functional diversity (see results) considering the best examples to explain the proposed targets. In addition, morphospaces were graphed to show the position of species using geometric morphological analysis. They were defined using the convex hull enclosing all the species from each fish assemblages (Cornwell et al., 2006).

### 5.2.4 Comparison of indices



## 5.3 Results

### 5.3.1 Meaning of geometric morphological indices

The two selected fish assemblages (sandy <10 m and rocky-seagrasses) showed a high variability in structure, specific composition, specific richness, and dominance. The sandy fish assemblage was composed by 26 species of 16 families, with four species (*Solea solea*, *Sarpa salpa*, *Mugil cephalus* and *Chelon labrosus*) comprising 60% of total catch in number, whilst most species belonged to three families, Sparidae (32%), Soleidae (27%) and Mugilidae (19%). By contrast, rocky-seagrasses fish assemblage was represented by 43 species of 18 families. *Mullus surmuletus*, *Scorpaena notata* and *Pagellus acarne* provided 60.7% of catch, which was dominated by three families, Mullidae (39%), Scorpaenidae (21%) and Sparidae (20%).

These differences in the specific composition of both fish assemblages were showed in the values obtained of geometric morphological indices. The sandy sample showed greater relative variability of taxonomical groups, taking into account the number of species, attaining a higher morphological disparity ( $MD= 0.054$  versus  $0.025$ ) and morpho-geometric diversity ( $EMI= 0.19$  vs  $0.16$ ) (Table 4). Nevertheless, morphological richness attained higher values in rocky-seagrasses sample ( $MR2= 6.98$  vs  $4.75$ ), whose habitat favoured variety of life strategies which was reflected in an increase of the functional diversity ( $FD= 101.80$  vs  $67.50$ ) (Table 4).

## 5. Geometric morphology for measuring biodiversity

**Table 4.** Ecological, taxonomic, morphological and functional indices obtained for the localities considered.  $H'$ , Shannon's diversity index;  $S$ , specific richness;  $S'$ , Simpson index;  $J'$ , Pielou's evenness index;  $\Delta$ , taxonomic distinctness;  $\Delta^+$ , average taxonomic distinctness;  $\Delta^*$ , variation in taxonomic distinctness;  $EMI$  and  $EMI2$ , morphological evenness;  $MD$  and  $MD2$ , morphological disparity;  $MR$  and  $MR2$ , morphological richness;  $FD$ , functional diversity.

Locality	Fish assemblages	Ecological					Taxonomic				Morphological		
		$S$	$d$	$J'$	$H'$	$S'$	$\Delta$	$\Delta^*$	$\Delta^+$	$\Delta^*$	$EMI$	$MD$	$MR$
North	Gravel-Sandy 25-50 m	22	4.15	0.68	2.11	0.81	67.04	82.41	75.11	462.65	0.153	0.026	2.9
	Rocky-Sandy 10-25 m	16	3.66	0.72	2.01	0.79	60.82	77.17	84.17	478.47	0.197	0.038	2.7
	Sandy 10 m*	26	6.33	0.90	2.92	0.94	86.52	91.93	88.23	317.25	0.193	0.054	4.6
	Sandy 10-20 m	21	4.71	0.80	2.44	0.88	71.51	81.54	85.36	413.56	0.192	0.044	3.8
	Sandy-Rocky 20 m	25	5.31	0.64	2.09	0.78	58.48	75.16	85.39	336.39	0.183	0.040	4.2
	Sandy-Muddy 26-50 m	22	5.26	0.87	2.68	0.92	84.77	91.76	89.72	232.50	0.201	0.042	4.2
	Muddy 30-35 m	18	4.06	0.74	2.13	0.82	61.89	75.13	81.21	312.75	0.184	0.035	3.1
Central	Sandy 10 m	30	6.04	0.77	2.62	0.88	69.17	78.57	82.64	330.94	0.178	0.034	5.1
	Sandy-Rocky 15-19 m	40	8.33	0.84	3.11	0.94	73.52	78.45	84.20	324.84	0.162	0.029	4.6
	Sandy 20 m	27	6.79	0.92	3.02	0.95	79.93	83.90	85.26	339.96	0.209	0.045	5.8
	Rocky-Seagrass 10-14 m*	43	6.89	0.63	2.37	0.82	68.37	83.28	83.48	315.85	0.156	0.025	5.4
	Rocky-Sandy 10-25 m	37	5.96	0.82	2.92	0.93	81.91	88.53	87.82	316.86	0.177	0.046	4.4
	Reef-Sandy 15-19 m	48	6.69	0.74	2.78	0.89	78.56	88.30	88.90	322.10	0.163	0.051	4.7

\*, it indicates the fish assemblages selected to as example to graphical illustration of morphospaces, its relation to morphological indices

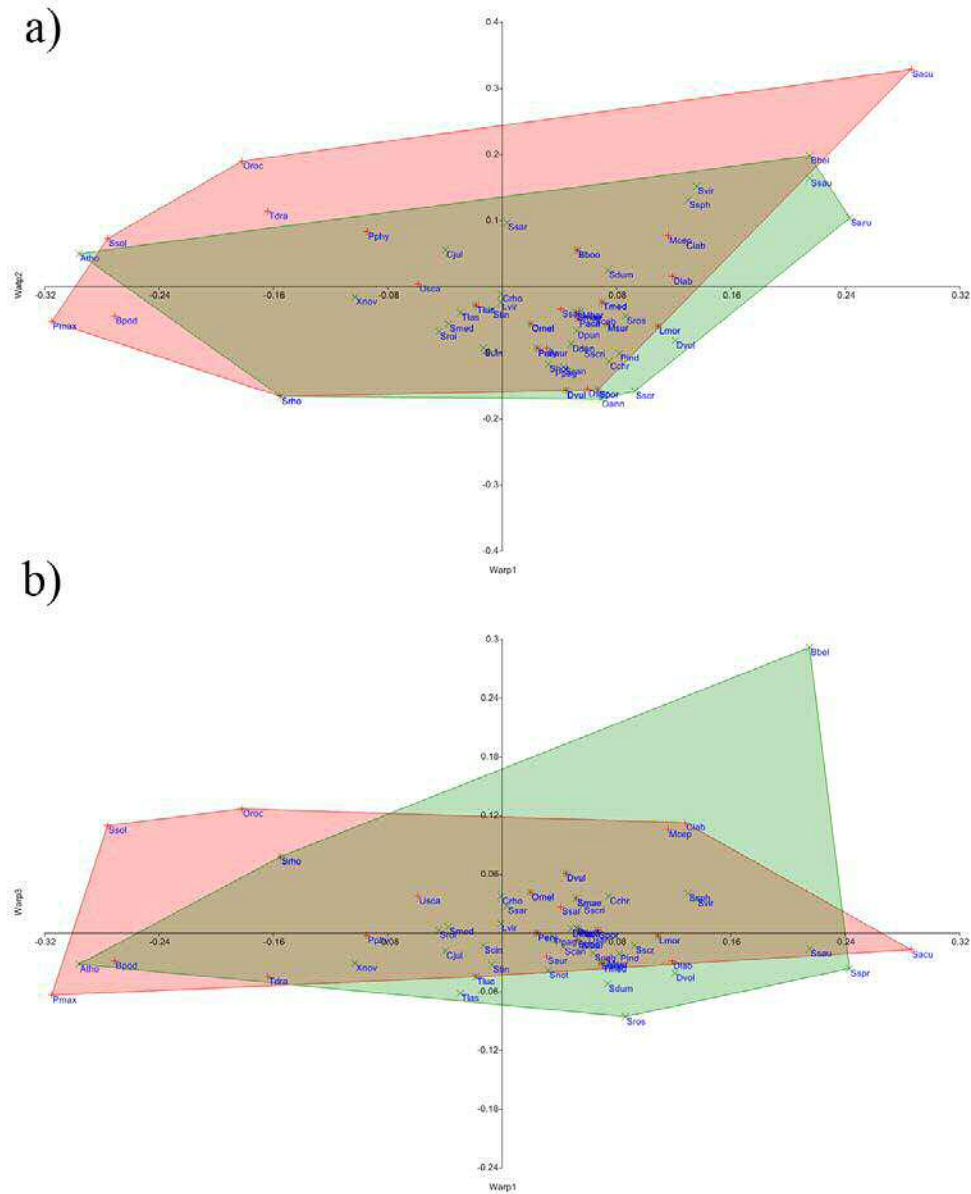
lesser grade some flattened fishes (Pleuronectiforms as *Arnoglossus thori* and *Scophthalmus rhombus*). The extreme shapes largely determined the space occupied for the remaining species, resulting in a high overlap between both communities. Thus, morphological disparity (*MD*) represented better the morphospace to maximize the distance among species; whilst, the higher dispersion of species in the space favoured the increase of morpho-geometric diversity (*EMI*) and the morphological richness (*MR*) is associated to specific richness.

The interpolation of these results to whole data reinforced the idea that each geometric morphological index provides different information because they were not correlated among them. In addition, it is interesting to highlight that similar results were obtained using quantitative or qualitative (presence/absence) data (Table 5).

### 5.3.2 Comparison of diversity indices

The analysis of Spearman's correlation showed a high and positive relationship between richness indices, morphological richness and functional diversity (Table 5). Moreover, Margalef' richness index (*d*) was also correlated to Shannon (*H'*) and Simpson (*S'*) indices although to a lesser degree; whilst specific richness (*S*) was significant correlation to *d* ( $r_s = 0.821$ ) and *H'* ( $r_s = 0.601$ ) indices. The remaining ecological indices were correlated among them and with some taxonomical indices as taxonomic diversity ( $\Delta$ ) and taxonomic distinctness ( $\Delta^*$ ). Similarly to richness index, the Shannon diversity index was linked to morphological richness and functional diversity

(MR2, 0.962) (Table 5).



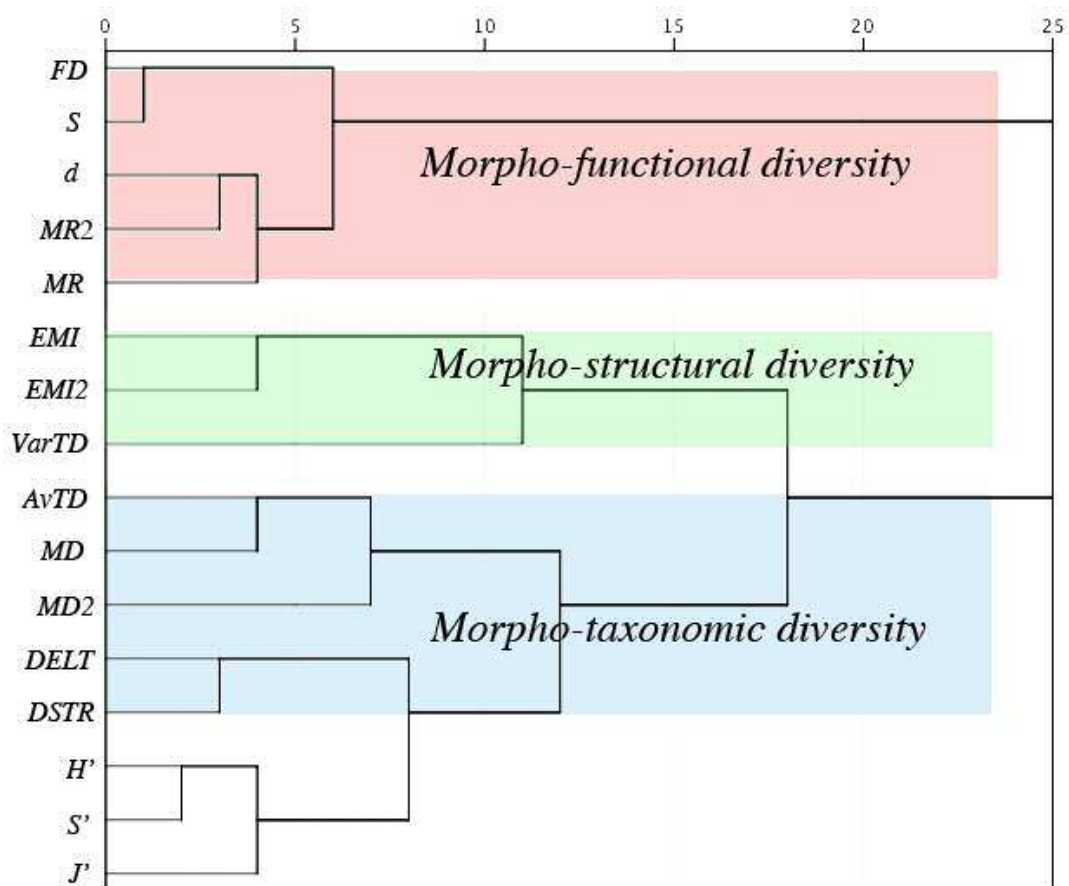
**Figure 3.** Morphospaces of two fish assemblages selected, sand < 10 m (red) and rocky-seagrasses (green), using relative warps1-2 (a) and 1-3 (b). In blue the acronyms of fishes.

**Table 5.** Spearman's correlation among ecological, taxonomic, morphological and functional indices. Shannon's diversity index;  $S$ , specific richness;  $S'$ , Simpson index;  $J'$ , Pielou's evenness index;  $\Delta$ , taxonomic distinctness;  $\Delta_+$ , average taxonomic distinctness;  $\Delta^+$ , variation in taxonomic distinctness;  $EMI$  and  $EMI2$ , morphological disparity;  $MR$  and  $MR2$ , morphological richness;  $FD$ , functional diversity. Bold values indicate variables significantly correlated.

Indices		Ecological					Taxonomic				Morphological			
		$S$	$d$	$J'$	$H'$	$S'$	$\Delta$	$\Delta^*$	$\Delta^+$	$\Delta^+$	$EMI$	$MD$	$MR$	
Ecological	$S$	1												
	$d$	<b>0.821</b>	1											
	$J'$	0.063	0.292	1										
	$H'$	<b>0.601</b>	<b>0.726</b>	<b>0.815</b>	1									
	$S'$	0.448	<b>0.618</b>	<b>0.905</b>	<b>0.974</b>	1								
Taxonomic	$\Delta$	0.385	0.456	<b>0.831</b>	<b>0.842</b>	<b>0.894</b>	1							
	$\Delta^*$	0.393	0.363	0.525	<b>0.572</b>	<b>0.632</b>	<b>0.879</b>	1						
	$\Delta^+$	0.237	0.231	0.473	0.443	0.458	<b>0.665</b>	<b>0.637</b>	1					
	$\Delta^+$	-0.311	-0.258	-0.182	-0.316	-0.302	-0.423	-0.357	-0.324	1				
Morphological	$EMI$	-0.505	-0.275	<b>0.561</b>	0.074	0.254	0.264	0.126	0.379	0.038	1			
	$MD$	0.061	0.055	<b>0.575</b>	0.435	0.505	<b>0.632</b>	<b>0.571</b>	<b>0.797</b>	-0.099	0.522	1		
	$MR$	<b>0.825</b>	<b>0.907</b>	0.327	<b>0.669</b>	<b>0.604</b>	0.473	0.407	0.192	-0.297	-0.088	0.154	1	
	$EMI2$	<b>-0.693</b>	-0.468	0.344	-0.132	0.030	0.083	-0.058	0.297	-0.077	<b>0.839</b>	0.308	-0.41	1
	$MD2$	0.124	0.052	0.425	0.353	0.409	<b>0.573</b>	<b>0.567</b>	<b>0.802</b>	-0.168	0.441	<b>0.953</b>	0.13	1
	$MR2$	<b>0.941</b>	<b>0.934</b>	0.259	<b>0.724</b>	<b>0.615</b>	0.533	0.478	0.385	-0.481	-0.280	0.214	<b>0.88</b>	1
Functional	$FD$	<b>0.991</b>	<b>0.901</b>	0.113	<b>0.630</b>	0.498	0.423	0.401	0.308	-0.346	-0.451	0.115	<b>0.84</b>	1

5.3.3 Morphology as biodiversity metric

The hierarchical clustering and index correlations allowed to differentiate three levels of diversity based on the geometric morphological indices (Fig. 4): a) a morpho-functional diversity group ( $MR$ ,  $MR2$ ,  $d$ ,  $S$  and  $FD$ ), where morphology richness and functional diversity were related together and with specific richness; b) a morpho-structural diversity group ( $EMI$ ,  $EMI2$  and  $VarTD$ ), that measured the morphological and taxonomical distinctness of fishes within assemblages; and c) a morpho-taxonomical diversity group ( $MD$ ,  $MD2$ ,  $AvTD$ ,  $DELTA$ ,  $DSTR$ ), where the morphological disparity depended on taxonomical groups.



**Figure 4.** Hierarchical clustering of biodiversity indices using Ward distance indicating several clusters: 1, morpho-functional diversity (red); 2, morpho-structural diversity (green); 3, morpho-taxonomical diversity (blue).

### 5.4 Discussion

The results from this study confirmed that geometric morphological indices could be a useful tool to measure the diversity of fish assemblages. This agrees with findings from studies on actual fish and gastropods assemblage structure (McClain et al., 2004; Lombarte et al., 2012).

The species richness ( $S$ ) is an inadequate measure missing 88.6% of total biodiversity (Lyashevskaya and Fransworth, 2012), although it is, by far, the most common measure of biodiversity used by scientists, conservationists, and policy makers (Magurran, 1988; Gray, 2000, Wilsey, 2005; Flynn et al., 2009). Most studies reveal a clear relationship between specific richness and functional diversity ( $FD$ ) independently of the method used for classifying species of functional groups (Micheli and Halpern, 2005; Stelzenmüller et al., 2009; Pease et al., 2012; present study). Nevertheless, functional diversity is the key to understand the structure of communities being its conservation vital for the maintenance of species diversity (Lyashevskaya and Fransworth, 2012). The high species diversity is frequently associated to a fine-scale niche partitioning of resource specialists, where each species occupy a part of the ecological space available (Wainwright and Richard, 1995; Ricklefs, 2010). In fact, species richness may not be a good proxy for functional diversity because functionally unique species may be lost more quickly than functionally redundant species and, therefore, functional diversity loss does not always parallel species richness loss (Halpern and Floeter 2008; Flynn et al., 2009). Morphological richness is a relevant variable quantifying variation of shapes and it is not necessarily linked to species richness. For example, the sandy (10 m) fish assemblages of north presented similar specific richness and functional diversity that sandy (20 m) sample of the central region (Table 4). The morphological disparity ( $MD$ ) was higher in the north because the number of taxonomical groups was higher and more extreme; however the morphological richness ( $MR$ ) was higher in the central sample because the species are more dissimilar including pelagic, benthopelagic and benthic species. None of the ecological diversity indices measured such variability except the morphological richness index. Therefore, this index does not infer the role of ecological mechanism in the diversification of evolutionary lineages as occurs in studies of ecomorphology traits (Winemiller, 1991;

Motta et al., 1995a; Fulton et al., 2001; Wainwright et al., 2002; Wagner et al., 2009), but it is useful to compare the diversity among fish assemblages.

The specific richness ( $S$ ), or morphological richness ( $MR$ ), is not always linked to variations in the morphospace as consequence of an increment of the taxonomic diversity (Campbell et al., 2011) or extreme shapes (Heino et al., 2005; present study). By contrast, the morphological disparity ( $MD$ ) is a diversity metric providing an invaluable source of information complementing taxonomic approaches (McClain et al., 2004; Gerber et al., 2008; present study). If the number of species is increased next to morphospace centroid, then morphological disparity decrease; whilst if the species tend to be preferentially added to the margins of morphospace, then morphological disparity and morphospace occupied could increase (Roy and Foote, 1997; Neige, 2003). That is clearly illustrated in the two fish assemblages used as example in our study. The morphological disparity ( $MD$ ), morpho-geometric index ( $EMI$ ) and taxonomic diversity ( $\Delta$ ) were higher in sandy than rocky-seagrasses; however the richness ( $S$ ), functional diversity ( $FD$ ) and morphological richness ( $MR$ ) were lower. In both cases, three families attained around 80% of abundance, but they corresponded to three different orders (Mugilliforms, Perciforms and Pleuronectiforms) in sandy sample instead one order (Perciforms) in the rocky-seagrasses assemblage. Morphological disparity increases because species have different life strategies and also represents distantly related lineages; by contrast, the functional redundancy decreases because there are less specialist species which are more flexible ecologically to avoid competition (Schoener, 1974; Roy et al., 2001).

Several studies have demonstrated that changes within a community, resulting from natural or anthropogenic perturbations, can be measured using morphological and functional traits (Ernst et al., 2006; Mason et al., 2007; Olden et al., 2008; Flynn et al., 2009; Villéger et al., 2010). Lombarte et al. (2012) showed that morpho-geometric diversity ( $EMI$ ) provided excellent results to explain the structural changes occurring in two South African estuaries fish assemblages, being more sensitive to diversity changes than Shannon ( $H'$ ) and taxonomic indices. The morpho-geometric diversity estimates how many clusters of shapes are present in the morphospace, and this index increases when the species are distributed heterogeneously and the number of clusters is high. That is the reason why this index is the most related to structural complexity of fish assemblages.



In conclusion, the geometric morphological indices are useful tools for comparing the diversity among fish assemblages when ecological information is absent or scarce, which is very common: by studying the variation in species shapes we can gain understanding on the function of these species, even if complete information on habitat structure is lacking. In addition, the morphological indices based on abundance and presence/absence provided similar results and were strongly correlated. This would open the possibility to analyse the evolution of fish assemblages over time simply from landmark analysis from species in historical checklists collected in experimental surveys from the late XIX century to the present, facilitating the analysis of long-term trends in fish diversity changes.

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## **Section 2**

# **Applicative Part**



# 6

## **A comparative study of morphospace occupation of mesopelagic fish assemblages from the Canary Islands (North-eastern Atlantic)**



**A comparative study of morphospace occupation of mesopelagic fish assemblages from the Canary Islands (North-eastern Atlantic)**

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See the original publication in the Appendix 2 section

### **Abstract**

The morphology of fishes plays a very important role in the ecosystem biodiversity to show the different evolutionary strategies. The morphological variations among species can be graphically represented in a morphospace and analysed using different methods. In this study we used different assemblages of mesopelagic fishes living in the Canary Islands (North-eastern Atlantic) to compare two methods: convex hull and patterning. The results demonstrated that the patterning of morphospace allowed understanding better the specific ecological strategies and structure of fish assemblages. By contrast, the convex hull is focused on a reduced number of species with a high level of morphological diversity which is located in the periphery of morphospace. The study demonstrates that patterning analysis is a better tool for comparing these assemblages than convex hull, and it highlights the relevance of the distribution of points within the morphospace for characterizing fish assemblages.

**Keywords:** Morphology; Patterning; Convex hull; Biodiversity; Fishes.

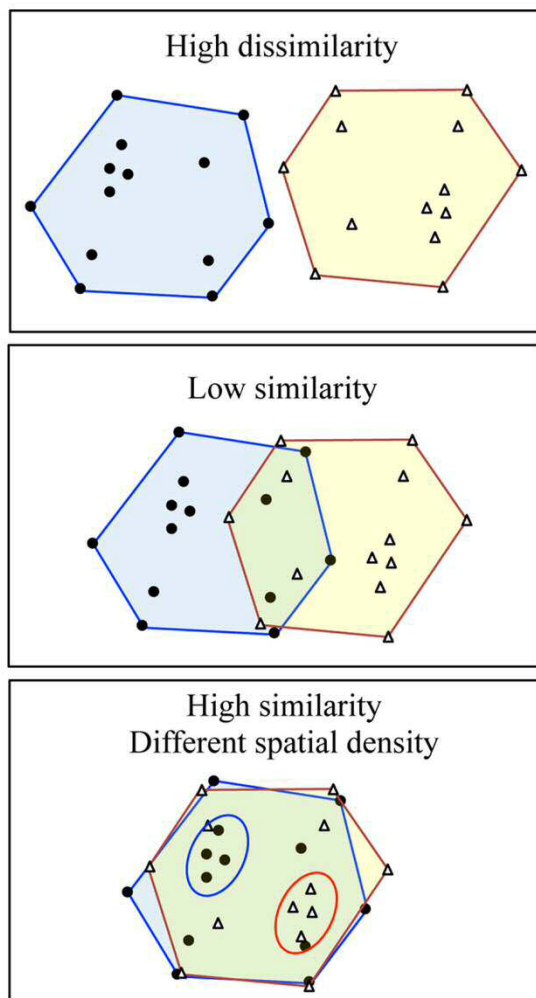


### Resum

La morfologia dels peixos desenvolupa un paper molt important en la biodiversitat dels ecosistemes marins, ja que permet percebre les diferents estratègies evolutives que hi coexisteixen. La variabilitat morfològica entre espècies que coexisteixen pot ser representada gràficament en un morfoespai, i al mateix temps analitzada mitjançant diferents mètodes. En el present estudi, es van analitzar els morfoespais de diferents comunitats de peixos mesopelàgics provinents de les Illes Canàries (nord-est de l'oceà Atlàntic) mitjançant dos mètodes: el "convex hull" i el "patterning". Els resultats van demostrar que l'aplicació de tècnica del "patterning" en el morfoespai ajuda a entendre millor les estratègies ecològiques de les espècies, i per tant també la estructura de les comunitats de peixos. En canvi, la tècnica del "convex hull" únicament ressalta la presència d'un nombre reduït de espècies, les que presenten un nivell més alt de variabilitat morfològica, i que es localitzen en la perifèria del morfoespai. Per tant, l'estudi demostra que l'anàlisi de "patterning" representa una eina més apropiada a l'hora de comparar la estructura de comunitats de peixos que la tècnica de "convex hull", ja que destaca la rellevància i importància de la distribució de punts dins el morfoespai a l'hora de caracteritzar la estructura i organització interna de les comunitats de peixos.

### 6.1 Introduction

Species richness is the most common measure of biodiversity used by scientists, conservationists and policy makers (Gotelli and Colwell, 2001; Drew et al., 2012). Nevertheless, the morphology of organisms has been also used as alternative (Foote, 1997; McClain et al., 2004; Shen et al., 2008; Pierce et al., 2009; Goatley et al., 2010; Villéger et al., 2011). Theoretical morphology is a scientific discipline arising from the early monographs of the 20th century on the ‘form, shape, and function’ of animal morphologies (Tyzka, 2006). Distance measurements or landmark-based morphometric methods are common tools for assessing the degree of change in shape, although the



morphological geometry is most powerful for describing different visual patterns (Bookstein, 1991; Rohlf and Marcus, 1993; Rohlf, 2001). The morphological variations among species are plotted from data matrices into a multidimensional space, called morphospace, where space occupying is used to determine the structural complexity of the system. Although there are a great variety of indices and methods, the disparity index (the spread or spacing of forms in a morphological space) and the convex hull (area or volume enclosing all the species from this assemblage) are mostly used (e.g., Foote, 1997; Roy and Foote, 1997; McClain et al., 2004; Villéger et al., 2011). However, it is also essential to take into account the distribution of a data set in the space (Fig. 1), also called patterning. Recently, morphological studies have used the quadrant analysis as an approach to

**Figure 1.** Similarity between theoretical spaces showing spatial distribution variation in the set data (coloured circles).

describe this patterning (Shen et al., 2008; Goatley et al., 2010; Ricklefs, 2012; Werdelin and Lewis, 2013).

In fishes, body shape is a multitasking, single factor at a lower level contributing to multiple traits at a higher level such as swimming, searching for food, striking and capturing prey, evading predators, migration, courtship dances, defending territories and spawning (see Walker, 2010). Fish fins are not included in morphological geometry since they are not rigid structures and including them in analyses would lead to bias. Admitting this reasoning, it is also true that in some species, fins and other sensorial organs (“singular structures”) are also key factors in behaviours (Colgate and Lynch, 2004; Yamamoue et al., 2010). The elongated shape of the pelvic and caudal fin rays help to hold the body above the sediment (Davis and Chakrabarty, 2011), pelvic and pectoral fins can be used such as “walking”, perching or probing for food items (Gosline, 1994), the transformation of the dorsal fin into a powerful suction disc allows a commensal relationship between organisms (Muss and Nielsen, 1999), sensorial chin barbells favour the finding of food (Lombarte and Aguirre, 1997); and transformations of the dorsal spine serve as decoy to capture preys (Shimazaki and Nakaya, 2004). The usefulness of analysing the morphological traits of species is based on the premise that these traits can be used to infer ecological strategies (Ricklefs, 1990; Lavin and McPhail, 1985; Kassam et al., 2003), thus the lack of information about special fins and sensorial organs also bias the morphological studies. Although many researchers question their use, fins are applied with successful in ecological (Recasens et al. 2006; Lombarte et al. 2012) and biodiversity studies (Farré et al., 2013).

The Canarian archipelago (North-eastern Central Atlantic) is a group of oceanic islands of volcanic origin having a narrow shelf and a steep slope. These special topographic conditions around such islands intensify the interactions among coastal, oceanic, benthic, and benthopelagic organisms (Uiblein and Bordes, 1999). This phenomenon is especially highlighted in diel migrations of mesopelagic fishes (Wienerriither et al., 2009). In this context, the main goal of this study was to compare the changes in the biodiversity of mesopelagic assemblages of the Canary Islands from the morphospace occupation using two graphical methods, convex hull and patterning. Our initial hypothesis is that mesopelagic fishes with singular structures (called “non-typical shape” versus “typical shape”) are located in the morphospace periphery indicating what species provide a major morphological diversity. Likely, they affect the

estimation of convex hull, but only the patterning help us to explain better the ecosystem structure.

### 6.2 Materials and Methods

#### 6.2.1 Fish data

The mesopelagic fish database from the Canary Institute of Marine Science of Government of the Canary Islands was used to carry out the study. The data were constructed based on the presence/absence of each species in the fish assemblages studied (see Table S1 in Supplementary Material). Data were collected during two pelagic trawling surveys with the research vessel B/E 'La Bocaina' in the southeast of Fuerteventura Islands (Canary Islands, North-eastern central Atlantic) (see Fig. S1 in Supplementary Material): "ECOS 04/99" (April 1999) and "BOCAINA 03/02" (March 2002). The trawl tows were conducted horizontally during the night at different depths and classified as: a) neritic, haul depth below 50 m and the bottom depth less than 200 m; b) epipelagic, haul depth below 200 m and the bottom depth range more than 200 m; c) mesopelagic, trawl tows deeper than the 200 m depth line (Wienerroither et al., 2009). Trawl tows were also performed in the mesopelagic area during the day. In addition, the mesopelagic trawl tows were further divided into two groups, the upper (200-600 m) and lower layers (600-1000 m), depending on whether the trawl tows were above or below the deep-scattering layer (*DSL*, around 600 m) (Bordes et al., 2009) respectively. The time of day was also divided into two categories to avoid the influence of the diel vertical migration (*DVM*) at sunset and sunrise: daytime (09:45-7:45 hours) and nighttime (20:10-2:00 hours). Consequently, six fish assemblages were studied: neritic-night (*NN*), epipelagic-night (*EN*), upper mesopelagic during the day and night (*UMD* and *UMN* respectively), and lower mesopelagic during the day and night (*LMD* and *LMN* respectively). More details on the duration, location, trawling, bottom depth, vessels and net, as well as a description of the fishing operations are given in Bordes et al. (2009) and Wienerroither et al. (2009).

### 6.2.2 Morphospace analysis

The changes in fish shapes were quantified using geometric morphometric techniques (Bookstein, 1991; Rohlf and Marcus, 1993). Due to the special morphology of many deep fishes, we decided to use semilandmarks to detect the presence of special fins and sensorial organs following previous studies (Recasens et al., 2006; Lombarte et al., 2012; Farré et al., 2013). The *x-y* coordinates of landmarks and semilandmarks (see Fig. S2 in Supplementary Material) were digitalised with tpsDig 2.16 (Rohlf, 2010a) according to points proposed by Recasens et al. (2006). The coordinates of each species were digitised, then rotated, scaled (to unit centroid size) and translated using a generalised least-square superimposition procedure (GLS, generalised Procrustes) to remove scale and orientation distortions using tpsRelw 1.49 (Rohlf, 2010b). Changes in fish shape were visualised using relative warp analysis of superimposed landmark coordinates (Rohlf and Marcus, 1993). This procedure produces multiple morphological axes in a way that best explains the variance in body shape among specimens. Each relative warp axis represents a set of specific morphological characteristics (Layman et al., 2005).

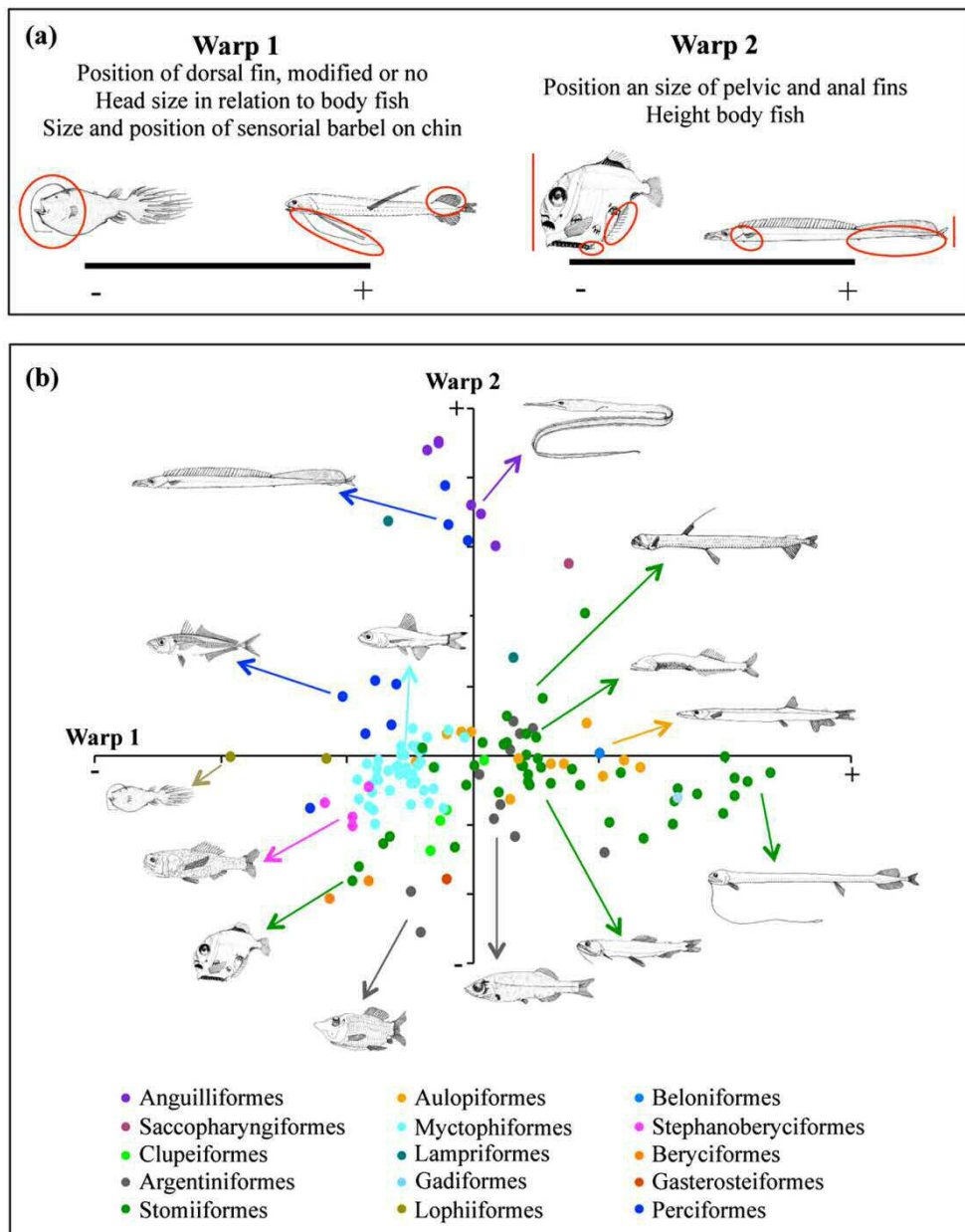
The warps 1 and 2 provided higher morphological variance and were used to build the morphospace of each assemblage (Recasens et al., 2006; Pierce et al., 2009). To determine the patterning, a grid-based model (or quadrant analysis) was constructed over the morphospace counting the number of species per quadrant. The Bray Curtis index was selected for the pairwise comparison of quadrants. To reduce this weighting to certain abundance, data were standardised using the square root. The pairwise values of the Bray Curtis similarity index were calculated for all possible combinations among quadrants and then classified by hierarchical agglomerative cluster analysis using the UPGMA algorithm. A multidimensional representation of the distribution of fish assemblages based on their similarity was then obtained by applying a non-metric multidimensional scaling technique (nMDS). In addition, the kernel density was determined for the localization of clusters in the quadrants using a Gaussian function:

$$f(x, y) = \frac{1}{2\pi r^2} \sum_i e^{-\frac{d_i^2}{2r^2}}$$

where  $d_i = \sqrt{(x - x_i)^2 + (y - y_i)^2}$ ,  $x$  and  $y$  the coordinates of points and  $r$  is the radius. The convex hull was defined as the area enclosing all the species among warps and was drawn for each fish assemblage. A dissimilarity matrix was gained across pairwise comparisons. Morphological dissimilarity equals zero when the portions of the morphological area filled by species assemblages are perfectly overlapping and equals unity when assemblages do not intersect in that functional space (Villéger et al., 2011). Fish assemblages were also analysed with hierarchical agglomerative cluster analysis and nMDS. All statistical calculations were carried out using the PRIMER V 6.1.13 computer program (Clarke and Gorley, 2006) and PAST v. 2.10 (Hammer and Harper, 2006).

### 6.3 Results

A total of 145 species belonging to 37 families and 15 orders were used to build the morphospace. The first warp was related to the relative position of the dorsal fin and its enlargement into an illicium (a sensorial organ), the relative head size in relation to body size and the length and position of the sensorial barbell on the chin. The second warp was correlated with fish body height and the position and size of the pelvic and anal fins (Fig. 2a). According to initial hypothesis, it was confirmed that species with a “non-typical shape” were located on the periphery of the morphospace, while “typical-shaped” fish occurred close to the centre of the morphospace (Fig. 2b).



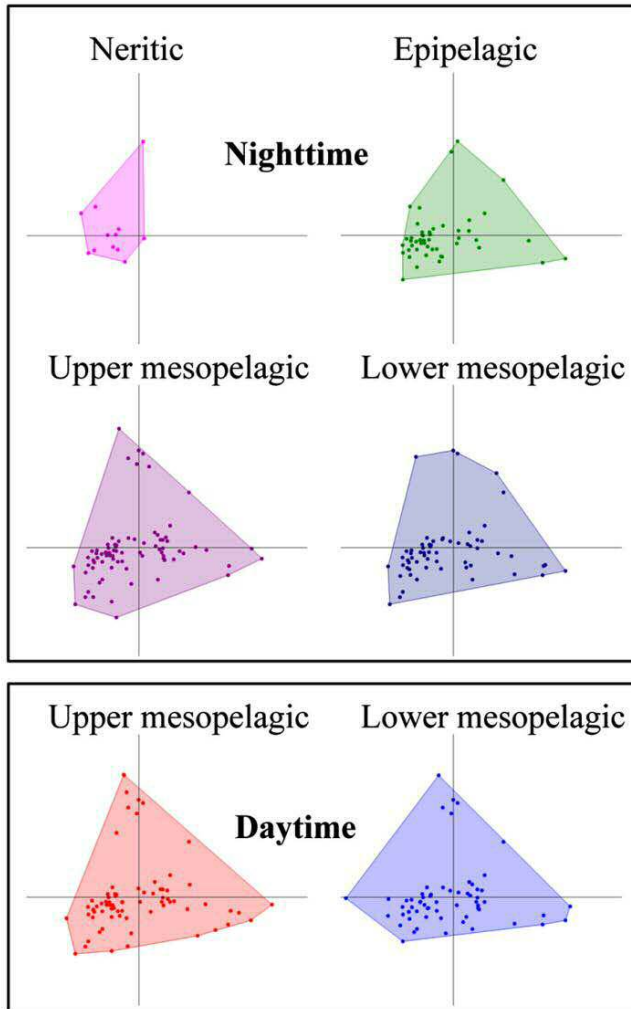
**Figure 2.** Morphological meaning of warps 1 and 2 (a), and plot representing all species in the morphospace helping to its comprehension (b).

### 6.3.1 Convex hull

Variations in the convex hull were mainly related to the presence of mesopelagic fish with extreme shapes: elongated tail (Anguilliformes), elongated body and large

## 6. Morphospace occupation of mesopelagic fish assemblages

sensorial barbels (Stomiidae, Stomiiformes), high body and big head (Sternoptychidae, Stomiiformes), big head and narrow caudal peduncle (Stephanoberyciformes), and high



**Figure 3.** Warp plot with convex hull delineating the morphospace realised by mesopelagic fish assemblages.

body and first spine of dorsal fin transformed into an illicium (Lophiiformes) (Figs. 2, 3).

The *NN* assemblage showed the smallest area and a noticeable dissimilarity with other assemblages (69.4-76.4%) due to absence of “non-typical shapes” (see Fig. S3 in Supplementary Material). The *EN* assemblage was defined by the absence of Stephanoberyciformes and Lophiiformes, which is why it was fairly similar to the mesopelagic assemblages (23.8-34.6%) (see Fig. S3 in Supplementary Material). In the remaining assemblages, only the *LMD* assemblage had Lophiiformes, which clearly conditioned its similarity with the other assemblages (25.4-33.3%) (see Fig. S3 in Supplementary

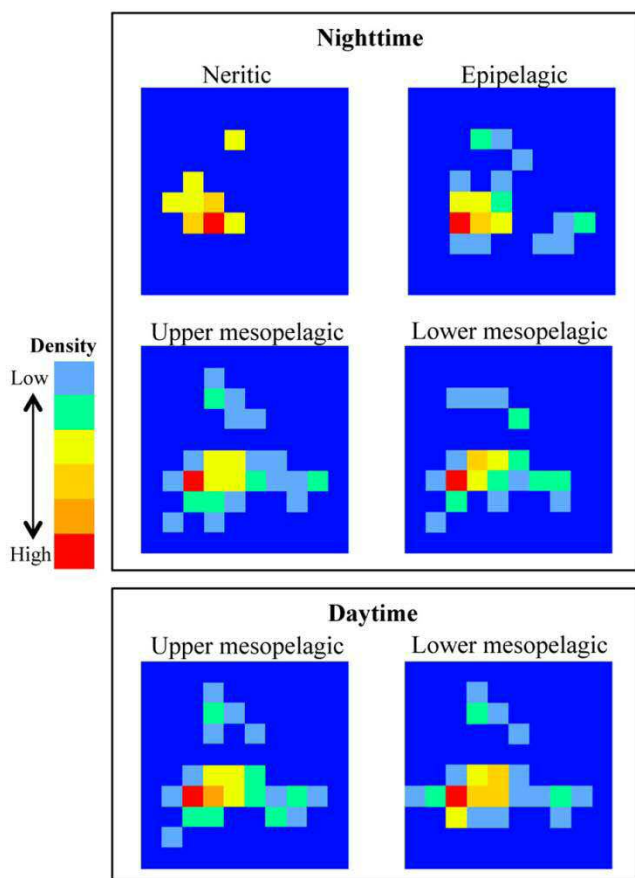
Material). The cluster and nMDS analyses grouped the upper mesopelagic assemblages with *LMN* and then with *LMD* (see Fig. S4a in Supplementary Material). This is consequence of the spatial distribution of *Oneirodes anisacanthus* (Lophiiformes) on the *x*-axis, improving the convex hull and dissimilarity among these assemblages.



## 6.3.2 Patterning

The fish assemblage modelling was determined by the species distribution in the morphospace, which was influenced by the high diversity of species belonging to the families Gonostomatidae and Stomiidae (Stomiiformes), and Myctophidae (Myctophiformes) (Figs. 1, 4).

The *NN* assemblage showed a patterning that was completely different to the remaining assemblages due to the low diversity of species and spatial homogeneity. The



**Figure 4.** Warp plot with patterning of morphospace realized by mesopelagic fish assemblages. Colours scale indicates the density of species in each cell.

*EN* assemblage was mainly composed of migratory species of the family Myctophidae and some species of Stomiidae, such as *Astronesthes* spp. and *Chauliodus* spp. The spatial distribution of the species abundance was quite similar to the mesopelagic assemblages and some extreme shapes were also present, which is why the *EN* assemblage was clustered with the mesopelagic assemblages (see Fig. S4b in Supplementary Material). The mesopelagic assemblages showed a similar patterning with slight differences in the density of species around the centre of the morphospace, which seems

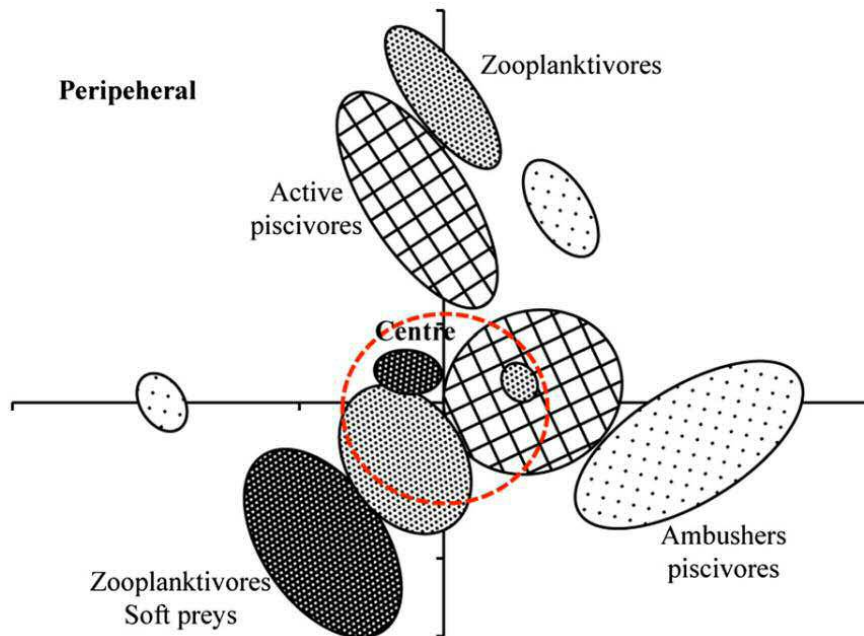
to be linked to vertical migration upwards into the surface layer at night. This variability in the morphospace was noticeable in the *LMN* assemblage, and hence the cluster analysis separated it from the other assemblages (see Fig. S4b in Supplementary Material).

### 6.4 Discussion

The morphological diversity within an assemblage depends on which mechanism is acting to promote species coexistence (Kneitel and Chase, 2004). The species that provide the highest biodiversity to the ecosystem have very specialised traits. This ecological premise is intrinsically contained in the convex hull analysis, and hence these species are located on the periphery of the morphospace. However, within the convex hull there may be species with a high level of morphological diversity (Salvanes and Kristoffersen, 2001), which are not considered in this analysis. In our study species such as *Oneirodes anisacanthus*, *Nemichthys* spp. (Anguilliformes), *Opisthoproctus* spp. (Argentiniformes) and some species of Stomiiformes show specific adaptations related to feeding or locomotion function. These species were the cause of the dissimilarity noted in the convex hull of the mesopelagic assemblages, where *LMD* was most different due to the presence of only one species, *Oneirodes anisacanthus*. It seems unreasonable that a single species can condition the comparison of morphological diversity among assemblages.

The patterning of morphospace helped to reveal the ecological strategies that allow the species coexistence (Fig. 5). We found that non-migratory species located on the periphery of the morphospace, or close to it, have common strategies for conserving energy (DeWitt and Cailliet, 1972). The ambusher piscivores (which mainly ingest fish) capture their prey by attracting them with a luminescent device projecting from the lower jaw or barbell chin, a modified dorsal fin or the tip of the caudal fin (Gartner et al., 1997; Haddock et al., 2010). Fish with an elongated shape are adapted to quick swimming, so that they can prey on small mesopelagic fish and cephalopods in deep waters (Hopkins et al., 1996; Cartes et al., 2009a). They are active predators with many different swimming styles and lifestyles that are associated with anatomical changes in the body and fins (Ward and Mehta, 2010). By contrast, some species, mainly crustacean zooplanktivores, have sensorial adaptations that allow distinguishing and feeding on other preys lesser visible, such as polychaetes and gelatinous organisms (Mauchline and Gordon, 1986; Hopkins et al., 1996; Collin and Partridge, 2006; Barlow and Sutton, 2008). The migratory species corresponded to mesopelagic eels that feed

primarily on zooplankton crustaceans in shallow or deep waters (Gartner et al., 1997) and compete with other species that have different ecological strategies.



**Figure 5.** Warp plot with feeding groups of mesopelagic fishes.

At the centre of the morphospace, the active piscivore foragers have well-muscled bodies, well-developed eyes and strong dentition. Most of these species were not collected from shallow waters, confirming that migratory piscivores generally make more restricted diel vertical migrations than zooplanktivores (Sutton and Hopkins, 1996). The species of the families Gonostomatidae and Phosichthyidae (Stomiiformes), Myctophidae (Myctophiformes) and Argentiniformes were the main contributors to the mesopelagic assemblages and were mainly crustacean zooplanktivores (Hopkins et al., 1996; Gartner et al., 1997; Pusch et al., 2004; Olivar et al., 2012). Although only the Myctophiformes and some species of the family Phosichthyidae perform diurnal vertical migration (*DVM*), not all individuals appear to exhibit *DVM* and the different species do not have the same migration range (Ross et al., 2010). This could explain why the spatial density was always higher in the part of the morphospace occupied by these groups (Fig. 5). Therefore, our results reinforce the idea that the distribution of

species within morphospace helps to explain better the understanding of the ecosystem structure.

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# 7

## **Habitat influence in the morphological diversity of coastal fish assemblages**



**Habitat influence in the morphological diversity  
of coastal fish assemblages**

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See the original publication in the Appendix 2 section

### **Abstract**

Ecological diversity based on quantitative data is widely used to characterise biological communities, but recently morphological and functional traits have also been used to analyse the structure of fish assemblages. This diversity and structure is usually linked to variables such as habitat complexity and composition, depth, and spatial and temporal variations. In this study, several fish assemblages off the Catalan coast (NW Mediterranean) were ecologically and morphologically analysed and compared. The morphological analysis was performed from body shape of fish species using geometric morphology. Moreover, a canonical correspondence analysis (CCA) was used to analyse the effect of local environmental variables such as habitat, locality and depth on the composition and abundance of assemblages. The results revealed greater differences among assemblages in the clustering performed from morphological data, which is linked to habitat complexity, than those shown by the ecological analysis. Moreover, the CCA analysis indicated that type of substratum and the location significantly influenced the composition and structure of the fish assemblages. These results evidenced that morphology provides different and complementary information than ecological analysis because it allows to predict the ecological and functional habits of species within the community, helping to improve the understanding of the fish assemblages structure.

**Keywords:** Morphology; Ecological structure; Environmental factors; Fish assemblages; Morphospace; Mediterranean Sea.



### Resum

La diversitat ecològica basada en dades quantitatives (riquesa o abundància específica) és el mètode més àmpliament utilitzat a l'hora de caracteritzar comunitats biològiques. No obstant, recentment l'ús dels caràcters morfològics i funcionals de les espècies ha començat a adquirir importància a l'hora de analitzar la estructura de comunitats de peixos. Aquests aspectes de la diversitat habitualment estan relacionats amb múltiples variables, com la complexitat de l'hàbitat, la composició de la comunitat, la profunditat o les variacions espacials i temporals. En el present estudi, es van caracteritzar, analitzar i comparar varies comunitats litorals de peixos provinents de la costa catalana (nord-oest del mar Mediterrani) des del punt de vista ecològic i morfològic. L'anàlisi morfològic es va basar en la forma corporal de les espècies i es va realitzar utilitzant tècniques de morfometria geomètrica. Addicionalment, es va aplicar un anàlisi de correspondència canònica (CCA) per analitzar l'efecte de les condicions ambientals locals, com ara el tipus d'hàbitat, la localització geogràfica o la profunditat, en la composició i abundància relativa de les comunitats. Els resultats van revelar que les diferències entre les comunitats estudiades eren majors quan es comparaven les seves estructures morfològiques, les quals estan lligades a la complexitat del hàbitat, que en el cas de les estructures ecològiques. A més, l'anàlisi CCA va indicar que el tipus de substrat i la localització geogràfica influenciaven la composició i estructura de les comunitats. Aquests resultats van evidenciar que la morfologia de les espècies proporciona informació diferent i complementària als anàlisis ecològics en estudis de comunitats, ja que permet predir els hàbits ecològics i funcionals de les espècies dins els ecosistemes, fet que contribueix a millorar el coneixement de la estructura i organització de les comunitats de peixos.

### 7.1 Introduction

There exist a wide number of studies regarding the effect of environmental factors in the structure and organization of fish assemblages. The circulation of water masses and currents, temperature, oxygen concentration and productivity have been considered factors influencing the structure of fish assemblages at large scale (García-Charton and Pérez-Ruzafa, 2001; Guidetti, 2000; La Mesa et al., 2010; Letourneur et al., 2001). Whereas, other variables such as the type of bottom (Demestre et al., 2000; Félix-Hackradt et al., 2014; Macpherson, 1994), depth (Gaertner et al., 1999, 2005; Menezes et al., 2006; Mérigot et al., 2007b), habitat complexity (Gratwicke and Speight, 2005; Kovalenko et al., 2012; McCormick, 1994) or the influence of terrestrial inputs in special zones such as estuaries and coastal lagoons (Akin et al., 2005; Franco et al., 2006; Maci and Basset, 2009) are contemplated also as key factors structuring biological communities but affecting at smaller scales.

However, in the nearshore fish assemblages, the habitat complexity and type of bottom are likely the two key factors. Several studies have demonstrated that the habitats formed by mixture of bottoms (i.e., coral reefs or seagrass meadows) contain greater diversity of fishes (García-Charton and Pérez-Ruzafa, 2001; Montaña and Winemiller, 2010). Usually, these complex habitats lead to an intense interspecific competition favouring the morpho-functional differentiation of species within assemblages (Gratwicke and Speight, 2005; Montaña et al., 2014; Price et al., 2011). Thus, fishes acquire singular behaviors in relation to their lifestyle and role within the community, such as the capture of food items (Costa and Cataudella, 2007; Labropoulou and Eleftheriou, 1997; Norton, 1995; Svanbäck and Eklöv, 2002), competition for resources (Peres-Neto, 2004), strategies of predators to capture preys (Eklöv and Svanbäck, 2006), territorial behaviors (Almany, 2004; Pitcher, 1986), and locomotion (Blake, 2004; Yamamoue et al., 2010). Therefore, the interspecific morpho-functional variation within fish assemblages can help to understand its structure and dynamics (Gatz, 1979; Langerhans et al., 2003; Montaña and Winemiller, 2010; Winemiller, 1991); and even, it can also be used as a measure of biodiversity that captures more ecological properties of fish assemblages than a simple enumeration of species (Farré et al., 2013; Foote, 1997; Karr and James, 1975; Ricklefs, 2010) or as a prediction tool of invasion and coexistence phenomena (Azzurro et al., 2014). In

addition, morphological traits of species are also useful to detect variations in the structure of assemblages caused by natural or external perturbations (Lombarte et al., 2012; Villéger et al., 2010), whereas simple ecological measures are unable to determine these changes within communities. Therefore, the incorporation of new approaches, such as morphological and functional information of species, to studies that only use ecological parameters such as specific richness, dominance or evenness, are important to improve the knowledge about the dynamics of communities (Farré et al., 2013; Somerfield et al., 2008).

In the Mediterranean Sea, very few studies had tried to explain the morpho-functional diversity and structure of fish communities (Albouy et al., 2011; Recasens et al., 2006). Recently, morphological analyses have been accepted as valid methods to define the community structure, offering an additional option when ecological or functional information of communities is absent or scarce (Farré et al., 2013; Lombarte et al., 2012). The aims of this study are (i) to characterize coastal fish assemblages of the Mediterranean Sea in relation to composition and abundance of species, (ii) to describe morphologically these assemblages from body fish shape and compare them to assess their variability, and (iii) to test how environmental factors (substrate composition, depth or location) affect the structure of the assemblages.

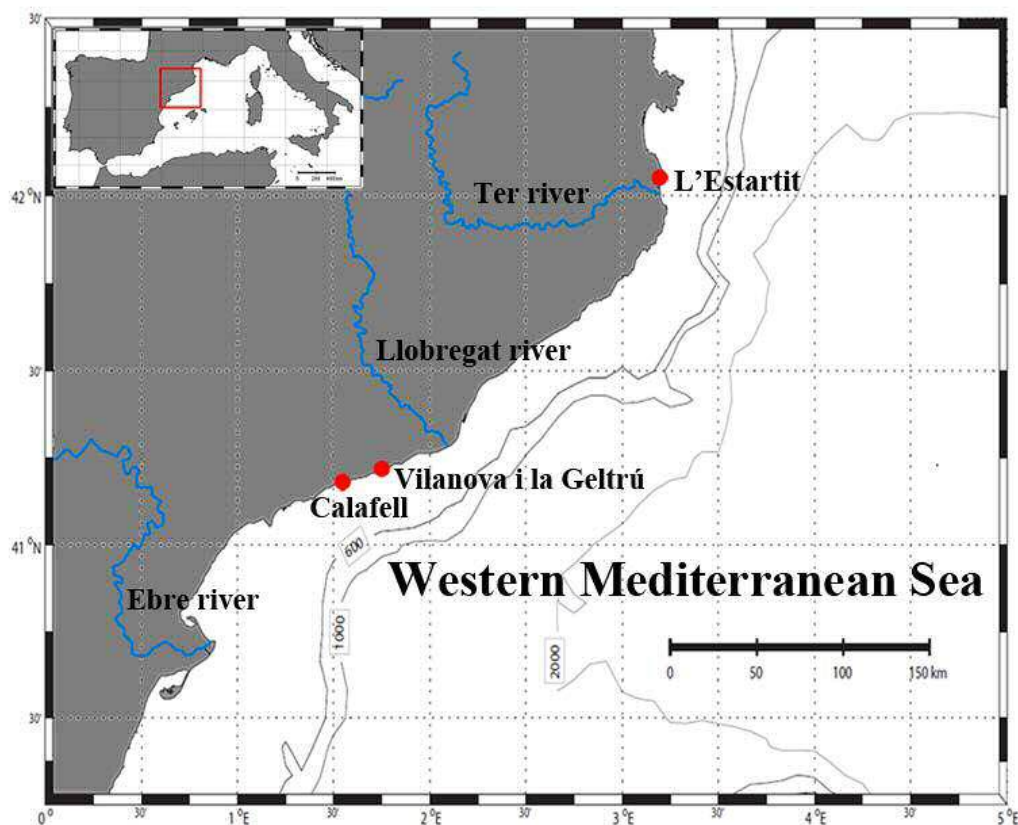
### 7.2 Material and methods

#### 7.2.1 Study area

Two coastal zones off the Catalan coast (NW Mediterranean Sea) were studied (Fig. 1). The rocky shores of the NW Mediterranean present a set of geologic and hydrologic characteristics that gives the zone a relatively high species richness compared with other habitats of the Mediterranean (García-Charton et al., 2008; Harmelin-Vivien et al., 2008). The littoral demersal fish fauna is dominated primarily by families such as Labridae, Sparidae, Mullidae, Serranidae and Scorpaenidae, which represent up to 50-70% of the total biomass (García-Rubies, 1999; Gordo, 2009; Macpherson et al., 2000, 2002).

## 7. Morphological diversity of coastal fish assemblages

The first study area was located in the vicinity (buffer zone) of the Medes Islands Marine Reserve (500 ha), near to the fishing port of L'Estartit and close to the mouth of the Ter River (henceforth, "Northern zone"). This marine reserve was established in 1983 to preserve its especially rich marine habitat, which primarily includes rocky substrates as well as several areas with sandy and muddy bottoms. Given its situation and dimensions, it is considered a small-sized MPA, as are most Mediterranean MPAs (Fraschetti et al., 2005; García-Rubies and Zabala, 1990; Tunesi et al., 2006). The marine reserve comprises an integral reserve or no-take zone (referred to as NTZ; 93 ha) where all fishing activities have been banned since 1991 and a buffer zone (418 ha) where only artisanal fishing by the local fleet is allowed (approximately 12 boats of less than 15 m in length using set gear only). Commercial fishing by the local fleet extends well beyond the boundaries of the buffer zone (the activity area of the fleet is approximately 3800 ha, Stelzenmüller et al., 2007).



**Figure 1.** Geographical localization of study areas: Vilanova i la Geltrú-Calafell or Central zone and L'Estartit or Northern zone.

In the second zone selected for the study, data were obtained from two nearby localities: Vilanova i la Geltrú and Calafell (henceforth “Central zone”). In Vilanova i la Geltrú, a total fleet of 21 artisanal netter boats was in operation (Maynou et al., 2011). The marine substrates of Vilanova are characterised by a wide sandy bottom with small interspersed rocky zones, rocky bottoms and a fragmented and dispersed seagrass meadow. In addition, samples from an artificial reef and rocky substrate surrounded by sandy bottom patches were incorporated from the nearby locality of Calafell (Recasens et al., 2006). Artificial reefs have been shown to be an effective approach to the prevention of illegal trawling in littoral zones and facilitate the feeding, spawning and protection of several fish species, producing significant changes in the species composition of assemblages (Charbonnel et al., 2002; Claudet et al., 2006).

### 7.2.2 Sampling

A total of 51 and 35 monthly experimental fishing samples, covering the entire year, were analysed in the Central and Northern zone, respectively. In the Central zone, the specimens were caught by small vessels at a depth of less than 50 m using trammel nets between February 2000–April 2001, December 2002–September 2003 and May 2009–April 2010. In Northern zone, the specimens were also captured using trammel nets between March and December 2003–2005, exclusively in the buffer area of Medes Islands Marine Reserve. The characteristics of trammel net fisheries in the study areas have been widely described in the literature (Martín et al., 2012; Maynou et al., 2011; Recasens et al., 2006; Stelzenmüller et al., 2009). In both regions, the entire fish catch for each operation (commercial plus the discarded fraction) was retained. The species were identified, classified (Mercader et al., 2001) and placed within a taxonomic hierarchy according to Nelson’s *Fishes of the World* (Nelson, 2006).

All of the fishing operations monitored were classified according to the characteristics of substrate, habitat and depth in each locality (Maynou et al., 2011; Recasens et al., 2006; Stelzenmüller et al., 2009) (see Table S1 in Supplementary Material). Given this information, six types of fish assemblages were established in the Central area: a) Sandy, <10 m depth (*CS10*, 3 samples); b) Rocky-Seagrasses, 10–14 m

## 7. Morphological diversity of coastal fish assemblages

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(*CSEA15*, 5 samples); c) Sandy-Rocky, 15-19 m (*CS15*, 6 samples); d) Sandy, >20 m (*CS20*, 3 samples); e) Artificial Reef, 15-19 m (*CA15*, 20 samples); and f) Rocky-Sandy, 15-19 m (*CR15*, 14 samples). Likewise, seven types of assemblages were recognised in the Northern study site: a) Gravel, 25-32 m depth (*NG20*, 3 samples); b) Rocky, 10-22 m (*NR15*, 3 samples); c) Sandy, <10 m (*NS10*, 13 samples); d) Sandy, 10-20 m (*NS15*, 4 samples); e) Sandy-Rocky with higher proportion of rocky bottom, >20 m (*NS20*, 5 samples); f) Sandy-Muddy, 26-50 m (*NSM20*, 5 samples); and g) Muddy, 30-33 m (*NM20*, 2 samples).

### 7.2.3 Ecological structure of assemblages

The structure and composition similarity of fish assemblages from each locality were investigated using a multivariate analyses performed with the software package PRIMER (Plymouth Routines in Multivariate Ecological Research) for Windows v. 6.0 (2008) (Clarke and Warwick, 2001), following the procedure carried out in similar studies (Gordoa, 2009, La Mesa et al., 2010; Maci and Basset, 2009). Abundance data were transformed using square root transformation to equalise the weight of all the present species in the analysis and reduce the effect of the most dominant species. A Bray-Curtis similarity matrix was calculated with these data, and the results were classified based on their similarity by hierarchical agglomerative cluster analysis using the Euclidean distance; then, a multidimensional scaling ordination (nMDS) was generated to show the distances between communities and their distribution in two-dimensional space (Gordoa, 2009; Mérigot et al., 2007b).

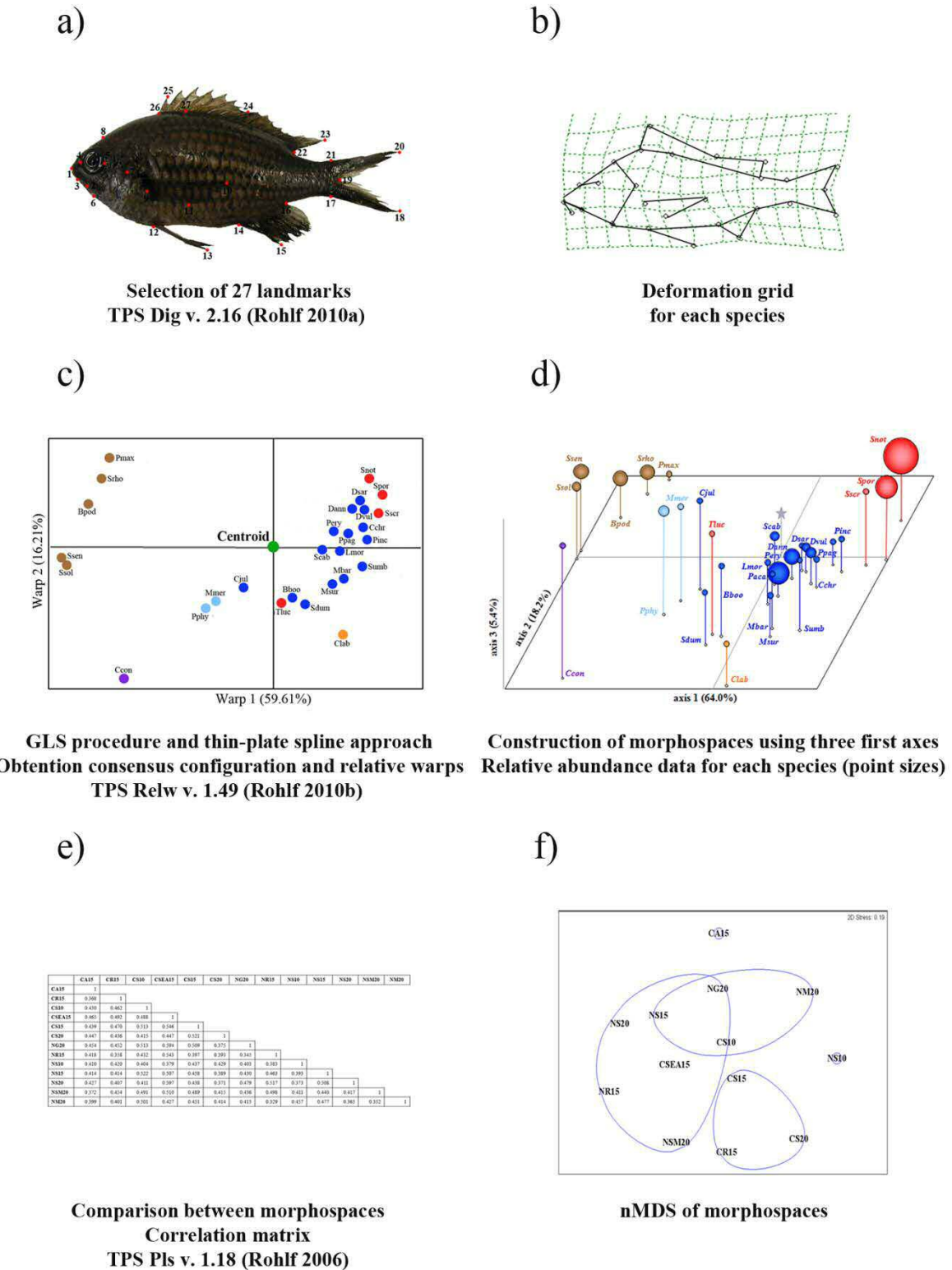
### 7.2.4 Morphological structure of assemblages

The configuration of the morphospaces of the fish assemblages was determined using the geometric morphological method. All steps realized during the morphological analysis process are schematically shown in Figure 2. The analysis of species morphology was realized using morphometric data obtained by the selection of 27

landmarks and semilandmarks (Fig. 2a) that describe the shape of each species from standardised images of the left side (Azzurro et al., 2014; Farré et al., 2013; Tuset et al., 2014). A consensus image of each species was used (Recasens et al., 2006) and in order to consider the abundance of species in the analysis, for each species it was calculated its proportion in % respect total abundance of each community. Then, the number of analysed images per species corresponded to the percentage abundance of the species within the community. All percentages from 1.0 to 99.9% were rounded downwards (e.g., 36.4% to 36%). The species with abundance equal to or less than 1% (between 19% and 73% of the species, depending on the community) were analysed as one image to include the largest number of species in the analysis (Lombarte et al., 2012).

Landmarks and semilandmarks were digitised using tpsDig v. 2.16 (Rohlf, 2010a), and their record included body shape, fins position and size and other sensory organs that are key traits in behaviors such as locomotion, feeding, spawning or defence against predation (Gosline, 1994; Yamanoue et al., 2010). Direct analysis of landmark coordinates contains other components not related with shape such as position, orientation, scale or size (Adams, 1999; Angeles et al., 2014). To remove these distortions, a generalised least-square superimposition procedure (GLS, generalised Procrustes analysis) was applied, translating all specimens to a common centroid position in the coordinates system, scaling them to unit centroid size and rotating them to minimize the distances between corresponding landmarks (Angeles et al., 2014; Kassam et al., 2002). Thus, superimposition methods allow realizing analysis of morphology independent of size (Layman et al., 2005). GLS procedure was conducted using tpsRelw v. 1.49 (Rohlf, 2010b), which it also provided the uniform components of shape variation for each specimen (relative warps). A consensus configuration was also computed by averaging the spatial coordinates of the landmarks that allows obtaining the deformation grids of each species (Fig. 2b) applying the thin-plate spline approach, which maps the deformation in shape between objects (Bookstein, 1991; Kassam et al., 2002; Langerhans et al., 2007). The comparison of the relative warps of each species with the reference configuration permits visualisation of changes in fish shape as well as shape differences between species (Kassam et al., 2002; Rohlf and Marcus, 1993; Zelditch et al., 2003).

**7. Morphological diversity of coastal fish assemblages**



**Figure 2.** Explanatory scheme of the different consecutive stages carried out for the computation of the morphological analyses of the different sampled fish assemblages.



Morphospaces for each assemblage were constructed using the obtained relative warps. To this end, a principal components analysis of the covariance matrix of the translated, rotated and scaled landmark coordinates of species was performed (Fig. 2c), creating multiple morphological axes that explain the variance in body shape among species. Thus, each relative warp axis represents a set of specific morphological characteristics, and the species are distributed in space according to these specific traits and the axis orientation (Layman et al., 2005). Herein, the first three axes of relative warps were selected to build the morphospaces. Besides, in the relative warp analysis, the relative abundance of the species within the assemblages was also considered (Fig. 2d).

Finally, the comparison among the morphological structures of the assemblages was evaluated (Fig. 2e) from the PLS method using tpsPls v. 1.18 (Rohlf, 2006). It assessed the pattern of covariation between two set of variables that have been treated symmetrically, assuming that they are independent variables between them. PLS operates as a series of interdependent OLS (Ordinary Least Square) regressions for each warp of the compared fish assemblages. Moreover, it is not necessary to standardise the shape variables since they are already in the same units (Rohlf and Corti, 2000). In our study, we used the position coordinates of each species within the morphospace as set of variables, and we only considered the correlation values  $>0$  for the estimation of average correlation between each pair of morphospaces. Finally, a non-metric multidimensional scaling ordination (nMDS) was generated (Fig. 2f) to show graphically the disposition and the distances between morphospaces.

### *7.2.5 Environmental effect study*

The influence of the recorded environmental factors in the abundance of fishes in each assemblage was tested using a correspondence canonical analysis (CCA) (Claudet et al., 2011; Selleslagh and Amara, 2008; ter Braak, 1986). According to previous studies performed in the areas (Martín et al., 2012; Maynou et al., 2011; Recasens et al., 2006; Stelzenmüller et al., 2009), three environmental traits were considered. The variable ‘type of substratum’ was divided in five different discrete categories according

to its consistency: muddy, sandy, gravel, mixture of sandy-rocky (including artificial reef such as rocky bottom), and rocky bottoms. The 'depth of capture' was categorized in three strata: <10 m, 10-20 m and >20 m. Finally, 'locality of capture' was split in north and central (see Fig. 1). Moreover, the abundance data of species were standardized using the square root transformation. Thus, two different matrices were created, one including the standardized abundance data for all the assemblages, and another classifying the assemblages in the selected environmental variables. To test the significance of the results, we used the Monte Carlo test (500 permutations). The analysis was executed using the software CANOCO for Windows 4.5 (ter Braak and Šmilauer, 2002).

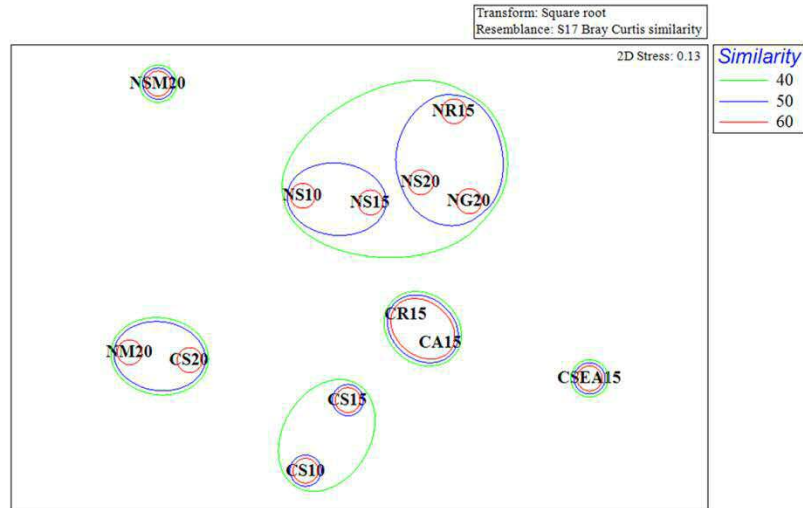
### 7.3 Results

#### 7.3.1 Structure of fish assemblages

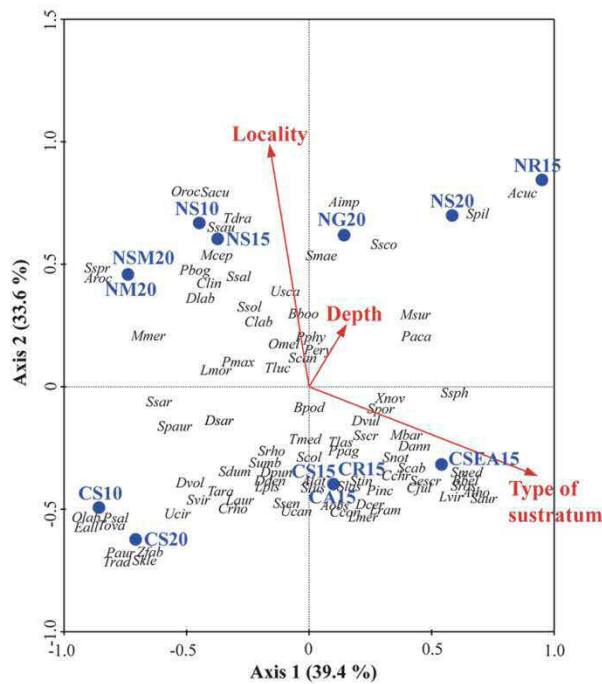
A high variability in specific composition and richness was noted among the different assemblages (see Table S1 in Supplementary Material). The results indicated low levels of similarity among them (<60%), with the most resemblance (69.1%) occurring between artificial reef (CA15) and rocky-sandy (CR15) assemblages (Fig. 3a), both sharing high abundance (>5%) of species such as *Bothus podas* and *Scophthalmus rhombus* (Pleuronectiformes), *Pagellus acarne* and *Pagellus erythrinus* (Sparidae) or *Scorpaena notata* and *Scorpaena porcus* (Scorpaenidae). The nMDS analysis showed a group formed by five exclusively northern assemblages, more specifically divided according on the type of substratum. This clustering was defined by the strong dominance exerted by species such as *Mullus surmuletus* (Mullidae), *Pagellus acarne* and *Pagellus erythrinus* (Sparidae) specially in the assemblages containing hard substratum (NG20, NR15 and NS20), whereas the assemblages from sandy bottoms (NS10 and NS15) were also characterised by the increased presence of flatfishes (*Solea solea*) and mugilids (*Mugil cephalus*, *Chelon labrosus*). The remaining assemblages were clustered pairwise or were isolated. Only one case (CS20 and NM20) demonstrated a grouping between central and northern assemblages, characterised by typical species

of soft substrates such as *Sparus aurata* (Sparidae), *Sarda sarda* (Scombridae) or *Uranoscopus scaber* (Uranoscopidae).

a)



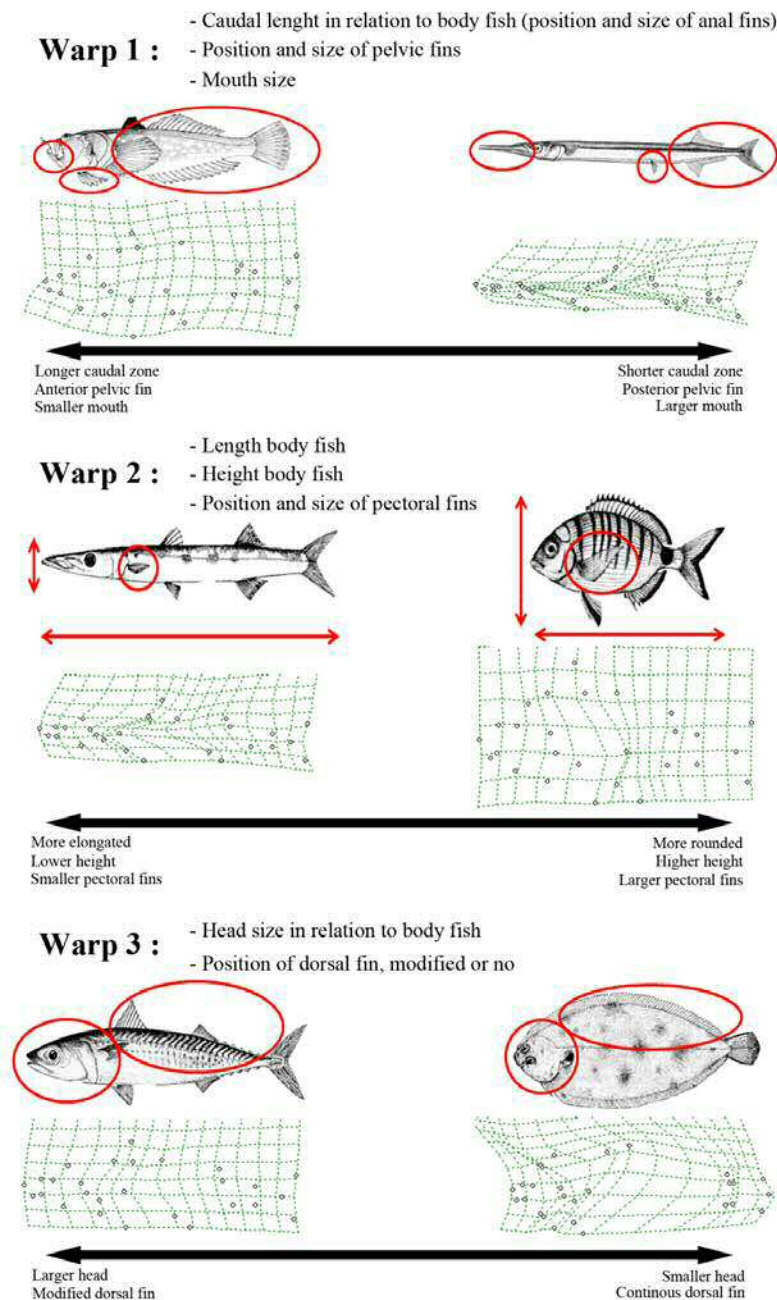
b)



**Figure 3.** Non-metric multidimensional scaling ordination (nMDS) from abundance data of the assemblages using the Bray-Curtis similarity (a) and correspondence canonical analysis (CCA) based on specific abundances, with the communities represented by points and environmental variables by vectors (b). The percentage of variance explained by the first two axes is provided. See Table S1 in the Supplementary Materials for communities and species acronyms.

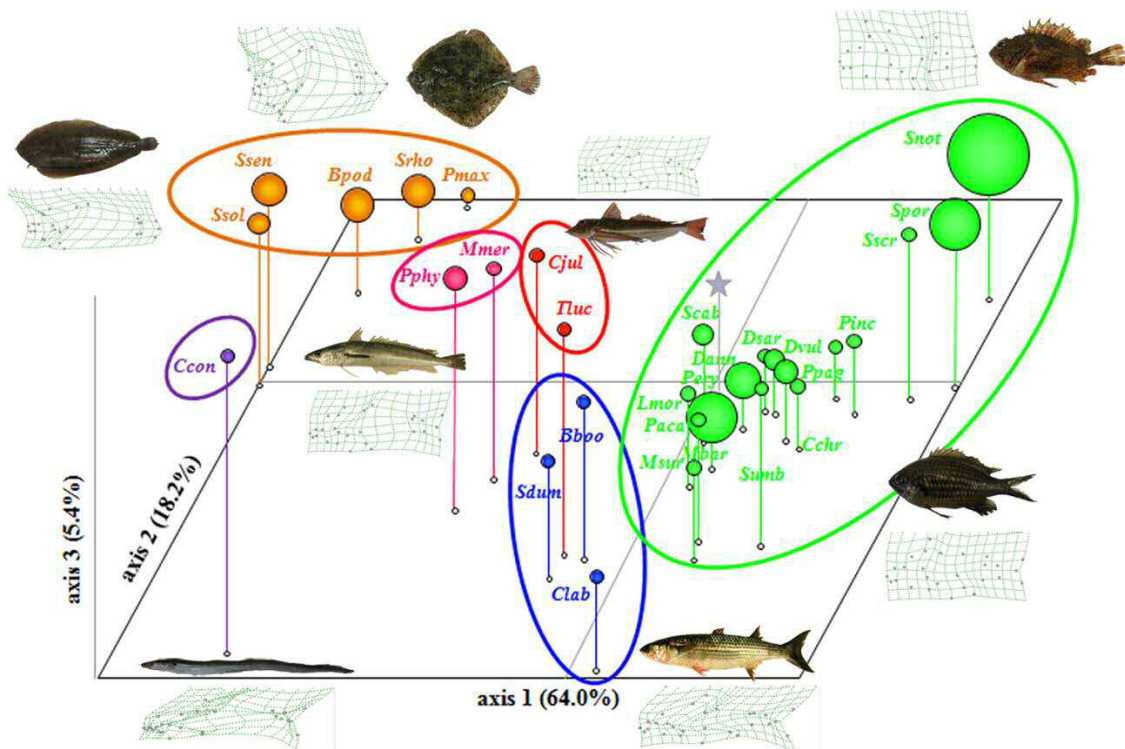
## 7. Morphological diversity of coastal fish assemblages

For all built morphospaces, the first axis (warp 1) was related with the length of the caudal zone in relation with the overall body, delimited for the origin and size of the anal fin, and also with the position and size of the mouth and pelvic fins (Fig. 4). The second axis (warp 2) defined the variation in length and the height of the body, as well as the relative position and size of the pectoral fins. And the third axis (warp 3) described the variation in two different traits: the head size in relation to the overall body size and the position and type of dorsal fin.



**Figure 4.** Scheme representing the main morphological characteristics defined by the three axis of the morphospace, coinciding with the first three relative warps.

All fish assemblages presented several clustering of species following a similar morphological pattern (Fig. 5): asymmetrical bodies, with small heads, rounded and dorsal-ventrally flattened shapes and with very elongated dorsal and anal fins (Pleuronectiformes); rounded and laterally compressed species with longer heads and smaller fins (Scorpaenidae, Sparidae; Mullidae, Serranidae, Labridae); elongated shapes with longer fins adapted to swimming near to the bottom (Gadiformes); pelagic species with fusiform shapes favouring permanent movement and relatively small fins respect the overall body (Carangidae, Scombridae, Sphyraenidae) or even more complex shapes with anatomical extreme traits mixed with other groups (Triglidae, Zeidae) or isolated in the periphery of the morphospace (Lophiidae, Congridae, Syngnathidae, Ophidiidae, Dactylopteridae). However, the comparison of the more specific internal distribution of morphospaces showed greater differences among assemblages.



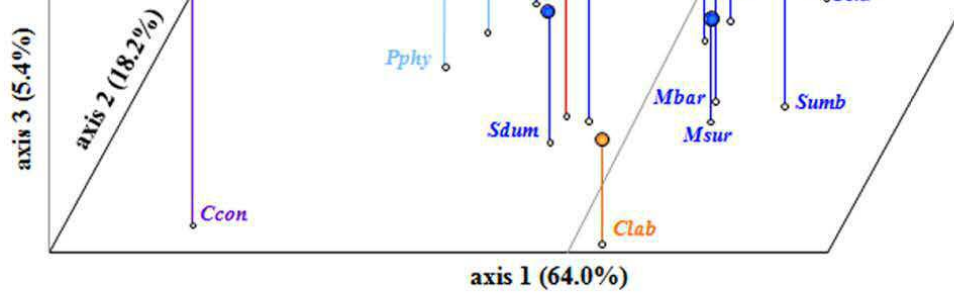
**Figure 5.** Example of the main morphological groups differentiated within the morphospaces, each of them represented by different colours. Deformation grids indicating shapes found within each group are provided, as well as images of the represented species.

## 7. Morphological diversity of coastal fish assemblages

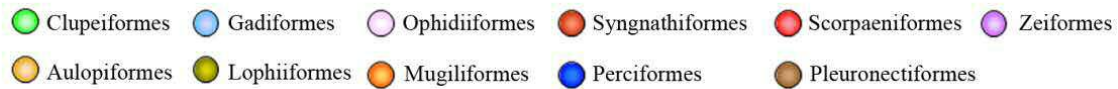
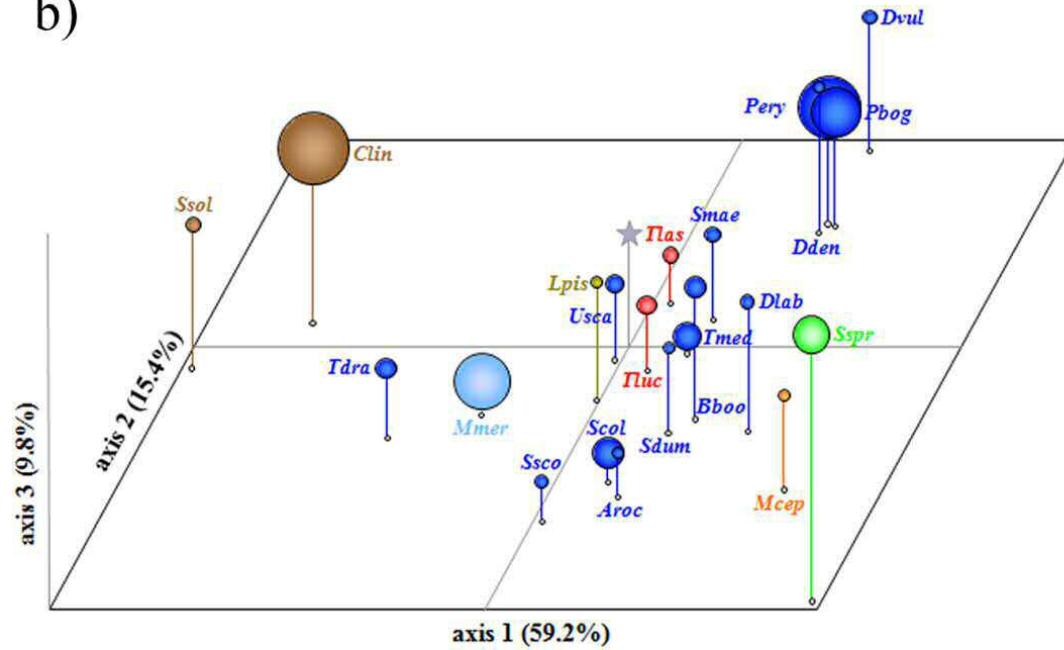
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The morphological structure of the assemblages (two illustrative examples were selected and are shown in Fig. 6; for the remaining assemblages, see the Supplementary Material, Fig. S1-S6) showed differences between them. The maximum average correlations between morphospaces were always lower than 60% ( $CSEA15-NS20=0.597$  and  $CSEA15-NG20=0.594$ , Table 1). The nMDS only distinguished three heterogeneous groups, supporting the differences given the low correlation levels between assemblages (Fig. 7). A first group was composed by assemblages of the Central zone (*CR15*, *CS15* and *CS20*), whose morphospaces were dominated by sparids (*Pagellus* spp., *Diplodus* spp., *Pagrus pagrus*) and secondarily by scorpaenids, flatfishes and some pelagic species (*Trachurus mediterraneus*, *Sarda sarda*). *CS10*, *NS15*, *NG20* and *NM20* formed a sub-group characterized by high proportion of Perciformes, both rounded laterally compressed and elongated forms (especially abundant in *CS10*), and a decrease (excepting *NS15*) of flatfishes (Pleuronectiformes) and scorpaenids. Moreover, the great abundance of demersal species such as *Mullus surmuletus* or *Pagellus* spp., shared with some assemblages of the second group (*NG20*, *NS15*), and an increased presence of scorpaenids defined the association of *CSEA15*, *NS20*, *NR15* and *NSM20* assemblages. The remaining assemblages (*CA15* and *NS10*) showed high level of morphological heterogeneity, but the presence of morphologically extreme species such as *Conger conger*, *Syngnathus acus*, *Ophidion rochei* or mugilids determined lower correlation with the other morphospaces and their isolation in the nMDS.

**Figure 6.** Representation of the morphospaces of two fish assemblages: artificial reef assemblage (*CA15*) (a) and sandy-muddy assemblage (*NSM20*) (b). The first three relative warps represent the three axes of the morphospace, providing each of them the corresponding percentage of total morphological variability. The size point of each species represents its specific abundance within the assemblage, and the colour represents the taxonomical order to which it belongs.



b)

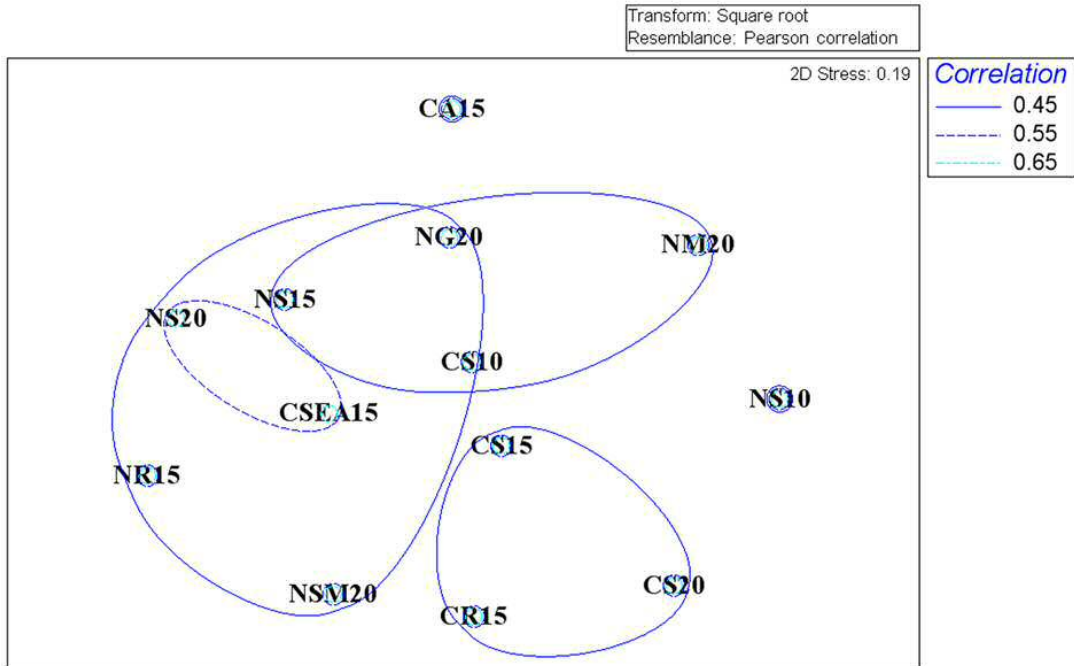


## 7. Morphological diversity of coastal fish assemblages

**Table 1.** Average correlation values among assemblages based on the PLS analysis (tps Pls v. 1.1) indicate correlations > 0.45.

Locality	Assemblages	Central zone						Northern zone			
		CA15	CR15	CS10	CSEA15	CS15	CS20	NG20	NR15	NS10	NM20
Central zone	CA15	1									
	CR15	0.368	1								
	CS10	0.430	<b>0.462</b>	1							
	CSEA15	<b>0.465</b>	<b>0.492</b>	<b>0.488</b>	1						
	CS15	0.439	<b>0.470</b>	<b>0.513</b>	<b>0.546</b>	1					
	CS20	0.447	0.436	0.415	0.447	<b>0.521</b>	1				
Northern zone	NG20	<b>0.454</b>	<b>0.452</b>	<b>0.513</b>	<b>0.594</b>	<b>0.509</b>	0.375	1			
	NR15	0.418	0.358	0.432	<b>0.543</b>	0.397	0.393	0.345	1		
	NS10	0.410	0.420	0.404	0.379	0.437	0.429	0.403	0.383	1	
	NS15	0.414	0.414	<b>0.522</b>	<b>0.507</b>	<b>0.458</b>	0.389	0.430	<b>0.463</b>	0.393	1
	NS20	0.427	0.407	0.411	<b>0.597</b>	0.438	0.371	<b>0.479</b>	<b>0.517</b>	0.373	0.373
	NSM20	0.372	<b>0.454</b>	<b>0.491</b>	<b>0.510</b>	<b>0.489</b>	0.415	0.436	<b>0.498</b>	0.411	0.411
	NM20	0.399	0.401	<b>0.501</b>	0.427	<b>0.451</b>	0.414	0.413	0.329	<b>0.457</b>	0.457





**Figure 7.** Non-metric multidimensional scaling ordination (nMDS) from the average correlation matrix between morphospaces using Pearson correlation.

### 7.3.2 Effect of environmental variables

The permutation test of CCA analysis indicated the existence of a linear relationship between the environmental and the abundance matrices ( $F$ -ratio=1.947,  $p$ -value <0.0001), confirming that the environmental factors considered affect the composition of the fish assemblages. The analysis also provided the individual influence of each variable (Fig. 3b): the type of substratum ( $F$ -ratio=1.96,  $p$ -value=0.002) and the location ( $F$ -ratio=1.90,  $p$ -value=0.004) affected significantly to the structure of communities, explaining 30% and 28% of the total variance observed respectively, whereas the gradient of depth ( $F$ -ratio=1.59,  $p$ -value=0.062) did not influence significantly in the observed variability between assemblages (21% of total variance). Along the axis 1, assemblages were distributed based on the nature of the substratum (Fig. 3b): from soft bottoms (CS10, CS20, NS10, NS15, NSM20, NM20) characterized by species such as *Mugil cephalus*, *Synapturichthys kleinii*, *Syngnathus acus*, *Merluccius merluccius* or *Trachinus* spp.; to hard bottoms (CSEA15, NG20, NR15) and

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mixture bottoms with rocky predominance (*CA15*, *CR15*, *CS15*, *NS20*) represented by species such as *Serranus scriba*, *Arnoglossus imperialis*, *Aspitrigla cuculus*, *Sphyraena sphyraena* or *Symphodus* spp. (hard bottoms) or *Conger conger*, *Solea lascaris*, *Sardina pilchardus*, *Labrus merula* or *Aspitrigla obscura* (mixture bottoms). By contrast, the axis 2 differentiated the geographic zone of assemblages: species such as *Sprattus sprattus*, *Arnoglossus imperialis*, *Syngnathus acus*, *Trachinus draco* or *Aspitrigla cuculus* characterized the assemblages of the Northern area; while *Solea senegalensis*, *Caranx rhonchus*, *Chromis chromis*, *Symphodus* spp. or *Labrus* spp. appeared as representative in the assemblages of the Central area.

### 7.4 Discussion

Our results support the role of environmental variables as drivers of the ecological organization of coastal fish communities (Claudet et al., 2011; Pessanha Pais et al., 2010; Pinault et al., 2014). The assemblages inhabiting areas with mixture of bottoms showed higher number of species (*CA15*, *CSEA15*, *CS15* or *CR15*), agreeing with many studies that assure that more complex substrates support richer and more diverse assemblages (Barros et al., 2001; García-Charton and Pérez-Ruzafa, 2001; La Mesa et al., 2010; Martins et al., 2013). The presence of hard substrata allows the development of a great biodiversity of epibenthic fauna and algae species, potential food resources for fishes living on different bottoms, i.e. *Pagellus* spp. and *Diplodus* spp. (Martins et al., 2013; Ruitton et al., 2000). Moreover, holes or caves provide shelters for benthic species, which can settle or hide reducing encounter rates with predators, such as scorpaenids (*Scorpaena* spp.), serranids (*Serranus cabrilla*) or conger eels (*Conger conger*) (Almany, 2004; Humphries et al., 2011; Wedding et al., 2008). By contrast, soft bottoms usually suffer a higher degree of physical disturbances, and consequently their fish assemblages are more sensitive to variations and usually are composed of a small number of species (Gili and Ros, 1985; Gratwicke and Speight, 2005; Guidetti, 2000). In our study, some sandy assemblages (*NS10*) were characterised by an increase in estuarine species with various life strategies resulting from the proximity of Ter River, although the effect was mitigated in space (*NS15*). Input of nutrients from rivers can enhance pelagic and benthic production and fishery yields, resulting in a system of

lower diversity but higher productivity (Consoli et al., 2013; Letourneur et al., 2001). However, sandy and muddy ecosystems are based on relatively 'simple' trophic interactions because many epibenthic species are scantily developed, thus favouring ambush predators with sedentary habits and species with highly cryptic features such as flatfishes (Pleuronectiformes), *Trachinus* spp. (Trachinidae) or *Lophius* spp. (Lophiidae) (Franco et al., 2006; Guidetti, 2000; Letourneur et al., 2001; Martins et al., 2013; Tuya et al., 2005).

Although with lesser extent than the type of substratum, the geographical location of assemblages also influenced in the structure of the fish assemblages. A clear separation between the assemblages of localities studied was obtained, showing the Central area a higher abundance, diversity and composition. Likely, the different fishery schemes between two locations could contribute to explain the observed differences. In the Northern zone, the artisanal fishing is highly concentrated in a small area (Martín et al., 2012; Stelzenmüller et al., 2009), whereas in the Central zone the active small-scale fleet use a wide variety of nets and secondary fishing gears and follow different fishing strategies at different times during the year (Maynou et al., 2011). Moreover, the fishing area is larger and the fishing effort is widely distributed, which favors a lower impact on biodiversity and composition of assemblages. Besides, the introduction in this area in 90's of artificial reefs as a tool to preventing illegal trawling in littoral zones produced a spillover of diversity and significant changes in the species composition of assemblages (Farré et al., 2013; Recasens et al., 2006), because this structures facilitate the feeding, spawning and protection of some fish species (Charbonnel et al., 2002; Claudet et al., 2006).

However, these effects of environmental traits were not reflected in the morphological structure of the fish assemblages. The low morphological similarity among fish assemblages reinforces the hypothesis of a closer relationship between fish shape and habitat complexity (Villéger et al., 2010; Willis et al., 2005), independently of substrata or locality. In several cases, assemblages with different substrates showed higher correlations than assemblages with similar substrate composition. A clear example that serves to illustrate this effect is the artificial reef assemblage (CA15), consisting of mixed patches of soft and hard substrata, but it had low correlation with the remaining rocky-sandy assemblages. However, it reached the highest values of specific richness, morphological disparity and functional diversity (Farré et al., 2013).

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For that reason, artificial reefs are a useful tool for the recovery of degraded areas and the improvement of biodiversity (Charbonnel et al., 2002; Price et al., 2011; Recasens et al., 2006). The morphological analysis detected better the idiosyncrasy of these assemblages *versus* more classic ecological analyses due to the presence of species with special body shapes (i.e., *Conger conger*). That was also noted in the *NS10* assemblage as consequence of species such as *Ophidion rochei* and *Syngnathus acus*, conferring higher morphological disparity and lesser functional redundancy (Farré et al., 2013).

The comparison between ecological and morphological results indicated higher variability in the grouping from morphological data. The ecological approach grouped geographically separated assemblages based on the relative abundance of *Mullus* spp. and *Pagellus* spp. in the samples, the most abundant species in almost all communities. For this reason, assemblages such as *CA15*, *CR15* and *CSEA15* were located closer to north assemblages. In contrast, the morphological analysis of assemblages primarily reflected the distribution of species within the morphospace, showing that assemblages with similar specific composition and abundance may present low correlation due to differences in their morphospace configurations. Ecological analyses including environmental variables are useful to detect changes in the composition of assemblages, but they can be biased by the relative specific abundance and are ineffective to predict the richness, diversity, redundancy and structure within communities (Mouillot et al., 2005; Petchey and Gaston, 2006; Somerfield et al., 2008; Willis et al., 2005). On the contrary, the morphological structure of assemblages is independent of the abundance and provides supplemental information that allows predicting the ecological habits of species and functional richness within assemblages. Besides, it has been demonstrated that the morphological analyses present high correlations with functional diversity analyses performed in these communities (Farré et al., 2013). Thus, the power of this morphological approach lies in its ability to supply information related with ecological and functional roles of species (Azzurro et al., 2014; Cooper and Westneat, 2009; Costa and Cataudella, 2007; Friedman, 2010; Kassam et al., 2003; Wainwright et al., 2004), which are key factors that help to improve the knowledge about the structure and diversity of communities (Farré et al., 2013; Lombarte et al., 2012; McClain et al., 2004; Montaña and Winemiller, 2010; Tuset et al., 2014; Willis et al., 2005). Therefore, our results support that the analysis of the morphology of species represents a useful

tool in studies of description of community structure, and reinforce its use as an alternative or complement with functional or traditional ecological diversity analyses.

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# 8

## **Depth-related trends in morphological and functional diversity of demersal fish assemblages in the western Mediterranean Sea**





**Depth-related trends in morphological and functional diversity of  
demersal fish assemblages in the western Mediterranean Sea**

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### Abstract

The morphological and functional traits of fishes are key factors defining the ecological and biological habits of species within ecosystems. However, little is known about how the depth gradient affects these factors. In the present study, several demersal fish assemblages from the Balearic Islands (western Mediterranean Sea) along a wide depth range (40-2200 m) were morphologically, functionally and ecologically described. The morphological characterization of communities was performed using geometric morphometric methods, while the functional structures were obtained by the functional categorization of species and the application of principal coordinates analysis (PCoA). The results revealed that morphospaces presented less richness of body forms as depth increases, although they showed a progressive spreading of species towards the periphery, with a proliferation of more extreme body traits, demonstrating lower morphological redundancy. In addition, a trend towards the elongation of body shape was also observed with depth. Moreover, functional diversity increased with bathymetry up to 1400 m, where it sharply decreased downwards. This decrease was parallel to a progressive fall of  $H'$  (ecological diversity) up to 2200 m. Functional redundancy progressively decreased until the deepest assemblage (more constantly in the deeper levels), which was almost exclusively dominated by benthopelagic wandering species feeding on suprabenthos. Redundancy analysis (RDA) demonstrated that both morphological and functional spaces showed high variation along the bathymetric range. Mantel test indicated that the majority of species presented similar spatial distribution within the morphospace and functional space, although in the functional space the more abundant species were always located at the periphery. These results demonstrate that the assessment of the morpho-functional variation between marine communities helps to understand the processes that affect the structure and functioning of communities, such as resource partitioning, trophic interactions, or interspecific relationships within ecosystems such as coexistence and dominance.

**Keywords:** Fish assemblage structure; Deep water; Morphometry; Functional analysis; Ecological diversity; Western Mediterranean Sea.

### Resum

Les característiques morfològiques dels peixos son factors clau a l'hora de definir les estratègies ecològiques i biològiques de les espècies dins els ecosistemes. No obstant, l'efecte de la profunditat sobre aquests factors és poc conegut. En el present estudi, es van descriure, des del punt de vista morfològic, funcional i ecològiques, vàries comunitats de peixos demersals al llarg d'un fort rang batimètric (40-2200 m) provinents de les Illes Balears (nord-est del mar Mediterrani). La caracterització morfològica es va realitzar utilitzant morfometria geomètrica, mentre que l'anàlisi funcional es va obtenir caracteritzant funcionalment les espècies i aplicant un anàlisi de coordenades principals (PCoA). Els resultats van revelar que els morfoespais presentaven menys variabilitat de formes corporals a mesura que la profunditat augmentava, tot i que mostraven una progressiva propagació de les espècies cap a la perifèria, amb una proliferació de formes corporals més extremes, demostrant menor redundància morfològica. A més, també es va observar una tendència cap a l'allargament de la forma corporal. Per altra banda, la diversitat funcional va incrementar al llarg de la batimetria fins als 1400 m, límit a partir del qual va començar a decreixer dràsticament. Aquesta reducció va anar en paral·lel a una caiguda progressiva de  $H'$  (diversitat ecològica) fins als 2200 m. La redundància funcional va reduir-se progressivament fins les comunitats més profundes (de manera més constant en els nivells més profunds), les quals van estar dominades de manera pràcticament exclusiva per espècies bentopelàgiques que s'alimenten de suprabentos. L'anàlisi de redundància (RDA) va demostrar que tant els espais morfològics com els funcionals presentaven variacions importants al llarg del gradient batimètric. El test de Mantel va indicar que la majoria d'espècies presentaven distribucions semblants tant en l'espai morfològic com en el funcional, tot i que en l'espai funcional les espècies més abundants sempre es localitzaven prop de la perifèria. Aquests resultats demostren que l'avaluació de la variació morfo-funcional entre comunitats marines ajuda a entendre processos que afecten a la estructura i funcionament de les comunitats, com ara la repartició dels recursos, les interaccions tròfiques o les relacions de coexistència, competència i dominància entre espècies dins els ecosistemes.

### 8.1 Introduction

In the study of marine benthopelagic communities, depth has been considered one of the strongest gradients affecting composition, zonation, structure and biodiversity (Bianchi, 1992; Stefanescu et al., 1993; Fujita et al., 1995; Labropoulou and Papaconstantinou, 2000; Magnussen, 2002). As the bathymetric level increases, several environmental factors (temperature, salinity, light availability, water pressure, etc.) and ecological conditions (resources availability, trophic relationships, intraspecific and interspecific competition, etc.) significantly change, creating evident bathymetric gradients (Rex, 1977; Gage and Tyler, 1991; Childress, 1995; Cartes et al., 2009b; Drazen and Haedrich, 2012). Many studies have analyzed these variations across wide depth ranges in fish assemblages (Stefanescu et al., 1992, 1993; McClatchie et al., 1997; Cartes et al., 2004, 2015; Menezes et al., 2006; Campbell et al., 2011; Papiol et al., 2012) concluding that, in general, species adapt their ecological, biological and physiological habits to the requirements imposed by the ecosystems (Moranta et al., 1998; Cartes et al., 2002; D'Onghia et al., 2004; Drazen, 2007; Fernandez-Arcaya et al., 2013).

There exist evidences of high variability in depth-related gradients for many biological and ecological factors within communities (Levin et al., 2001; Rex and Etter, 2010; Mindel et al., 2015). Although they can not be generalized worldwide, several trends have been usually described in the structure and composition of fish assemblages over extensive geographical ranges: a usually perceived progressive reduction of abundance and biomass of species below 500 m (Haedrich and Rowe, 1977; Stefanescu et al., 1993, 1994; Powell et al., 2003; Menezes et al., 2006); a usual decrease of biodiversity levels with depth, especially below 1000 m, generally associated with productivity and food availability (Haedrich et al., 1980; D'Onghia et al., 2004; Rex and Etter, 2010; Papiol et al., 2012); a depth-size relationship, tending to smaller sizes especially below 1200-1400 m especially in the deep Mediterranean, determined by food availability, environmental restrictions and intraspecific or interespecific competition (Macpherson and Duarte, 1991; Stefanescu et al., 1992, 1993; Cartes and Carrassón, 2004; Massutí et al., 2004), and a reduction of activity and metabolic rates with increasing depth, affecting functional characteristics (feeding strategies,

reproduction, locomotion, morphology, etc.) of species (Carrassón and Cartes, 2002; Drazen and Seibel, 2007; Fernandez-Arcaya et al., 2013; Neat and Campbell, 2013).

The functional characteristics of species are directly related to foraging and diet strategies, trophic level in food webs, size, locomotion, mobility, lifestyle, activity or distribution in habitat, all key factors for defining the role of species within communities (Petchey and Gaston, 2006; Halpern and Floeter, 2008; Villéger et al., 2011; Mouillot et al., 2014). Theoretical studies of ecosystem functioning suggest that species diversity effects on ecosystem processes can be explained by two major acting mechanisms: i) the occurrence of functional trait variation that allows a complementary, and thus more complete and efficient, use of the available resources to ensure better collective resource partitioning; and ii) selective processes, such as resource limitation or interspecific competition, that promote the dominance of species with special functional traits that perform best under determined ecosystem conditions (Loreau, 2000; Loreau and Hector, 2001; Petchey and Gaston, 2006). Likewise, morphological traits, including body shape, are also considered good predictors of the ecological habits of species, assuming that the adaptation to the environment depends on the use of resources, which is directly linked to the phenotype of species (Gatz Jr., 1979; Douglas and Matthews, 1992; Walker, 2010; Farré et al., 2015). However, few studies have asked how morphology and functional traits of fishes vary depending on the ecosystem that they inhabit, affecting the structure and composition of assemblages. As depth increases, an evolutionary trend toward the elongation of the body shape has been detected (Neat and Campbell, 2013; Claverie and Wainwright, 2014), with anguilliform shapes as dominant morphologies. The locomotion types, directly linked to body shape, have also evolved towards the elongated line, identified as the most efficient strategy because, at low speeds, it is the metabolically most economic mode to overcome the flow resistance, high hydrostatic pressures and water viscosities found in deep ecosystems (Langerhans and Reznick, 2010; Tytell et al., 2010; Vorus and Taravella, 2011). Moreover, commonly abundant deep-sea species have also developed exclusive functional adaptations not found in fishes inhabiting shallower waters. For instance, tripodfishes (Ipnopidae) possess extremely developed rays in the pelvic and caudal fins to allow them to settle on the sea floor and displace along the bottom, while the pectoral fins orientate in vertical position over the head, apparently to detect potential near-bottom swimming prey (Carrassón and Matallanas, 2001; Davis and Chakrabarty,

2011). Mesopelagic species such as Myctophiformes and Stomiiformes have large tubular eyes adapted to capture the maximum amount of light in environments with low light availability, whereas deeper bathypelagic fishes have evolved reduced eyes only for detecting bioluminescence flashes (Warrant and Locket, 2004; de Busserolles et al., 2013). Meso-bathypelagic species such as Stomiiformes or Saccopharyngiformes present oversized mouths and enlarged teeth and jaws to assure the ingestion of any size of food and allow it to be swallowed directly (Herring, 2002; Sutton, 2005). Or deep-sea anglerfishes that show a transformed first dorsal fin spine with a bioluminescent mobile lure on the extremity of the spine acting as a bait to attract preys (Shimazaki and Nakaya, 2004; Pietsch, 2009). Moreover, deep-sea species have also progressed to reduce their metabolic rates and mobility given the decrease of oxygen levels (Drazen and Seibel, 2007; Seibel and Drazen, 2007). In fact, many deep-sea fishes manifest an enlargement of the anterior body region that allows an increased the gill surface and thus elevates the ability to capture oxygen from the environment (Childress and Seibel, 1998; Drazen and Seibel, 2007).

Thus, the analysis of changes in morphological and functional diversity from surface to deep-sea levels, a domain whose environmental gradients are considered as the most extreme on the planet (Gage and Tyler, 1991; Levin et al., 2001), is essential to understand the structure, functioning and transitions between fish assemblages along the bathymetric range. Therefore, the general aim of this study was to assess variation in the morphological and functional structure of fish assemblages with increasing depth. Accordingly, we studied different fish assemblages located around the Balearic Sea (western Mediterranean) across a wide bathymetric range (from 40 to 2200 m). More specifically, the goals of the study were i) to characterize the morphological and functional diversity of the fish assemblages dwelling along the depth range, from shelf to deep slope, as well as analyze the changes of the indices along the bathymetry and their relationship with the ecological diversity, ii) to assess if there exists similarity between the morphological and functional spaces along depth, and iii) to check the usefulness of the study of morpho-functional variation within marine ecosystems as a valid tool for discussing key aspects affecting the dynamics and structure of fish assemblages, such as trophic relationships and prey partitioning among species.

### 8.2 Materials and methods

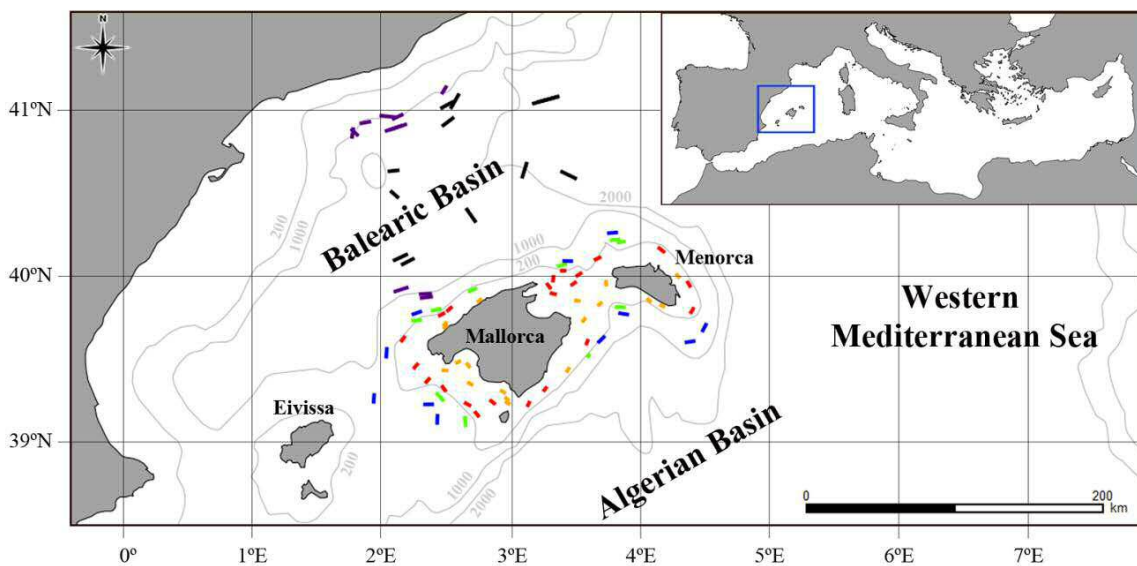
#### 8.2.1 Study area

The study was performed around the coasts of Mallorca and Menorca (Balearic Islands, north western Mediterranean), including a small transect between the NW of Mallorca and the Catalan coast, along the Balearic Basin (Fig. 1). The area presents certain oceanographic variability at shelf (i.e., comparing the areas N and S of the Balearic Islands). The continental shelf of Balearic Islands is especially narrow, with pronounced slope along its edge. Moreover, the slope is very steep, with absence of large marine canyons, and its topography, that plays an important role in the circulation of water masses and transport of resources (Moranta et al., 1998), is more conditioned by geological processes than for cumulative sediment inputs due to absence of river runoff (Massutí and Reñones, 2005). Over the slope (200 to 2000-3000 m depth), the deep Mediterranean is characterized by high stable temperatures and salinity compared, for instance, with neighbouring Atlantic depths. Some oceanographic variability, which influences different biological processes (i.e., communities composition, trophic webs), has been evidenced by the comparison of upper slope communities inhabiting the slopes of the Balearic and Algerian basins (Massutí et al., 2004; Cartes et al., 2008; Moranta et al., 2008a, 2008b). To the north, the Balearic basin is characterized by the presence of large submarine canyons, which greatly affect the environmental conditions of the ecosystems (Puig et al., 2000). In the south, the dynamics of the currents are more driven by atmospheric phenomena, such as wind and temperature, and geomorphological structures such as canyons are absent (Massutí et al., 2014). Despite this mesoscale variability, it has been observed that the fish fauna dwelling on the slopes of both basins is composed of the same species with similar dominance (Stefanescu et al., 1993; Morales-Nin et al., 2003).

The temperature of the surface waters is variable depending on the season, ranging between 13°C (winter) and 27°C (summer) and creating intense gradients between 50 and 100 m (Fernández de Puellas et al., 2004). However, below depths of 200 m, the zone is characterized by a high degree of environmental stability in factors such as temperature (12.8-13°) and salinity (38-38.6‰) (Hopkins, 1985). The deep

## 8. Depth trends in morphological diversity of demersal fish assemblages

Mediterranean Sea has been considered as an oligotrophic environment with respect to adjacent areas, such as the Atlantic Ocean (Pérès, 1985). The oligotrophy of marine systems is directly related with the poor availability of some essential nutrients that affects to the surface productivity and thus to the supply of food resources to deeper levels. However, these particular higher temperatures of the deep Mediterranean can also contribute to the more rapid degradation of the organic matter falling down along the water column below 200 m, causing a decrease in food availability with depth and, consequently, a decrease in the biomass of deep-living organisms (Cartes et al., 2015).



**Figure 1.** Map of the geographical location of the study area: Mallorca and Menorca Islands (Balearic Islands, western Mediterranean) and Balearic Basin, showing the position of the trawl hauls performed during the BALAR survey (in orange hauls performed between 40-80 m, in red 80-250 m, in green 250-500 m, in blue 500-800 m) and during the ANTROMARE 1, 2, 3 and PreTREND cruises (in violet 800-1400 m, in black 1400-2200 m).

### 8.2.2 Sampling

Including all the sampled area, a total of 84 bottom trawl hauls were performed. Data from depths between 40 and 800 m were collected in the trawl fishing grounds along the continental shelf and slope of Mallorca and Menorca Islands (Fig. 1) during the BALAR survey (2002). A total of 61 hauls with durations of 20 to 60 minutes depending on the depth were conducted during May 2002 using the experimental bottom trawl gear GOC73 (commonly used in bottom trawling along the Mediterranean Sea, MEDITS surveys, Bertrand et al., 2002). The tows were carried out during daylight



hours on board of the vessel R/V “Francisco de Paula Navarro” (length: 30 m; engine power: 1100 hp), with an average towing speed of 3 knots. The horizontal and vertical openings of the net (16.4 m and 2.8 m on average, respectively), as well as the position and operation of the net in the bottom and the swept area, were controlled using a SCANMAR system. All details of the sampling can be found in Massutí and Reñones (2005) and Ordines and Massutí (2009).

Otherwise, data from 800 to 2200 m were obtained between the NW slope of Mallorca and the Catalan coast, along a transect that covered the maximum depths of the Balearic Basin (2200 m) (Fig. 1). A total of 23 hauls with durations between 60 and 120 minutes depending on the depth were conducted between June and July 2010-2011 (ANTROMARE 1, 2 and 3 cruises) and May 2012 (PreTREND cruise) on board of the vessel R/V “García del Cid” (length: 37 m; engine power: 1160 hp, average trawling speed of 2.7-2.8 knots). The tows were performed using a standard trawl for the analysis of deep-sea megafauna (Haedrich et al., 1975; Rucabado et al., 1991), the OTSB-14 bottom trawl gear, of 6 mm mesh at the cod end, a bridle length of 8 m and a vertical opening of 1.2 m. More details of this gear and sampling in Cartes et al. (2009c, 2015).

To provide a complete continuous picture of the depth trends of diversity for the entire slope, several ecological diversity indices (see section 8.2.5) were calculated for both datasets (BALAR and ANTROMARE-PreTREND samplings) and including 166 OTSB-14 hauls performed in the Balearic Basin at depths between 149-2263 m in the period 1987-2012 (see section 8.3.5 of Results). These new hauls were added only to perform the ecological diversity analysis (see section 8.2.5), not for the remaining analyses. The characteristics of the hauls were the same cited above for the 23 hauls of the ANTROMARE and PreTREND cruises. We performed the calculations of the ecological diversity for GOC73 and OTSB-14 hauls by separate, since the collecting gears used in both samplings (GOC73 vs. OTSB-14) were different. In spite this difference of gears, the only comparative study existing in the sampling area (Catalan Sea, NW Mediterranean) on the influence of these trawl types on the composition and diversity of deep benthopelagic fish assemblages (Cartes et al., 2009c) indicated that both gears provide equivalent estimates (by swept area) of composition, biomass, abundance and diversity of fish assemblages at mid-slope depths (<800 m), more similar than the results obtained with other trawl systems (Cartes et al., 2009c).

Therefore, both gears allow obtaining a valid representation of the demersal and benthic fish assemblages.

In the first two samplings (61 GOC73 hauls between 40-800 m and 23 OTSB-14 hauls between 800-2200 m), the fish fraction was separated from the remaining biological catch. For each haul, fish were sorted, identified to species level (Mercader et al., 2001), taxonomically classified according to Nelson's *Fishes of the World* (Nelson, 2006) and photographed. Abundance data ( $N/km^2$ ) of each species was also determined. Finally, all the realized fishing operations were classified according to the depth and the geological strata. Basing on this criteria, six fish assemblages were established as study objects (see Table S1 in Supplementary Material) (Stefanescu et al., 1992, 1993; Massutí and Reñones, 2005): Upper continental shelf, 40-80 m (*A*, 18 samples); Lower continental shelf, 80-250 m (*B*, 22 samples); Upper slope, 250-500 m (*C*, 10 samples), Upper-middle slope, 500-800 m (*D*, 11 samples), Lower-middle slope 800-1400 m (*E*, 11 samples), and Lower slope, 1400-2200 m (*F*, 12 samples).

### 8.2.3 Morphological analysis: morphospace configuration and diversity measures

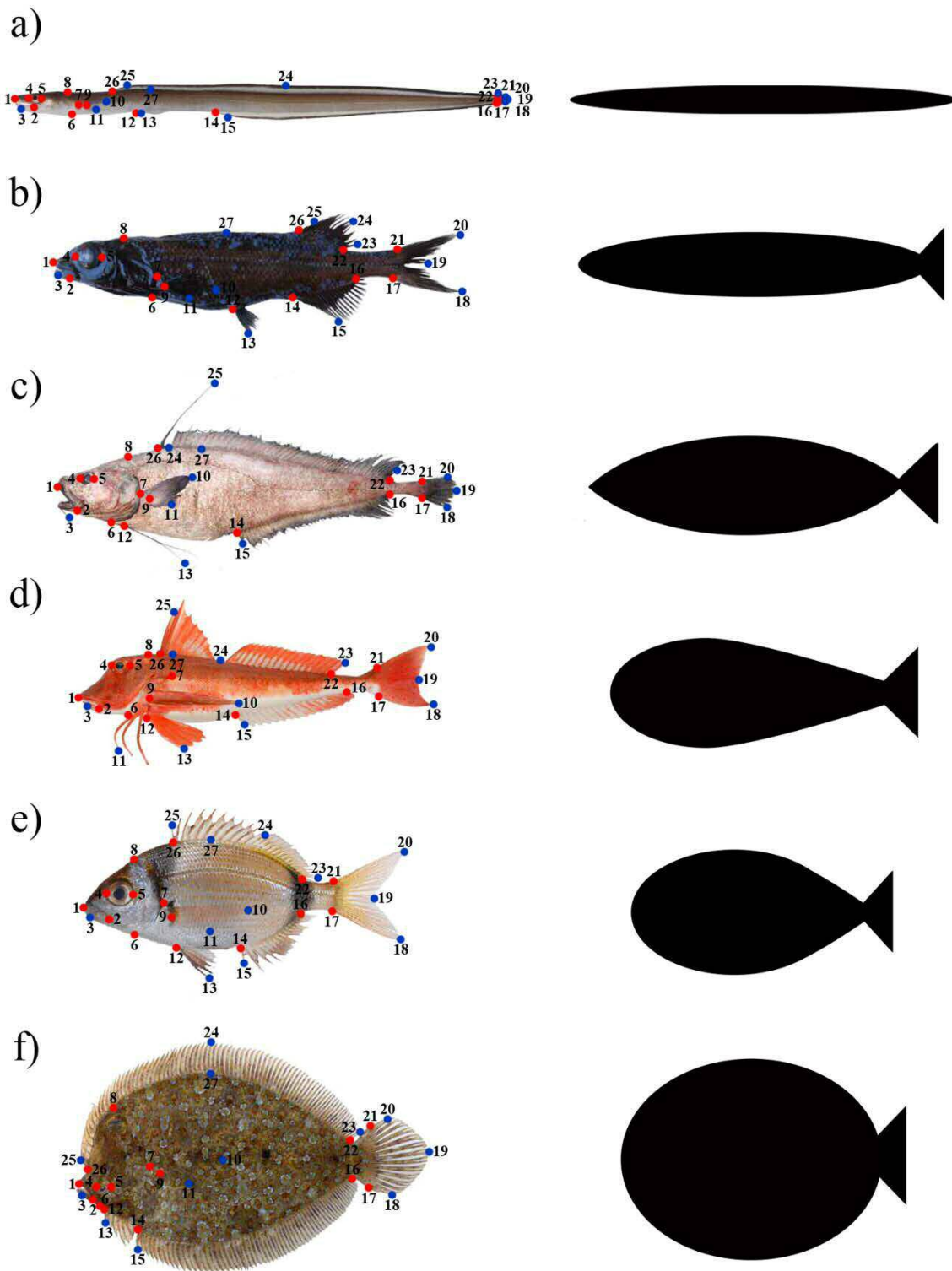
The configuration of the morphospaces of fish assemblages was determined using geometric morphometrics methods (Bookstein, 1991; Rohlf and Marcus, 1993). The analysis of morphological traits of species was realized from standardized images of the left side, previously obtained as a consensus figure from different specimens, selecting a total of 27 landmarks (fixed homologous points) and semilandmarks (sliding or mobile not homologous points) (Fig. 2) with anatomical, ecological and taxonomical meaning (Recasens et al., 2006; Lombarte et al., 2012; Farré et al., 2013, 2015) to describe the shape of each specimen (using tpsDig 2.16; Rohlf, 2010a). The digitized coordinates of the landmarks created a metric map of each species, and this map was translated and rotated to remove scale and orientation distortions not related with shape by the method of generalized least squares (GLS, Procrustes analysis; Bookstein, 1991). The variation in landmark positions (relative warps) of each species was obtained by comparing each specimen to the consensus configuration created with the application of the thin-plate spline approach, which maps the deformation of shape between objects. The GLS

analysis and the obtaining of the relative warps were carried out using tpsRelw 1.49 (Rohlf, 2010b). However, GLS Procrustes coordinates are not expressed in Euclidean shape space. Therefore, these coordinates should be previously projected in a Euclidean tangent space in order to test if the shape variation is small enough to consider this new tangent space as a good representation of the Procrustes data in a Euclidean space (Rohlf, 1999). Then, to check the variation between both spaces, we computed the correlation between the tangent and Procrustes distances using tpsSmall v. 1.28 (Rohlf, 2013). The result of the correlation (unc centred correlation=0.999910, root mean square error=0.000713) confirmed that both spaces were nearly identical for our data.

The analysis of the relative warps allows visualization of the changes in shape between species (Rohlf and Marcus, 1993; Zelditch et al., 2003) and the distribution of species in the morphospace based on their morphological differences. Thus, species were distributed in space according to their morphological characteristics and the axis orientation. Morphospaces were plotted using two-dimensional representations of the first four values of the relative warps because they represent a high percentage (>75%) of the total morphological variation. They were performed using PAST software v. 2.15 (Paleontological Statistics software package, Hammer et al., 2001). Assuming that intraspecific variability is lower than interspecific variability, only one representative image of each species was used (more details of morphometric procedure and description of landmarks scheme in Lombarte et al., 2012; Farré et al., 2013, 2015).

In addition, three morphological diversity indices were also estimated: a) the morphological disparity (*MD*) (Zelditch et al., 2003; Farré et al., 2013), calculated using the first eight relative warps, because they provide more than 88% of the total morphological variability (Recasens et al., 2006; Lombarte et al., 2012). *MD* measures the total amount of morphological variability between species within a community, defining the size and shape of the morphospace; b) the morpho-geometric diversity index (*EMI*) (Lombarte et al., 2012; Farré et al., 2013), more sensitive to the morphological changes between species, allowing species to be grouped based on its morphological similarity. Thus, *EMI* determines the degree of clustering of species within morphospaces based on the relative locations of species, i.e., if they are located together or more distant in space; and c) the morphological richness (*MR*) (Farré et al., 2013), that quantifies the total amount and diversity of different morphological shapes within an assemblage and is directly linked with the specific richness.

## 8. Depth trends in morphological diversity of demersal fish assemblages



**Figure 2.** Location of the 27 landmarks (red points) and semilandmarks (blue points) used to characterize the body shape of fishes using geometric morphometry analyses, as well as geometric figures of the different body shapes considered in this study: *Conger conger*, anguilliform shape (a), *Alepocephalus rostratus*, elongated shape (b), *Lepidion guentheri*, fusiform shape (c), *Chelidonichthys cuculus*, oblong shape (d), *Diplodus vulgaris*, oval shape (e), *Bothus podas*, assymetrical flat shape (f). Fish images obtained from Iglésias, 2013.

### 8.2.4 Functional analysis: functional space configuration and diversity measures

The functional diversity of communities was examined based on indices that describe different dimensions (Mason et al., 2005; Villéger et al., 2008). Initially, several functional traits with biological importance for the fitness of species and their associated categories (Table 1) were selected (Cartes et al., 2002; Halpern and Floeter, 2008; Somerfield et al., 2008; Farré et al., 2013). A functional-trait matrix with the categorization for each species was created (see Table S2 in Supplementary Material). All the nominal variables of the matrix were transformed to binary presence/absence variables, and a principal coordinates analysis (PCoA) was performed with the obtained matrix (Villéger et al., 2011; Claverie and Wainwright, 2014; Mouillot et al., 2014) using InfoStat software (Di Renzo et al., 2008). The coordinates of the first four axes of the PCoA (56.5% of total functional variability) were kept to build the multidimensional functional space (Villéger et al., 2008; Mouillot et al., 2014) to observe the distribution of species of the assemblages within the functional space.

Moreover, the resulting PCoA axes and abundance data were used to calculate different functional indices: a) functional evenness diversity (*F<sub>eve</sub>*) (Villéger et al., 2008), which describes the regularity of species along the trait space taking in account the evenness of their abundance distribution (Mason et al., 2005). *F<sub>eve</sub>* is independent of specific richness and convex hull, and its value range between 0 and 1; b) functional divergence diversity (*F<sub>div</sub>*) (Villéger et al., 2008), an index that determines how the abundance of species spread within the volume of the functional space occupied by species. The index is also constrained between 0 and 1 and shows high values when most abundant species present extreme functional traits, whereas when most dominant species have functional traits close to the centre of functional space, the divergence is lower; c) functional dispersion index (*F<sub>dis</sub>*) (Laliberté and Legendre, 2010), which has no upper limit and represents the average distance of species to the centroid of the functional trait space, taking into account the relative abundances of species. The position of the centroid is weighted by the relative abundance of species and is displaced towards the most abundant species; and d) functional redundancy (*FR*) (Mouillot et al., 2014), an index that represents the number of species within a community per functional entity, where functional entities are each of the unique

## 8. Depth trends in morphological diversity of demersal fish assemblages

combinations of the considered categorical functional traits. The index has no upper limits and provides the degree of functionally similar species within each assemblage. The estimation of the first three functional indices was conducted using statistical software specialized for functional diversity analysis, *FDiversity* (Casanoves et al., 2008; Di Renzo et al., 2008).

**Table 1.** Definition of the 6 selected functional traits and their associated categories used to perform the functional analyses (Cartes et al. 2002; Stergiou and Karpouzi 2002; Colgate and Lynch 2004; Halpern and Floeter 2008; Farré et al. 2013).

Trait	Code	Definition	Trait	Code	Definition
<b>Body shape</b>	Ang	Anguilliform	<b>Size</b>	S	Small 0-10 cm
	Elo	Elongated		SM	Small-Medium 10-20 cm
	Fus	Fusiform		M	Medium 20-30 cm
	Obl	Oblong		ML	Medium-Large 30-40 cm
	Ova	Oval	L	Large >40 cm	
	Sym	Symmetrical flatfish	<b>Vertical distribution</b>	EPIP	Epipelagic
	Asy	Asymmetrical flatfish		MESP	Mesopelagic
		BENTP		Benthopelagic	
<b>Swimming type</b>	Ang	Anguilliform	EPIB	Epibenthic	
	Sub	Subcarangiform	ENDB	Endobenthic	
	Car	Carangiform	BATHYP	Bathypelagic	
	Dio	Diodontiform	<b>Diet (feeding guild)</b>	nmM	Non-migrator macroplankton
	Ami	Amiiform		mM	Migrator macroplankton
	Bal	Balistiform		NS	Nectobenthos-suprabenthos
	Lab	Labriform		EPIB	Epibenthos
Bat	Bathypteroiform	INF	Infauna (endobenthos)		
<b>Motility</b>	S	Sedentary or territorial	EPIP	Macroplankton epipelagic	
	R	Roving			
	H	High mobile or migratory			

### 8.2.5 Ecological diversity indices

To provide a broader overview of the overall diversity of the communities, two ecological measures commonly used in diversity studies related to abundance and richness were also computed for each assemblage (Mérigot et al., 2007a; Farré et al.,

2013): species richness ( $S$ ) and Shannon-Wiener diversity index ( $H'$ ) (Shannon and Weaver, 1949).  $S$  and  $H'$  were calculated per haul along all the depth range and studied by separate for GOC73 and OTSB-14 samplings, including the additional data covering the entire depth range previously explained (section 8.2.2). The indices were obtained using the multivariate software package PRIMER (Plymouth Routines in Multivariate Ecological Research) for Windows v. 6.0 (2008) (Clarke and Gorley, 2006).

### 8.2.6 Statistical analyses

To compare the morphological and functional structure of assemblages along the bathymetry, two methods were used: a) a Mantel test (Mantel, 1967; Smouse et al., 1986), using 5000 matrix permutations and the Euclidean distance as similarity measure. We obtained the Euclidean distance matrix of the morphological (using the first 8 relative warps) and functional structures (using the 17 obtained PCoA values) and we tested the correlation between both matrices; b) the Voronoi polygons, a tessellation method commonly used due to its applicability for multiple purposes, including packing and distribution patterns of species within biological communities (Okabe et al., 2009; Azzurro et al., 2014). The cells are constructed by calculating the perpendicular bisector of the line that separates each individual species from the surrounding species. Thus, the polygons created by the bisectors delimit the space belonging to each species, enclosing all the points in the plane that are closer to that species than to any other species. Within the morphological space, each species is represented by an individual point, whereas within the functional space, points are defined by categorical data, so that different species with similar functional traits may overlap in identical position and thus prevent the application of the Voronoi tessellation. These analyses were conducted using PAST software v. 2.15 (Paleontological Statistics software package, Hammer et al., 2001) and Delone software v. 1.0.1.19.

To determine whether the presence/absence of species influences the morphological and functional characterization of fish assemblages along the depth gradient, a redundancy analysis (RDA) (Legendre and Legendre, 1998) was performed. RDA is an extension of multivariate linear regression, consisting of a constrained ordination that seeks the axes that best represent the linear combination of the explanatory variables.

Moreover, the examination of the obtained canonical coefficients allows the identification of the most important variables explaining the different axes (Ibañez et al., 2007b; Tuset et al., 2015). Three matrices were used to perform the correlation: a presence/absence checklist of species for each community and two matrices with the relative warps (morphological) and the PCoA values (functional) of all the species. A Monte Carlo test (9,999 permutations) was applied to check the statistical significance of the obtained results. Finally, second order polynomial regression models were used to test the relationship between the obtained diversity indices and depth gradient (Zar, 1996; Moranta et al., 1998; Labropoulou and Papaconstantinou, 2000). The analyses were performed using the software XLSTAT v. 2015.3.01, a statistical plug-in of MS Excel 2007.

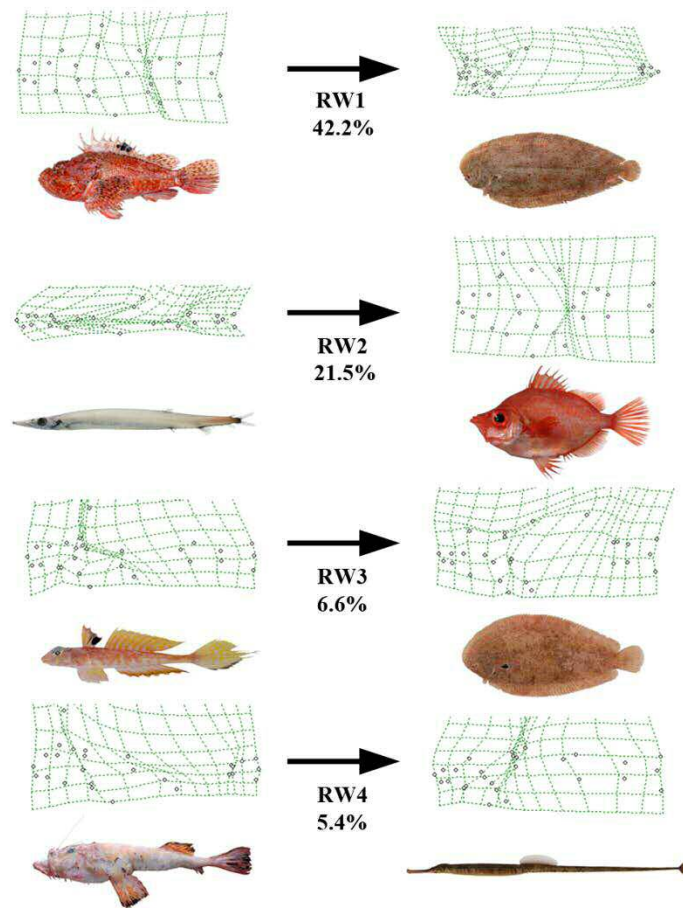
### 8.3 Results

#### 8.3.1 Morphospaces analysis

The representation of morphospaces of the assemblages was performed using the first four relative warps, which explained 75.4% of the total morphological variability, and species were distributed along the axes based on their morphological traits. The RW1 axis (42.2%) separated species based on the type of fins and head size (Fig. 3), where positive values corresponded to species with elongated anal fins beginning near the anterior part of the body; lengthened or continuous dorsal fins extending for most of body surface; small or absent pectoral fins and smaller heads (i.e., Pleuronectiformes, Anguilliformes, Albuliformes, most of Gadiformes); whereas negative values represented species with shorter anal fins originated in the posterior zone of the body, diverse types of shorter dorsal fins; larger or modified pectoral fins and larger heads in relation to the body size (i.e., most of Perciformes, Scorpaeniformes, Argentiniformes, Myctophiformes). The RW2 axis (21.5%) defined the general body shape related to its height and length (Fig. 3). Negative records represented species with elongated (to anguilliform) shapes and positive ones indicated rounded and oval (deep-bodied and laterally compressed) forms. Nevertheless, the negative extreme also indicated some



displacement of the origin of the dorsal fin towards the posterior zone of the body (*Stomias boa*, *Arctozenus risso*, *Syngnathus acus*, *Argentina sphyraena*, *Glossanodon leioglossus*). The RW3 axis (6.6%) differentiated fishes based on the presence of two wide-developed dorsal fins (negative extreme; Triglidae, most of Gadiformes, Perciformes such as *Callionymus maculatus* or *Synchiropus phaeton*) and species with one continuous dorsal fin (positive extreme; Pleuronectiformes, Anguilliformes,



Ophidiiformes, Perciformes such as *Diplodus* spp.). Finally, the RW4 axis (5.4%) also reflected characters of the dorsal fin, from short fins in central or posterior position of the body in high scores (i.e., *Syngnathus acus*, *Notacanthus bonapartei*, *Alepocephalus rostratus*) to large dorsal fins extending for the dorsal surface of the body, with presence of developed or modified first spines in the negative extreme (i.e., *Lophius* spp., *Chauliodus sloani*, *Blennius ocellaris*).

**Figure 3.** Explanatory scheme of the morphological variation observed along each of the first four axes (coinciding with the first four relative warps) from negative (left images) to positive extreme (right images), including images of representative species, the deformation grids and the percentage of variance represented by each axes.

A strong variation in shape was noticed along the bathymetric range between the morphospaces of the different assemblages (RW1-RW2 representations in Fig. 4, RW3-RW4 in Fig. S1 of Supplementary Material). In the A assemblage (40-80 m), the most abundant species were modern Actinopterygian fishes (Perciformes) located close to centroid of morphospace, noting high degree of morphological redundancy. They were

## 8. Depth trends in morphological diversity of demersal fish assemblages

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characterized by rounded/fusiform laterally compressed body shapes, with large heads and with one (*Spicara smaris*, *Booops boops*, *Serranus* spp.) or more dorsal fins (*Trisopterus capellanus*, *Trigloporus lastoviza*). Other fish orders with extreme morphological traits (i.e., Pleuronectiformes, Anguilliformes, Gasterosteiformes, Zeiformes) were poorly represented, distributed on the periphery of the morphospace. Downwards, the morphological structure became more dispersedly distributed within space, and the elongated shapes began to prevail as most abundant species. In general, morphological shapes were progressively moving away from the centroid and the most abundant species were separated more widely between them. In the *B* assemblage (80-250 m), although some shallower abundant shapes remained (*Centracanthus cirrus*, *Serranus hepatus*), more elongated shapes with reduced fins (*A. sphyraena*) also predominated. The *C* assemblage (250-500 m) was dominated by oblong shapes with well-developed fins close to the centroid (*Gadiculus argenteus*), although some shapes more distant from the centre, both fusiform and elongated forms with reduced fins (*A. sphyraena*, *Chlorophthalmus agassizi*) as rounded shapes with large heads (*Helicolenus dactylopterus*) were also importantly present. Oblong species with reduced fins and large eyes displaced from the centroid (*Lampanyctus crocodilus*) were strongly predominant in *D* assemblage (500-800 m), followed by far by more fusiform and elongated forms with longer and modified fins (*Phycis blennoides*, *Nezumia aequalis*). Finally, the deepest assemblages (*E* and *F*, 800-1400 m and 1400-2200 m, respectively) presented morphospaces particularly different, characterized by exclusivity of elongated forms (absence of rounded deep-bodied shapes), lesser redundancy caused by the noticeable shape differences between species and by the dominance of extreme morphologies with strange characters isolated from the centroid, such as *Lepidion lepidion*, *N. bonapartei* in *E* assemblage or *Bathypterois mediterraneus*, *Coryphaenoides guentheri* and *L. lepidion* in *F* assemblage.

### 8.3.2 Functional spaces analysis

Species were scattered throughout the space based on their functional characteristics, whose axes were described by the first four PCoA values representing 56.48% of the total functional variability. The PCoA1 axis (23.51% of total functional variability) was

mainly related to body shape, motility and vertical distribution of species. At the left extreme were placed species with fusiform and oval shapes, with high or medium (roving) mobility and inhabiting the benthopelagic domain (Perciformes such as Sparidae, Mullidae, Serranidae, Carangidae or Centracanthidae, Gadiformes, Argentiniformes), while at the opposite extreme were located species with oblong, symmetric and asymmetrical flat shapes, with epibenthic or endobenthic sedentary habits (Pleuronectiformes, Scorpaeniformes, Lophiiformes, Perciformes such as Trachinidae, Blennidae or Gobiidae). The PCoA2 axis (13.69%) separated species based on functional traits such as the swimming type, body size or diet: positive values defined species with small or small-medium sizes (<20 cm) and carangiform or anguilliform locomotion (most of Perciformes, Pleuronectiformes, Myctophiformes, Stomiiformes, Argentiniformes). Conversely, negative values represented species with bigger sizes (>20 cm) and subcarangiform locomotion (most of Gadiformes, Scorpaeniformes, Albuliformes, Lophiiformes). Moreover, the PCoA3 axis (10.49%) distributed species based on the combination of their own functional traits, although it was mainly driven by the body shape and the swimming type. On the negative side, fusiform or oblong forms with subcarangiform swimming (Scorpaeniformes, most of Gadiformes) were found. The positive side was occupied by species with anguilliform and asymmetrically flat bodies with anguilliform locomotion (Anguilliformes, Pleuronectiformes, Ophidiiformes). In the medium zone were located species with diverse body shapes and carangiform swimming (most of Perciformes, Aulopiformes, Argentiniformes, Stomiiformes). Finally, the PCoA4 axis (8.79%) was mainly linked to the body size of species: in the positive zone were placed species with lengths greater than 20 cm (medium, medium-large or large sizes), while the negative area included species with sizes between 10 and 20 cm (small-medium sized).

Similarly than in the morphospaces analysis, the occupation of functional spaces varied as bathymetry increased (PCoA1-PCoA2 representation in Fig. 4, PCoA3-PCoA4 in Fig. S1 of Supplementary Material). The functional spaces were characterized by an absence of species close to the centroid, and the most dominant species were located in the periphery. The functional spaces of the shallower assemblages (*A* and *B*, 40-250 m) were clearly differentiated into two main areas: a wider and more dispersed zone (left quadrants) of abundant benthopelagic mobile or wandering species with fusiform or oval shapes, and a dense packing of epibenthic and

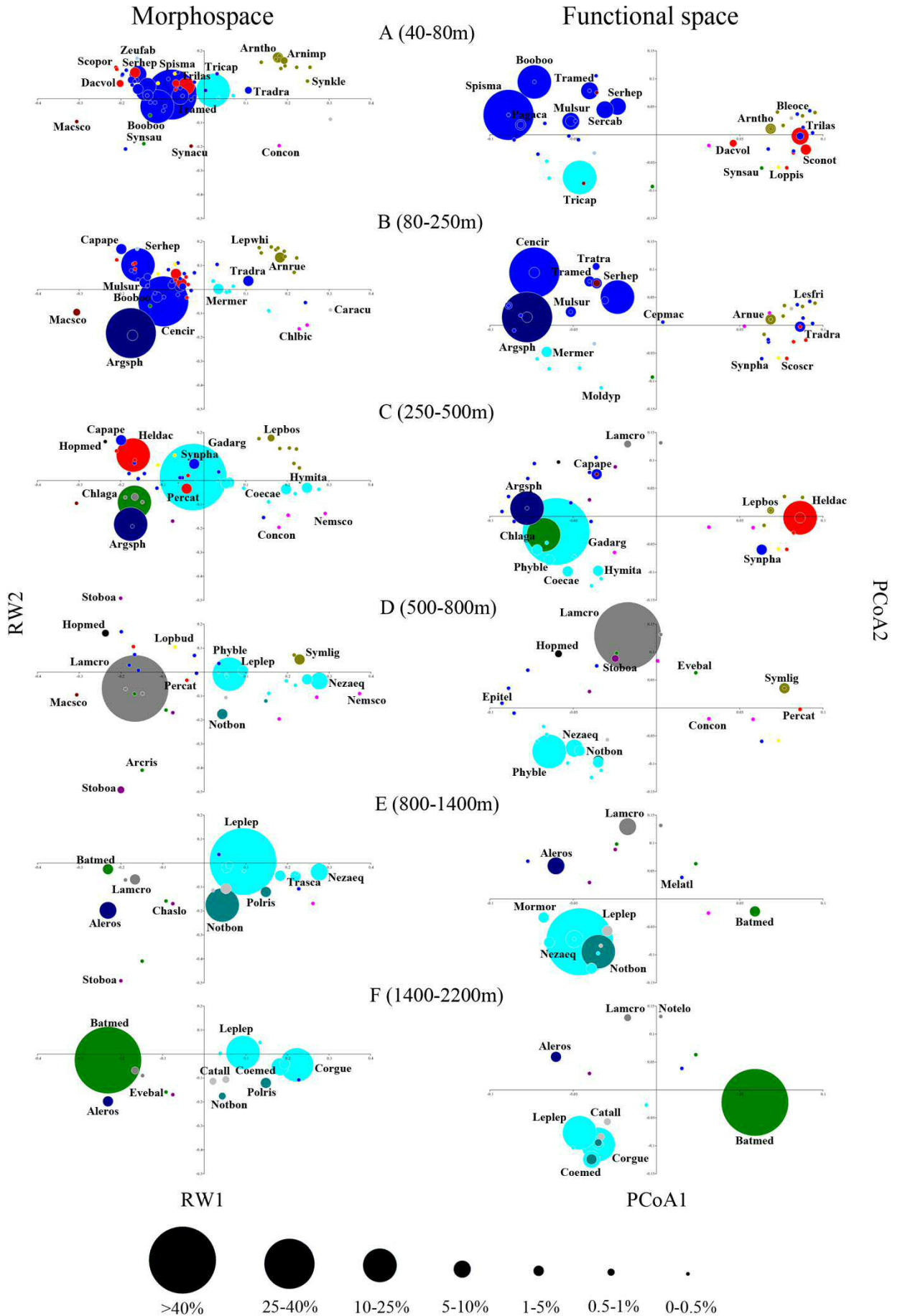
## 8. Depth trends in morphological diversity of demersal fish assemblages

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endobenthonic species scarcely represented (right quadrants), with asymmetric or oblong shapes and low motility. The functional structure showed an expansion in the PCoA2 axis in the intermediate assemblages (*C* and *D*), which was due to the occurrence of mesopelagic and bathypelagic migratory species (*L. crocodilus*, *Notoscopelus elongatus*, *C. sloani*, *S. boa*). In the *C* functional space (250-500 m) elongated or fusiform non-migrant species with subcarangiform locomotion were abundant, although some epibenthic oblong species remain well represented. In contrast, the number of epibenthic and endobenthic sedentary species progressively decreased in the *D* assemblage (500-800 m), simultaneously showing an increased abundance of benthopelagic wandering species of deeper habits with subcarangiform locomotion (Macrouridae, Gadidae, Phycidae or Notacanthidae). Furthermore, mesopelagic migratory species began to strongly dominate, as well as, to a lesser extent, larger and more elongated benthopelagic wandering species. Finally, the deepest assemblages (*E* and *F*) suffered a significant reduction of functional spaces. Most abundant species corresponded to benthopelagic fusiform or elongated shapes, with subcarangiform locomotion and roving habits adapted to deep-sea ecosystems (lower-left quadrant) especially in the *E* assemblage (800-1400 m), although some macroplanktonic active feeders, both mesopelagic (*L. crocodilus*) or highly mobile bigger species (*A. rostratus*), remained noticeably represented. However, an epibenthic and low active species with uncommon and exclusive functional traits (*B. mediterraneus*) became the most dominant species in the *F* assemblage (1400-2200 m).

**Figure 4.** Representation of the morphospace (first column) and functional space (second column) for each assemblage along the bathymetric gradient. In the morphospaces, axes were represented by the first (RW1) and second (RW2) relative warp, and in the functional space by the first (PCoA1) and second (PCoA2) PCoA values. The size of point represents the relative abundance of species (%) within the assemblage, and the colour represents the order to it belongs: Albuliformes (turquoise), Anguilliformes (pink), Argentiniformes (dark blue), Aulopiformes (green), Beryciformes (black), Gadiformes (light blue), Gasterosteiformes (maroon), Lophiiformes (yellow), Myctophiformes (dark grey), Ophidiiformes (light grey), Perciformes (blue), Pleuronectiformes (brown), Scorpaeniformes (red), Stomiiformes (violet), Zeiformes (sky blue). The acronyms of each species are defined in Supplementary Table S1.

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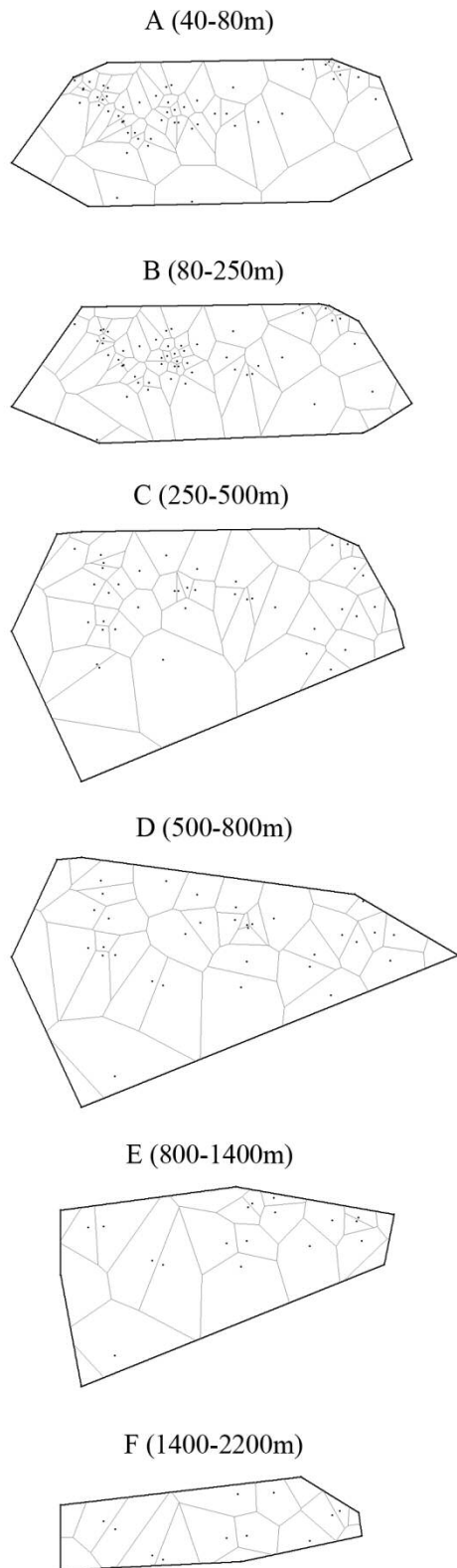
### 8.3.3 Comparing morphological and functional spaces

The Mantel test results indicated a significant correlation between distances of morphological and functional structures for all the fish assemblages (*A* assemblage  $R=0.237$ ,  $p=0.0012$ ; *B* assemblage  $R=0.3232$ ,  $p=0$ ; *C* assemblage  $R=0.237$ ,  $p=0$ ; *D* assemblage  $R=0.3049$ ,  $p=0.0008$ ; *E* assemblage  $R=0.2968$ ,  $p=0.003$ ; *F* assemblage  $R=0.314$ ,  $p=0.012$ ), confirming similarity in the distribution of species within morphospaces and functional spaces.

Moreover, the Voronoi representations evidenced variation in the packing pattern of species between morphospaces, showing a progressive disaggregation of morphologically similar groups of species as depth increased (Fig. 5). The shallower assemblages (*A* and *B*, 40-250 m) were characterized by a high concentration of species (small-sized polygons) in two cores in the left part of morphospace, one more extreme and one closer to the centroid. However, in deeper assemblages, species were progressively more dispersedly distributed, showing bigger Voronoi cells and causing the absence of species aggregations. This dispersion entailed an increase of species in the right zone of the morphospace characterized by elongated shapes (i.e., Macrouridae, Albuliformes or Anguilliformes). The scattering of species reached its maximum degree in the deepest assemblages (*E* and *F*, 800-2200 m), where species were widely separated from each other along the morphospace.

### 8.3.4 Variation in morphological and functional composition along depth gradient

The variation of the different functional categories showed noticeable changes with increasing depth, manifesting a reduction in the number of represented categories in most of the functional traits along the bathymetric range (Fig. 6). Fusiform and oblong bodies were the most abundant in the shallower levels (<500 m), although the elongated forms strongly proliferated to become the dominant shapes downwards. Subcarangiform and carangiform were the most common swimming types, being the first the most abundant as depth increased. Referring to its activity, sedentary species dominated in

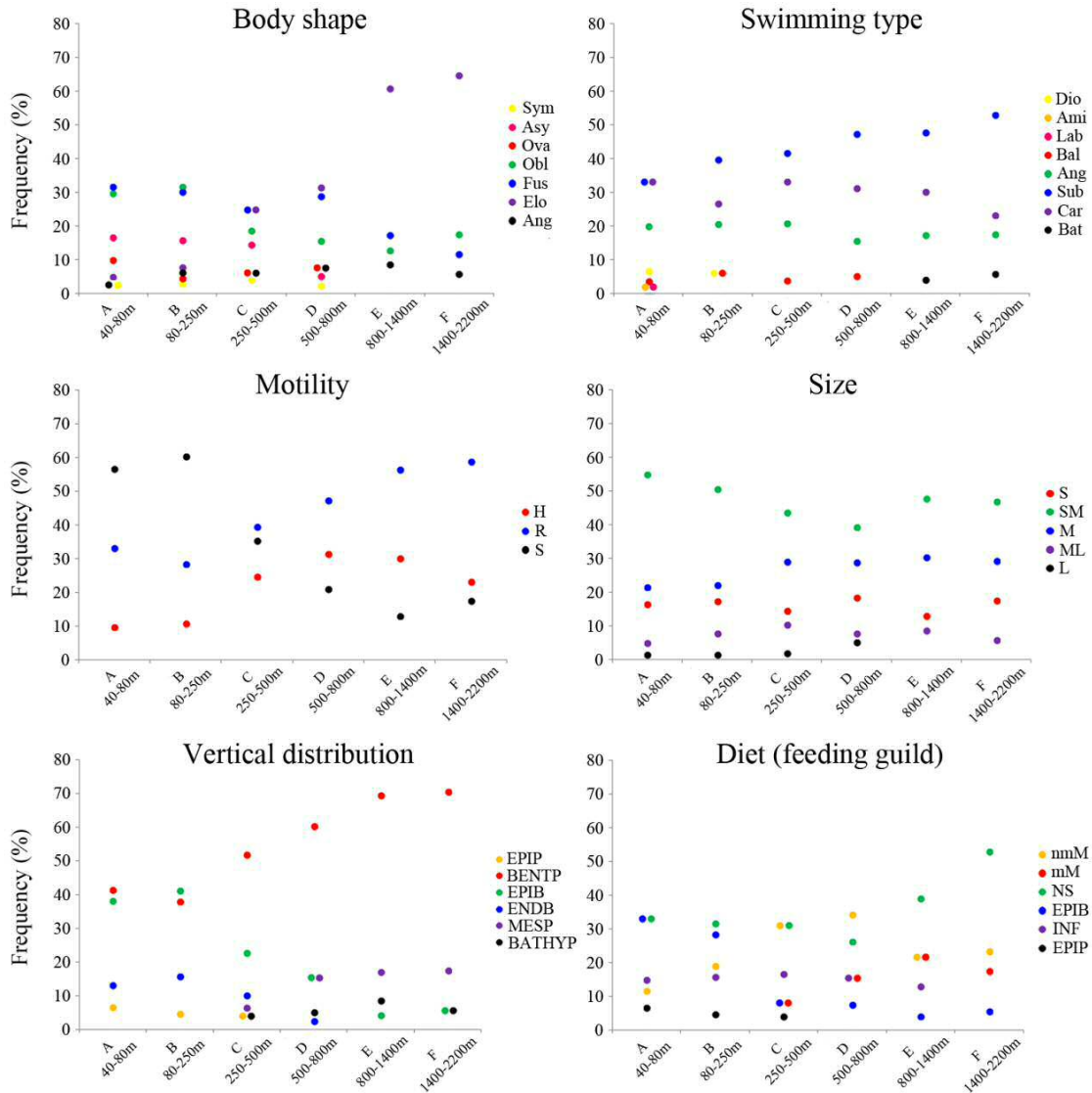


**Figure 5.** Representation of the Voronoi polygons from the morphospace RW1-RW2 for each assemblage along the bathymetric gradient. Each species are represented by a point.

the shallowest assemblages, although they drastically decreased along the depth range analyzed, whereas mobile species increased progressively with depth, with wandering species proportionally the most dominant in the deepest assemblages. Regarding sizes, small-medium (10-20 cm) and medium (20-30 cm) specific sizes were the most common within all the assemblages, showing a trend towards a general size increase (simultaneously growing the medium-sized proportion and decreasing the small-medium proportion) until 800 m. Finally, the vertical distribution and feeding strategies of species followed similar trends. Benthopelagic and nectobenthonic (NS) species were the most common within the assemblages, especially with increasing depth. Epibenthic and endobenthic species, as well as epibenthos feeders, were also abundant in the shallowest assemblages, although they sharply decreased downwards. Conversely, mesopelagic species increased their proportion with increasing depth, similarly to non-migrant and migrant macroplankton feeders, which also increased until 800

and 1400 m, respectively.

## 8. Depth trends in morphological diversity of demersal fish assemblages



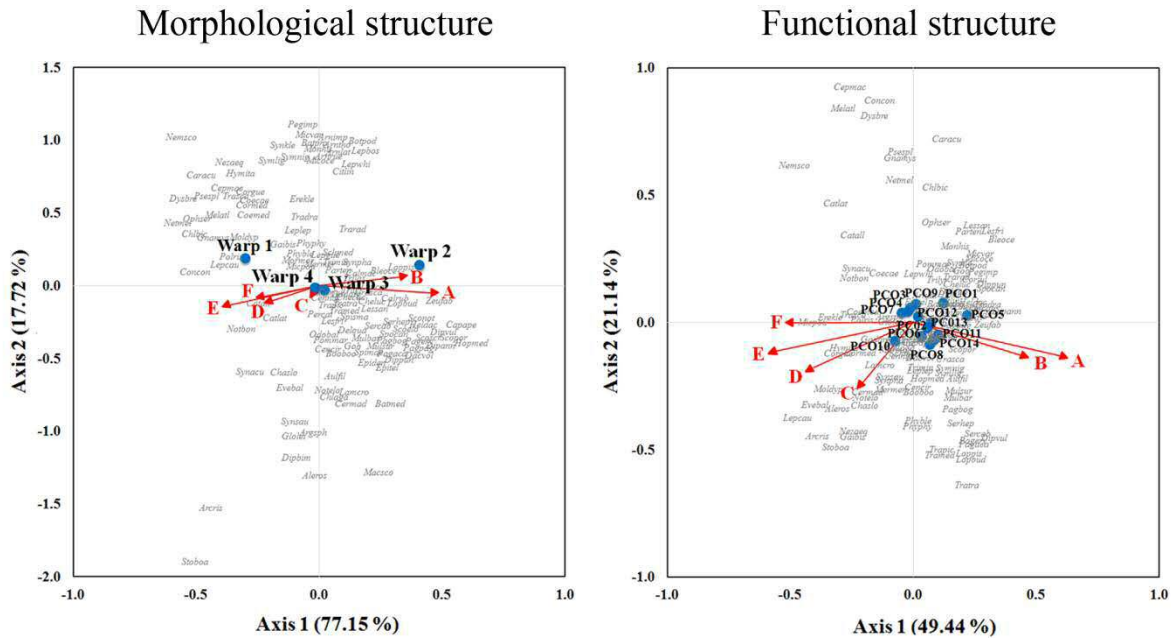
**Figure 6.** Changes of the occurrence frequency of the functional traits along the bathymetric range. Points of colours represent the different categories within each functional trait; X axis represents the assemblages with depth and Y axis the occurrence frequency (% of species) of each functional category.

The RDA permutations evidenced a linear correlation between specific composition and the morphological ( $Pseudo-F=0.159$ ,  $p<0.01$ ) and functional structure ( $Pseudo-F=0.192$ ,  $p<0.01$ ) of assemblages with depth (Fig. 7), demonstrating changes in both structures with increasing depth. In the morphological comparison, the model represented only 13.8% of the total variability, of which the first two RDA axes represented 94.9% of the total variation. The RDA1 axis explained 77.2% of the variance and was correlated with warp 2 ( $r=0.640$ ), which determined the body shape relative to the height and length: from elongated shapes (predominant in the D, E and F



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assemblages) to rounded and oval forms (most abundant in the *A* and *B* assemblages). In contrast, the RDA2 axis was linked to warp 1 ( $r=0.631$ ), was related to the fins type and head size, and determined 17.7% of the total variability.



**Figure 7.** Redundancy analysis (RDA) applied to the morphological and to the functional structure based on presence/absence data of species. The percentage of explained variance by the first two axes is provided. The vectors in red represent each assemblage, and the blue point represents the position of the first four warps (morphological structure) and of the first fourteen PCoA values (functional structure).

In the analysis of the functional structure, the model only explained 7.6% of the total variability. The first two axes of the functional structure explained 70.6% of the total variance, but the variables were not generally related to the axes. The RDA1 axis represented 49.4% of the variance, and the most strongly related variables were PCoA5 ( $r=0.475$ ) and PCoA1 ( $r=0.141$ ). The assemblages were distributed along the axis based primarily on the vertical distribution, motility, diet and body shape of the species, distinguishing the shallowest assemblages (*A* and *B*) from the remaining deeper assemblages. The RDA2 axis defined 21.1% of the variability and was weakly correlated with PCoA8 ( $r=0.171$ ), PCoA1 ( $r=0.144$ ) and PCoA9 ( $r=0.128$ ).

### 8.3.5 Biodiversity-depth relationships

The morphological diversity indices showed differences between communities (Table 2). In general, *MD* and *EMI* exhibited a similar pattern, increasing with depth until 1400 m (*E* assemblage, 800-1400 m) and then decreasing, to a lesser extent in the case of *EMI*, in the deepest *F* assemblage (1400-2200 m). By contrast, *MR* slowly diminished up to 800 m (*D* assemblage) displaying a strong decrease downwards. However, all the indices were significantly correlated with depth in the polynomial regression: *MD* ( $R^2=0.934$ ,  $p=0.017$ ), *EMI* ( $R^2=0.970$ ,  $p=0.005$ ) and *MR* ( $R^2=0.943$ ,  $p=0.014$ ) (see Fig. S2 in Supplementary Material).

The functional diversity values also presented variations among the assemblages, although some of them remained constant along the whole bathymetric range (Table 2). For this reason, *Feve* and *Fdis* did not provide significant evidence of any relationship with depth ( $R^2=0.276$ ,  $p=0.616$ ;  $R^2=0.556$ ,  $p=0.296$ , respectively). By contrast, *Fdiv* and *FR* revealed significant correlations with the bathymetry: an increasing trend up to 1400 m (*F* assemblage) in *Fdiv* ( $R^2=0.926$ ,  $p=0.02$ ), and a decreasing correlation along the whole depth range in *FR* ( $R^2=0.867$ ,  $p=0.048$ ) (see Fig. S2 in Supplementary Material).

Ecological measures of diversity evidenced different trends along depth (Table 3). A clear decrease with increasing depth was observed for species richness (*S*), with significant tendencies for both GOC73 ( $R^2=0.331$ ,  $p<0.01$ ) and OTSB-14 hauls ( $R^2=0.443$ ,  $p<0.01$ ). In contrast, the Shannon-Wiener diversity index (*H'*) showed higher diversity at depths of 500-800 m for OTSB-14 hauls, when the entire slope (150-2300 m) was covered (*H'*:  $R^2=0.299$ ,  $p<0.01$ ). In the case of GOC73 sampling, covering only the continental shelf and upper slope (to 800 m), the maximum *H'* values occurred at shelf (80-250 m) and then also decreased (*H'*:  $R^2=0.161$ ,  $p=0.006$ ) (see Fig. S3 in Supplementary Material).

In addition, the comparison of the Shannon diversity index (*H'*) of the data set used in this study over the middle slope at ca. 600-800 m (Table 3 and Fig. S3) confirm that both gears used in the study (GOC73 and OTSB-14) provide similar estimates of composition, abundance and biodiversity of demersal and benthic fish assemblages at mid-slope depths (< 800m) and thus that they are compatible in the comparative analysis of fish communities performed in the present study.

## 8. Depth trends in morphological diversity of demersal fish assemblages

**Table 2.** Morphological and functional calculated indices for the different communities along the bathimetric strata. *MD*, morphological disparity index, *EMI*, ecomorphological diversity index, *MR*, morphological richness index; *Feve*; functional evenness index; *Fdiv*, functional divergence index; *Fdis*, functional dispersion index; *FR*, functional redundancy index.

Assemblages	Morphological			Functional			
	<i>MD</i>	<i>EMI</i>	<i>MR</i>	<i>Feve</i>	<i>Fdiv</i>	<i>Fdis</i>	<i>FR</i>
<i>A</i> (40-80 m)	0.050	0.124	7.301	0.336	0.799	0.181	1.463
<i>B</i> (80-250 m)	0.045	0.115	7.138	0.301	0.858	0.172	1.575
<i>C</i> (250-500 m)	0.060	0.147	6.916	0.207	0.873	0.178	1.263
<i>D</i> (500-800 m)	0.067	0.174	6.420	0.389	0.916	0.172	1.226
<i>E</i> (800-1400 m)	0.078	0.185	4.059	0.374	0.948	0.191	1.150
<i>F</i> (1400-2200 m)	0.062	0.179	2.866	0.368	0.791	0.157	1.133

**Table 3.** Mean and standard deviation (SD) of the ecological indices calculated for GOC 73 and OTSB-14 hauls separately along the bathimetric range, following the bathimetric zonation previously established. *S*, number of species; *H'*, Shannon-Wiener diversity index.

Assemblages	GOC73				OTSB-14			
	<i>S</i>		<i>H'</i>		<i>S</i>		<i>H'</i>	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>A</i> (40-80 m)	19.4	4.90	2.528	0.23	-	-	-	-
<i>B</i> (80-250 m)	24.1	4.93	2.582	0.34	20.3	2.31	1.529	0.14
<i>C</i> (250-500 m)	23.1	4.38	2.551	0.21	16.2	2.37	1.684	0.26
<i>D</i> (500-800 m)	13.6	3.20	2.173	0.39	17.2	3.16	2.062	0.42
<i>E</i> (800-1400 m)	-	-	-	-	14.1	2.83	1.827	0.29
<i>F</i> (1400-2200 m)	-	-	-	-	11.2	2.15	1.452	0.29

### 8.4 Discussion

Many studies analyzing biodiversity patterns with depth have detected a general increasing trend of the diversity values until intermediate levels. This phenomenon has been observed along the continental slope (deep sea), because at intermediate depths, where the highest diversity occurs, coincide: i) several optimal environmental and ecological factors, such as higher food supply due to accumulation of primary production from shallower levels or optimal oxygen levels (Levin et al., 2001) and ii)

intermediate gradients of biological disturbance, i.e., high/moderate production by low trophic levels and moderate control by top predators maintaining species abundance within levels of coexistence (Gage and Tyler, 1991; Roxburgh et al., 2004). These processes generate a general picture of a “bell-shaped” trend of diversity with depth, which progressively decreases along the bathymetry after reaching maximum values. There exist examples of this phenomenon in deep-sea fish and invertebrates (Gage and Tyler, 1991; Stefanescu et al., 1993; Moranta et al., 1998; D’Onghia et al., 2004; Rex and Etter, 2010; Cartes et al., 2011; Gaertner et al., 2013). Our results of diversity over the entire slope (OTSB-14 data) agree with this trend in indices considering species abundance ( $H'$ ), showing the highest values at 500-800 m and then decreasing downwards especially below 1400 m. The composition of fish assemblages also supports the first studies that analyzed the zonation of fish assemblages in the northwestern Mediterranean along the different levels of the slope (Stefanescu et al., 1992, 1993), including a critical boundary of reduction of food availability (1200-1400 m) that represents the lower limit of distribution of mesopelagic organisms such as lanternfishes and euphausiids, main food source of many demersal fishes, shrimps and crabs (Stefanescu et al., 1992, 1993; Cartes and Sardà, 1993; Cartes et al., 2002). Below this boundary, many species with high energetic requirements (i.e., large fish) are unable to resist these food restrictions (Cartes et al., 2002; Papiol et al., 2012), leading to a decline in diversity and biomass of the lower slope assemblages. Although this falling part of the “bell-shaped” diversity trend is characteristic in abyssal systems (Gage and Tyler, 1991), the particular paleoecology of the deep Mediterranean (Pérès, 1985) could cause the displacement of this fall to shallower (the lower slope) depths.

These changes are clearly reflected in our morpho-functional results, which confirm an evident transition along the bathymetric range of the morphological and functional structures of the fish assemblages. This transition is caused primarily by changes in the depth zonation of species and the substitution of the dominant and subdominant species with depth (Rex, 1977; Stefanescu et al., 1993; Merrett and Haedrich, 1997). Over the shallower levels (at shelf, *A* and *B* assemblages), where environmental factors are less restrictive and resources availability are assumed to be greater (Levin et al., 2001), we observed a higher specific richness. However, this higher number of species was not expressed as richer morphological and functional diversity, as those found from the upper to the lower-middle slope (*C*, *D* and *E* assemblages). The most abundant species

(*Spicara maena*, *C. cirrus*, *A. sphyraena*, *B. boops*, *Trachurus mediterraneus*) presented similar morphological and functional characteristics: rounded and laterally compressed body shapes with small fins or more elongated fusiform shapes with modified fins, and mobile species with good swimming ability feeding on macroplankton in benthopelagic habitats (Cartes et al., 2002, 2008). Thus, they possess similar habits and compete for similar resources, leading to higher morphological and functional redundancy (Guillemot et al., 2011; Mouillot et al., 2014; Villéger et al., 2012). However, on the upper-middle slope (250-800 m), the assemblages began to be dominated by species with different body shapes and lifestyles, from elongated or fusiform dwellers of benthopelagic habits (*G. argenteus*, *C. agassizi*, *P. blennoides*) to oblong sedentary epibenthic feeders (*H. dactylopterus*) or the mesopelagic migratory species (*L. crocodilus*), all of them exploiting mesopelagic zooplankton/micronekton to depths of 1000-1200 m (Cartes, 1998). This space distribution was maintained or even reached its maximum degree in the lower slope assemblages (*E* and *F* assemblages). There, new forms with specialized anatomical characteristics previously absent (*B. mediterraneus*, *A. rostratus*, *C. guentheri*), which coexist or even replace the species of shallower levels, appear as a consequence of the adaptation to the new environmental characteristics (Gatz Jr., 1979; Winemiller, 1991; Douglas and Matthews, 1992; Ingram, 2011). This situation entails an expansion of the morphological structure and a progressive spreading of species towards the morphospace periphery. This morphological diversification, combined with the decline in the number of species, reduced the occurrence of morphologically similar groups and the proliferation of more isolated body shapes, suggesting lower morphological redundancy. Concurrently, the diversity indices agreed with these trends: *MD* and *EMI* significantly increased with depth, while the sharp reduction in the number of species made that *MR* also decreased significantly.

In the functional space, in contrast to the morphospace, the most abundant species tended to be located at the periphery of the space, since that the extreme functional traits allow more efficient use of the available resources (Loreau, 2000; Loreau and Hector, 2001). This peripheral distribution of most abundant species influenced the estimation of indices based on abundance data (*F<sub>eve</sub>* and *F<sub>dis</sub>*), which remained relatively constants along the bathymetry. In contrast, functional divergence (*F<sub>div</sub>*) grew because, as depth increased, species acquired exclusive and peculiar functional traits (*L.*

*crocodilus*, *A. rostratus*, *N. bonapartei*, *B. mediterraneus*), indicating a higher degree of niche differentiation and thus less resource competition (Mason et al., 2005; Micheli and Halpern, 2005; Guillemot et al., 2011; Villéger et al., 2011; Mouillot et al., 2014). This pattern occurs particularly over the lower slope in parallel to the reduction of prey. Hence, among different macrourids, species are specialized consumers of, e.g., different groups of suprabenthic crustaceans (*Coryphaenoides mediterraneus* feeds mainly on mysids, amphipods and some natatian decapods, whereas *C. guentheri* consume less mobile taxa such as cumaceans, and also polychaetes, Carrassón and Cartes, 2002). Moreover, the fact that functional redundancy (*FR*) decreased significantly with depth also supports this higher functional specialization in deeper assemblages. This finding agrees with hypotheses suggesting that the functional assembly of species within communities follows a non-random distribution (Halpern and Floeter, 2008; Guillemot et al., 2011), where an increase in the number of species leads to the aggregation of species in some similar key functional groups (higher redundancy) rather than their addition to other ecosystem functions. However, several studies have revealed that functional diversity is strongly linked to species richness (Micheli and Halpern, 2005; Thurber et al., 2014), and a specific reduction may cause a lack of variety of functions to perform and consequently a loss of ecosystem functioning (Danovaro et al., 2008). This process was also noted in our results, where, for instance, the body shape and the locomotion modes ranged from 7 (shallowest *A* assemblage) to 4 (deepest *F* assemblage) different functional traits, demonstrating the effect of depth on the reduction of ecosystem functioning.

Deep-sea fish species have developed specific adaptations to overcome the constraining conditions of the deep environments (Gage and Tyler, 1991; Cartes, 1998; Cartes et al., 2002). For instance, a trend to the elongation of body shape as depth increases has been detected (Ingram, 2011; 2015; Neat and Campbell, 2013; Claverie and Wainwright, 2014). Our results strongly support this body elongation hypothesis, showing a progressive proliferation of elongated and slender shapes with depth (40-800 m) especially below 800 m, where deep-bodied species were not represented. This elongation phenomenon is attributed to the greater food resource limitation as bathymetry increases, a particularly severe situation in an oligotrophic system such as the deep Mediterranean (Pérès, 1985). Moreover, the body elongation is considered as a more efficient strategy related to swimming and feeding performance in deep-sea

ecosystems (Sfakiotakis et al., 1999; Langerhans and Reznick, 2010; Neat and Campbell, 2013). In the deep Mediterranean, this tendency seemed to be linked to the consumption on a single food compartment in the deepest assemblages: the suprabenthos (or hyperbenthos; swimming macrofauna living close to the bottom, at 0-2 meters above bottom). Some studies have considered that anguilliform swimming is the optimal locomotion strategy in the deepsea given that it is the most energetically economic and efficient strategy at lower speeds (Borazjani and Sotiropoulos, 2009; Inoue et al., 2010; Tytell et al., 2010). In this sense, it is necessary to emphasize that anguilliform elongation (typical of true eels, Anguilliformes) differs from the stiffer-bodied elongation (Aulopiformes, Argentiniformes, Stomiiformes or some Gadiformes) (Ward and Mehta, 2010). The anguilliform elongation directly implies anguilliform swimming, as occurs in Anguilliformes, Ophidiiformes or some Perciformes (*Cepola macrophthalma*). In contrast, species that evolved with other elongation patterns present other swimming modes, usually subcarangiform (Gadiformes such as macrourids, *Gaidropsarus biscayensis* or *Molva dypterygia*, Perciformes such as *C. maculatus*, *S. phaeton*, Aulopiformes such as *Synodus saurus*). In fact, we observed a dominance of subcarangiform swimming over anguilliform as depth increases because it is also a common style in benthopelagic and benthic foraging species that allows manoeuvring, hovering and landing efficiently and economically in deep-sea habitats (Webb, 1984; Killen et al., 2010; Davis and Chakrabarty, 2011). This lifestyle trend along depth also would agree with the reduction of metabolic rates with depth linked to the light availability and to the search of less mobile prey suggested within the visual-interactions hypothesis (Childress et al., 1995; Seibel and Drazen 2007) for midwater fauna. Additionally, the elongation of the body shape entails an increase in body size, noting a trend to larger sizes as depth increases (Rex and Etter, 1998; Morales-Nin et al., 2003; Cartes and Carrassón, 2004; Massutí et al., 2004; Mindel et al., 2015). However, this “bigger-deeper” trend with depth has been demonstrated only until certain bathymetric levels. Our findings agree with this enlargement tendency, although from certain bathymetric layers where the food availability sharply declines (>1200 m), the pattern changes tending to smaller sizes (tendency commonly observed in the Mediterranean, Stefanescu et al., 1992; Moranta et al., 2004).

The benthopelagic deep-sea fauna mainly relies on a reduced portion of food resources originating in euphotic shallower zones, vertically transported downwards and

deposited on the deep-sea bottom (Miquel et al., 1994; Maynou and Cartes, 1998; Cartes and Carrassón, 2004; Papiol et al., 2012). Over the slope, the 250 m layer represented a transitional boundary, the shelf-slope break, regarding the feeding habits of species. The drastic reduction downwards of typically epibenthic (some Pleuronectiformes, Perciformes such as Gobidae, Blennidae or Trachinidae, Scorpaeniformes such as Triglidae) or endobenthic species (some Pleuronectiformes) caused that epibenthos feeders became a minority; upwards over the shelf, in contrast, they were one of the dominating feeding guilds. By contrast, migratory macroplanktonic feeders (Myctophiformes, Stomiformes and some Aulopiformes such as *Evermannella balbo* or *A. risso*) began to proliferate below the shelf-slope break until the deepest assemblage (> 1400 m), where they decreased due to the reduction of mesopelagic (*A. risso*, *Ceratoscopelus maderensis*) and bathypelagic (*S. boa*) species. To survive this food scarcity and coexist, deep-sea fishes have developed efficient resource partitioning strategies based on the bathymetric substitution of species that exploit prey of different size and swimming capacity near the bottom (Cartes, 1998; Carrassón and Cartes, 2002; Cartes et al., 2002, 2009b; Papiol et al., 2013). In the deepest assemblages (below 800-1000 m), we found that, due to the absence of zooplankton, nectobenthos-suprabenthos feeders (*B. mediterraneus*, *Coryphaenoides* spp., *Lepidion* spp., *Cataetyx* spp.) increased as the most dominant guild (Carrassón and Cartes, 2002), supporting the hypothesis that lower slope species are trophically adapted to essentially prey on the suprabenthos compartment (Cartes et al., 2002, 2013).

In conclusion, the present study evidences that the morphological and functional structure of demersal fish assemblages in the Mediterranean Sea noticeably changes with the bathymetry. The food limitation and the fact that the Mediterranean Sea is a partly closed area implies that ecological diversity measures ( $S$  and  $H'$ ), as well as morphological and functional diversity, oscillate differently until 800 m, where they critically decline downwards (Stefanescu et al., 1993; Moranta et al., 1998; D'Onghia et al., 2004; Cartes et al., 2009b; Papiol et al., 2012). We also demonstrate that morphological and functional structures are similar along the bathymetry because the most abundant species are separated by distances that are comparably similar between them and even many species are located at the periphery in both spaces. In contrast, the variation of their indices with depth was different: the morphological changes were sharper than those functional. This result reinforces the idea that body shape allows



inferences about functional diversity from the variety of body forms represented in a fish community (Ingram, 2015). Finally, the results also displayed that morphological and functional redundancy decreases with depth. Most of dominant species are located at the periphery of the functional space suggesting that, in ecosystems where food availability is scarce and environmental restrictions are strong, some ecological strategies are better adapted to overcome the constraints. Thus, as depth increases, these strategies are more efficient and, consequently, more frequent than other ones.

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# 9

## **General Discussion**



The purposes of the present thesis were to characterize and assess the morphological diversity of different fish assemblages using landmark-based GM methods, highlighting the importance of the morphology of the species in the structure and organization of communities. These GM techniques have been applied and tested in several fish assemblages from different life history, geographical locations and environmental conditions, and the outcomes have demonstrated their ability as appropriate and accurate methods capturing the morphology and shape of organisms. In addition, the obtained results have allowed supporting the usefulness and the applications of the study of the morphology of species in several research fields: in biodiversity studies, as a tool that allows computing morphological diversity measures complementary with other diversity components that provide valid information about the functioning of communities; as well as a proxy in studies of structure of communities, emphasizing the role of morphology and shape of species in the understanding of internal processes and relationships that drive the structure and organization of fish communities.

In biological research, many questions can be addressed by the assessment of morphology and shape of organisms or their structures (Thompson, 1917; Bock and von Walhert, 1965; Slice, 2007). The anatomical building of organisms has been seen as a trait dependant of many variables (genetic design, environmental factors, etc.) and resultant of multiple adaptations that allow maximizing the fitness of the organism in a given environment (Bock and von Walhert, 1965). Given its huge plasticity present within the biosphere, morphology is a propriety of species that was early identified as an essential trait driving the lifestyle and ecological and biological habits of species, and consequently also for the functioning of communities (Karr and James, 1975; Ricklefs and Miles, 1994; Wainwright and Reilly, 1994). Following these theoretical premises, the morphology and shape of species was quickly highlighted as a topical factor and its use in scientific studies began to progressively increase, becoming basic in different ecological research fields until nowadays (Bock, 1990; Adams et al., 2004, 2013).

Concerning to the measurement and acquisition of the morphological data of organisms, many techniques have been used across the different research fields with interests in studying the morphology (Zelditch et al., 2004). Currently, the selection of landmarks and semilandmarks has been established as a widely applied technique in order to compute the shape proprieties of structures (Corti, 1993; Rohlf and Marcus, 1993; Adams et al., 2004; Mitteroecker and Gunz, 2009). The results of the present

thesis are another example of application of these GM landmark-based methods in fishes, confirming its effectiveness and success in the study of overall body shape at community level. Landmarks selection is a faster and easier method to compute compared to other more time-consuming methods, such as the linear measurements. Their selection can be performed only using appropriate photographs and software associated, being unnecessary to physically possess the individuals (Clabaut et al., 2007; Maderbacher et al., 2008). This aspect supposes a great advantage because allows analyzing historical data that can be obtained from individuals recorded by images, or even preserved in collections. Besides, the combination of landmarks and semilandmarks allows describing the shape of organisms or structures with a high level of accuracy and detail, as the results of the present thesis demonstrate.

However, the main drawback of this method is the lack of consensus to choose the criteria for selecting the homologous landmarks and semilandmarks between organisms, since differences in the selection schemes can affect to the obtained outcomes (Cadrin, 2000; Klingenberg, 2010; Van Bocxlaer and Schultheiß, 2010). In order to address this issue, the chapter 4 of the present thesis aimed to test the hypothesis if the set of landmarks and semilandmarks chosen to define the body shape of fishes is a factor influencing the morphological variation results, and the conclusions supported this biased effect. In the particular case of the fishes, much of studies applying landmark methods basically highlight the overall body and head, including some particular traits such as mouth and eyes (Valentin et al., 2002; Wainwright et al., 2004; Costa and Cataudella, 2007; Cooper and Westneat, 2009; Young et al., 2009). These anatomical characters are essential defining some lifestyle strategies of species, such as feeding ecology, locomotion, defensive behaviors or reproduction strategies. Instead, other structures with important roles in many habits of species within ecosystems, such as fins or sensory organs (Lombarte and Aguirre, 1997; Wainwright et al., 2002; Weissburg and Browman, 2005; Yamanoue et al., 2010), are usually not included under the arguments that they are not rigid structures, where is difficult to find homologous positions or that sometimes they are absent (Chakrabarty, 2005; Hankison et al., 2006). However, we consider that they should be incorporated (previously defining standardized positions) to the GM analyses since it supply additional morphological information that contribute to describe more completely the anatomy of the species. Therefore, the chapter 4 of this thesis applied and compared several sets of landmarks

commonly used in previous studies with a new scheme proposed in this thesis introducing these mobile structures. Although the results of the new method, in terms of morphological differentiation between species, were similar to other techniques, species with presence of special characters were morphologically better characterized and differentiated. Thus, the study demonstrates that the incorporation of landmarks and semilandmarks describing the position and shape of fins and sensorial organs, such as barbels or free radius in pectoral or dorsal fins, generate consistent results in comparison with previous selecting methods, but in addition helps to better differentiate morphologically the species since it provide a more accurate and detailed description of their overall morphology. Besides, the definition and selection of these landmarks do not require specific expert knowledge neither additional time-consuming maneuvers that entail difficulties in its application. However, although the outcomes of the work are conclusive and satisfactory, this study only represents an example of comparative of landmarks selection methods in order to determine the procedure capturing the maximum amount of morphological information of species and that helps to better differentiate them. More similar studies should be carried out in order to discuss the conclusions of the present thesis and establish generalizations about this topic.

In addition to effectively extract information about the shape of structures, the processing of the shape data allow to define a 'morphospace', a multidimensional space generated by multivariable analysis of the geometric shape data in which each morphologically defined structure locate based on its morphological characteristics (Motta et al., 1995b; Dryden and Mardia, 1998; Lombarte et al., 2012). In the case of defining the shape of the species of a specific community, the morphospace encloses all the shape variation present within a community, and the examination of their internal occupation allows addressing specific biological questions, such as the organization and structural complexity of communities (Wainwright et al., 2002; McClain et al., 2004; Clabaut et al., 2007; Tuset et al., 2016). The distribution and spread of species within morphospaces, as well as the distances between them, is important in order to address these ecological questions. Therefore, the use of analytical methods assessing the pattern of points (species) distribution is necessary (Zelditch et al., 2004; Perry et al., 2006; Werdelin and Lewis, 2013). The chapter 4, 6 and 8 of this thesis has investigated the distribution patterns of species within the morphospaces to infer in the structural complexity of communities using several analytical methods, including numerical

methods, point pattern analyses and graphical representations. The results concluded that, although graphical methods are more complete and provide more valuable information about the occupation patterns, a mixture of both numerical and graphical methods is necessary for the appropriate assessment of the occupation of morphospaces (Wiegand and Moloney, 2004; Perry et al., 2006; Van Bocxlaer and Schultheiß, 2010; Werdelin and Lewis, 2013). Graphical representations such as convex hull, Kernel density, Gabriel graphs, quadrant analysis, patterning or Voronoi cells are usually more intuitive visually and are able to discern the general distribution, density or clustering of points within morphospaces. However, the numeric methods, such as disparity indices or nearest-neighbour distances, are also useful to perform comparatives between very similar structures, since they focus in the distances between points at short scales that are close together (Ciampaglio et al., 2001; Perry et al., 2006; Korn et al., 2013). Besides, they are essential to test the statistical significance and validity of the results that are difficult to visually interpret.

As explained before, the morphological structure (morphospace) of fish assemblages helps to investigate on the ecological and functional habits of species that shape the organization of communities, as well as the mechanisms that drive the relationships between the coexistent species, such as resource differentiation, competence or dominance (Foote, 1997; Kneitel and Chase, 2004; McClain et al., 2004; Willis et al., 2005; Clabaut et al., 2007; Claverie and Wainwright, 2014). The application of GM methods on different fish assemblages with different conditions allowed examining the configuration of morphospaces and assessed its ability with this purpose. In Chapter 6 the morphospaces of epipelagic and mesopelagic fish assemblages at different daytimes were characterized, and their evaluation allowed highlighting that those species possessing special or more extreme morphological traits that are located in the morphospace periphery perform specialized functions adapted to their ecological habits and conditions (ambushers such as most of Stomiidae species or Lophiiformes; vertical migratory zooplanktivores such as *Serrivomer* sp., *Nemichthys* sp., *Opisthoproctus* sp.; etc.) (Loreau and Hector, 2001; Petchey and Gaston, 2006). Instead, more generalist species showed similar common shapes between them occupying closer positions the centroid, area that concentrated more density of species. These outcomes suggest that the morphological traits of species, reflected in their distribution within morphospace,



supply important information about the life habits of species and contribute to improve the knowledge about the functioning and structure of the ecosystems.

However, although morphospaces can be an exhaustive source of information about the structural complexity of communities, the interpretation of the patterns of morphospace occupation can be problematic. Usually, numerical measures quantifying the disparity of species can be more explicative, and in many occasions have been used with these purposes (Ciampaglio et al., 1991; Foote, 1993, Clabaut et al., 2007). These measures of the morphological diversity are complementary methods helping to examine the structure of morphospace, becoming essential tools in the assessment of the dynamics that drive the functioning of communities (Foote, 1997; McClain et al., 2004). Recently, GM landmark methods have also been used to generate indices of morphological diversity (Recasens et al., 2006; Lombarte et al., 2012). Using the components of shape variation extracted from the analytical process, it was possible to easily and quickly elaborate measures providing information about the morphological diversity of communities and at the same time about the structural complexity of fish assemblages, such the amount of morphological variation within morphospace that defines size and shape of the morphological structure (*MD*, Zelditch et al., 2003; Antonucci et al., 2009) or about the clustering and distribution of species within the morphospace (*EMI*, Lombarte et al., 2012). The Chapter 5 of the present thesis used GM techniques to compute these morphological indices on coastal fish assemblages and evaluate their ability and proprieties as good biodiversity metrics. In addition, a new morphological measure is presented (morphological richness, *MR*) able to quantify the total amount of different morphological forms within communities and therefore useful and effective as biodiversity index. Besides, given that the concept of biodiversity is considered as multicomponent enclosing many different biological aspects (Purvis and Hector, 2000; Lyashevskaya and Farnsworth, 2012; Magurran, 2013), the morphological indices were compared with other metrics also computed from other biodiversity components (ecological, taxonomical and functional diversity) in order to contrast and consolidate them as a valid and complementary biodiversity alternative. Each of the morphological indices correlated significantly with any of the other biodiversity components: *MD* was related with taxonomic indices, *EMI* was linked with some ecological indices and *MR* showed good relationship with richness and abundance indices as well as with the functional diversity. These results demonstrated their good

adaptability within the complex net of diversity competences as well as the success of this morphological approach in the assessment of the biodiversity and structure of fish communities. The characterization of the biodiversity of coastal fish assemblages of the Catalan Sea (Chapter 5 and 7) and demersal fish communities from the Balearic Basin (Chapter 8) performed in this thesis also confirmed that morphological indices are able to supply information about the ecological and functional role of species, and therefore are useful as a complementary tool in biodiversity indices, especially to the measures that only capture information related with abundance or specific richness. In addition, the results of the Chapter 5 also showed that the morphological indices computed with qualitative (presence/absence) data presented good correlations and similar results with those calculated with quantitative (abundance) data. This conclusion suppose an important finding and progress in studies of biodiversity of communities, since demonstrates that quantitative data is not necessary to assess the diversity of communities, providing the opportunity to analyze i) the evolution and changes of fish assemblages al large-temporal scales only from historical qualitative checklists, or ii) heterogeneous data obtained with multi-gear sampling, cases where is not possible to apply commonly used ecological diversity indices.

In Chapter 7, the aim was to analyze the morphological structure of several coastal fish assemblages of the Catalan Sea (NW Mediterranean), as well as to determine the environmental factors that affect to the composition and abundance of communities. The results determined that environmental factors, especially the type of substratum and at lesser extent the geographical location, are useful to identify the differences of composition and abundances between communities (Macpherson, 1994; Demestre et al., 2000a). Fish assemblages inhabiting bottoms with presence of hard substrata presented higher diversity, specific richness and abundance values, since i) favors the settlement and growing of a great variability of epibenthic fauna and macroalgae, potential food source for many demersal fishes (Ruitton et al., 2000; Ordines and Massutí, 2009; Martins et al., 2013, de Juan et al., 2013), ii) their configuration allows the occurrence of holes that act as optimal refuges to avoid predators or as nursery areas (Almany, 2004; Humphries et al., 2011). Moreover, the organization and functioning of assemblages associated to soft substrates usually is less complex because the epibenthos is less extended and developed and trophic relationships between species are more visually-based. These environment characteristics favor the increasing presence of

species with particular ecological habits (mimetic and cryptic traits, endobenthic habits, ambusher feeding strategies), but in general entail lower biodiversity of fish species (Guidetti, 2000; Letourneur et al., 2001; Tuya et al., 2005). Besides, the higher exposition to external physical disturbances, such as fishing activity, causes that soft-bottom environments usually are more sensible and vulnerable to perturbations and impacts, affecting to the composition, richness and biodiversity of their communities (Demestre et al., 2000b; Kallianiotis et al., 2000; Colloca et al., 2003; de Juan et al., 2013). The geographical location also influenced in the composition and diversity of fish assemblages, probably attributed to the different fishery management programs of the studied locations. In the north (L'Estartit) the artisanal fishery effort is concentrated in a small area (Martín et al., 2012, Stelzenmüller et al., 2009), affecting in higher extent to the abundance and biodiversity of fish assemblages than in the central zone (Vilanova i la Geltrú-Calafell), where the fishing area is larger and the active fleet use different fishery strategies at different seasons during the year to optimize the yields (Demestre et al., 1997, Maynou et al., 2011). However, the analysis of morphospaces focuses in the morphological and shape variability within the assemblages, which is directly linked to the complexity of the habitat (Willis et al., 2005; Villéger et al., 2010; Kovalenko et al., 2012). The performed comparisons demonstrated that assemblages with similar environmental conditions but differences in the habitat complexity presented low similarity in their morphospaces, whereas in some cases assemblages with differences in location or type of substrate manifested higher correlations. Thus, the analysis of morphospace configurations allows better differentiating the structure of communities than other ecological analyses, only able to detect changes in the specific composition and abundance. By quantifying the body shape of species and its variation within communities, it is possible to infer in the ecological and functional habits of species, key aspects defining the organization of communities (Winemiller et al., 1991; Wainwright et al., 2004; Petchey and Gaston, 2006; Costa and Cataudella, 2007). Therefore, the study support again that morphology of species is a useful source of information in the analysis and understanding of the structure of communities, as well as a complementary tool in studies of biodiversity of systems (Willis et al., 2005; Montaña and Winemillier, 2010; Lombarte et al., 2012; Azzurro et al., 2014).

In marine ecosystems, depth has been widely identified as one of the most important environmental gradient influencing to the dynamics, structure and functioning of

biological communities (Gage and Tyler, 1991; Bianchi, 1992; Fujita et al., 1995; Levin et al., 2001; Rex and Etter, 2010). Many environmental factors (temperature, salinity, pressure, oxygen concentration, light availability, etc.) noticeably change as the bathymetric range increases, causing that deep-sea levels are considered the domains with the most extreme conditions on the overall planet (Gage and Tyler, 1991; Levin et al., 2001). Thus, the species inhabiting these environments has adapted their life habits to overcome these strong restrictions. In fishes, depth-related changes have been addressed from multiple viewpoints. For instance, changes in body size (Stefanescu et al., 1992; Rex and Etter, 1998; Mindel et al., 2015), metabolism activity (Carrassón and Cartes, 2002; Drazen and Seibel, 2007; Fernandez-Arcaya et al., 2013) or modifications of many anatomical features (Merrett and Haedrich, 1997; Herring, 2002; Sutton, 2005; Lombarte and Cruz, 2007) have been commonly detected along the bathymetric range, among others. However, the evolution with depth of the general body shape of species is an aspect that has attracted much less attention (Neat and Campbell, 2013).

Given the importance of morphology of species in the ecological and biological behaviors within communities, Chapter 8 aimed to apply the morphological approach used during the entire thesis in order to examine the morphological transition of fish assemblages along a wide bathymetric range (40-2200 m), as well as to check again its ability as a descriptor of the processes that shape the structure and organization of communities. In addition, a parallel analysis of the functional diversity along the assemblages was performed. Analyses based on pooling of multiple functional traits from the species are currently a powerful and widely extended tool in marine studies addressing many ecosystem aspects, such as the ecological functioning of communities or the assessment of natural or anthropogenic disturbances on the ecosystem performance in order to integrate appropriate management measures, since functional traits of species are indicative of the role that organism play within the ecosystems (de Juan et al., 2007; Somerfield et al., 2008; Villéger et al., 2011; Mouillot et al., 2014; Muntadas et al., 2015). Therefore, they are interesting and useful complementary methods helping to complete the analysis of the variation of the structure of fish communities along wide depth gradients. The results of the study showed that the morphological diversity decreases along the bathymetry: the shallower assemblages possessed higher variability of different body shapes but also a higher morphological redundancy, whereas deeper assemblages manifested less morphological richness but

showed more extreme anatomical characteristics and less redundancy of forms. In addition, a trend to the elongation of the body shape was clearly perceived along the bathymetric (Neat and Campbell, 2013), even with total absence of deep-bodied shapes in the deepest assemblages. The analysis of the functional diversity and structure of assemblages provided similar results than those of the morphological analysis along depth, manifesting also i) less degree of redundancy as depth increases and ii) more peripheral position of most dominant species along the bathymetry (Loreau and Hector, 2001; Loreau et al., 2001; Danovaro et al., 2008). These results suggest that species acquire higher levels of functional specialization as depth increases. However, reduction in the number of species, which is known affecting to functional diversity of ecosystems (Micheli and Halpern, 2005; Danovaro et al., 2008; Guillemot et al., 2011), entail lesser degree of functional redundancy and increase the probability of loss of particular functions, which may affect to the vulnerability and the resilience of the ecosystem (de Juan et al., 2009; Mouillot et al., 2014, Muntadas et al., 2016). Our results reflects these statements, since as depth increases the number of different functional traits progressively declines, demonstrating the effect of depth in the reduction of the ecosystem functioning and stability.

The ensemble examination of the morphological and functional allowed addressing in some internal aspects of the communities, especially the food resources partitioning. While in the shallower levels coexist species with many morphological and functional strategies that exploit similar or different food compartments based on their adaptations, the progressive scarcity of resources as depth increases causes that species acquire higher degrees of specialization in the resource partitioning that allow them to survive and coexist within the community (Carrassón and Cartes, 2002; Cartes et al., 2002; Papiol et al., 2013). To overcome the strict restrictions of the deep environments, deep-sea fishes develop extreme morphological and functional adaptations directed to optimize and maximize the efficiency of the obtained resources, such as reduction of their metabolic and locomotor activity (Drazen and Seibel, 2007; Seibel and Drazen, 2007), specialization in determined food strategies (Cartes et al., 2002, 2013) and trends to determined body shapes and sizes (Stefanescu et al., 1992; Cartes and Carrasson, 2004; Neat and Campbell, 2013; Mindel et al., 2015). These bathymetric trends in the habits of species cause a progressive substitution and segregation of the most dominant species based on their adaptation abilities the new environments. Therefore, the results

## **9. General Discussion**

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of this chapter support again that the general morphology and shape in fishes is a factor that allows inferring in the functional and ecological role of species, which are essential to understand the different processes that determine the structure and functioning of fish communities, such as the resources partitioning, trophic interactions or specific relationships such as dominance, coexistence or competence.

# 10

## **Conclusions**





1. The specific method of selecting landmarks affects to the distribution of species within the morphospace. The inclusion of landmarks and semilandmarks defining the body shape and special anatomical structures of biological meaning, such as fins or sensory organs, provide a clearer differentiation between species, contributing to better define the species ecologically and helping to improve the interpretation of the morphospace occupancy.
2. A mixture of numerical and graphical analytical methods is the better option in order to assess the occupation of morphospaces. Graphical methods such as Kernel density, Gabriel graphs, patterning methods or Voronoi cells provide a visually more intuitive and interpretative approach, especially in zones with a high density of species. However, numerical analyses are also necessary to test the significance of the obtained results.
3. The application of GM methods on the fish body shape allows obtaining morphological diversity indices (*MD*, *EMI* and *MR*) that represents a valid and useful tool to complement studies of biodiversity of communities. They provide information about the variation in the shapes and morphologies (and therefore of functions, roles and strategies) within communities.
4. These morphological diversity metrics are independent between them and correlate significantly with other biodiversity components, demonstrating their appropriate assembly within the complex net of multiple components of biodiversity: *MD* is directly linked with the taxonomical variability within communities; *EMI* define the structural complexity and taxonomical structure of communities, while *MR* correlates with measures of specific richness and functional diversity. These results support and reinforce their ability as a complementary tool in studies of biodiversity of communities.
5. The GM procedure that allows computing the biodiversity metrics is easily and quickly applicable in comparison with other alternative methods, and do not require specialized degree of knowledge about morphology of species. In addition, the morphological indices yielded equivalent results based on both quantitative (abundance) and qualitative (presence/absence) data.

6. The obtained results confirm that the analysis of the fish shape variation based on GM methods is useful and essential to assess the structure of communities, especially when ecological and environmental information is lacking or scarce. In addition, it allows analyzing communities from qualitative databases, providing the possibility 1) to study the evolution of fish assemblages over long-time periods only from historical checklists avoiding the necessity of costly and hard to obtain quantitative data, or 2) to compare data from heterogeneous or multi-gear samplings.
7. The assessment of the morphospaces from coastal to deep-sea, including mesopelagic, fish assemblages from the Catalan coast, Balearic Sea (NW Mediterranean) and Canary Islands (NE Atlantic) also demonstrated that the analysis of the internal distribution of morphospaces contributes to better understand the structure, organization and functioning of fish communities.
8. In the studied coastal fish assemblages of the Catalan Sea, the ecological characterization of communities grouped communities mainly based on the geographical proximity and the proportion of the most dominant species. In contrast, the morphological approach showed greater differences among communities, was independent to the abundance and specific composition and grouped assemblages based on the distribution of species within the morphospace, allowing inferring in their ecological and functional habits within ecosystems.
9. The low similarity among the different analyzed morphospaces reinforces the theory that morphology of fishes is directly linked to the habitat complexity: the communities that presented higher habitat complexity (e.g., mixed bottom types or artificial reefs) possessed higher number of different body shapes because they allow supporting a higher variability of different ecological strategies and lifestyles.
10. The type of substratum and the geographical location affected significantly to the ecological composition of the coastal fish communities. Assemblages with mixture of different bottoms presented richer and more diverse compositions, whereas assemblages with soft bottoms were ecologically simpler and supported less number of species. River inputs, the different fishery policies and the introduction of artificial substrata also contributed to the observed differences among assemblages between locations.

- 11.** In the analysis of the morphospace transition along depth performed in demersal fish assemblages around the Balearic Islands, several general trends were observed: 1) a progressive reduction of the richness of different body shapes, linked to the decrease in the number of species; 2) a proliferation of morphologically more extreme shapes, causing a general dispersion of species towards the periphery of morphospace progressively reducing morphological redundancy; 3) the specific abundance followed a similar dispersed tendency, being the most dominant species more widely distributed and separated between them; and 4) a general trend towards the elongation of the body shape, considered as a more efficient strategy in deep-sea ecosystems, and a progressive reduction of deep-bodied shapes (dominant in shallower assemblages) until totally disappearing in the deepest levels.
- 12.** The pattern of the distribution of most of species was similar within both morphospaces and functional spaces along the bathymetric range. Both structures manifested evident changes as depth increases, mainly driven by the environmental restrictions, the replacement of the most dominant species and the food availability. The constraining conditions along depth caused that morphological and functional diversity, as well as the specific richness, progressively declines until middle slope depths (800 m), levels where they critically declined downwards.
- 13.** Functional diversity increased with depth up to 1400 m, from where drastically decreases. Downwards, the strong reduction in the number of species, linked to the functional diversity, causes an impoverishment on the ecosystem functioning (in terms variability of functions) in the deepest levels of the slope.
- 14.** Instead, morphological and functional redundancy constantly decreased until the deepest assemblage. The restrictive environmental conditions and the limitation of resources of deep-sea ecosystems select towards acquiring particular extreme strategies to overcome the restrictions. Among other adaptations, species develop higher specialization levels in the use of the available resources, causing a lower degree of competition and thus a high degree of niche differentiation.
- 15.** The general results of this thesis support and reinforce the hypothesis that the morphology of species is a good tool addressing and predicting the ecological and functional roles of species within ecosystems. The analysis of the morphospace allows inferring key aspects affecting the dynamics of communities, such as the

## **10. Conclusions**

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resource partitioning, the habitat differentiation, zonation or interspecific relationships such as competence, dominance and coexistence. Thus, the assessment of the morphological variability among species helps to better understanding the structure, organization and functioning of communities.

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# 12

**Resum  
de la tesi doctoral**



## 12.1 Introducció

L'anàlisi de la morfologia dels organismes ha estat una disciplina clau dins la comunitat científica des dels inicis del segle XX, quan va començar a establir-se una relació directa entre el fenotip (característiques anatòmiques) dels organismes i les condicions ambientals del seu entorn (Allen, 1907; Thompson, 1917; Bock and von Wahlert 1965). L'estudi de la variabilitat morfològica entre espècies va esdevenir un anàlisi essencial a l'hora d'entendre la evolució, adaptacions i estratègies dels organismes dins els ecosistemes on habiten (Bock, 1990). A mitjans de segle XX (anys 1950-1960), el camp científic va experimentar un salt important, quan la morfologia va començar a considerar-se com un component no només lligat a les condicions externes, sinó també com un factor que permetia definir i entendre els rols ecològics i funcionals de les espècies dins els ecosistemes. Els ecòlegs es van veure ràpidament atrets per aquestes idees, ja que els permetien abordar aspectes tradicionalment del seu d'interès, com ara la repartició de recursos o la diferenciació de l'hàbitat, que ajudaven a entendre el funcionament de les comunitats biològiques (Hutchinson, 1959; Keast and Webb, 1966; MacArthur, 1968; Schoener, 1974). En aquest context, aprofitant la creixent relació entre la morfologia i la ecologia de les espècies, un nou concepte (anomenat *ecomorfologia*; Karr and James, 1975) va ser definit amb l'objectiu d'analitzar les interaccions entre la morfologia de les espècies i els seu entorn dins un context ecològic i evolutiu (Motta et al., 1995a; Douglas and Matthews, 1992; Ricklefs and Miles, 1994). A més, aquestes relacions podien ser analitzades a diferents escales (des d'organismes individuals fins a nivell de comunitats), fet que va permetre que comencés a aplicar-se en estudis d'organització i estructura de comunitats (Gatz, 1979; Winemiller, 1991; Wainwright and Reilly, 1994).

Els mètodes de mesura i anàlisi de la morfologia de les espècies han evolucionat contínuament des dels inicis en la matèria. A principis del segle XX, l'estudi de la morfologia va manifestar una evolució important, des d'un camp tradicionalment descriptiu cap a un de quantitatiu i mesurable. Els estudis van començar a recopilar mesures de les característiques anatòmiques de les espècies. De fet, amb el temps i els avenços analítics i estadístics associats, la mesura i anàlisi de la forma corporal dels organismes (*morfometria*) va esdevenir el mètode més àmpliament aplicat a l'hora

d'avaluar la variabilitat morfològica existent (Bookstein, 1991; Dryden and Mardia, 1998; Adams et al., 2004). Inicialment, els estudis més tradicionals empraven mesures lineals de les estructures anatòmiques, juntament amb mètodes analítics complexos. No obstant, aquests mètodes van començar a ser qüestionats, ja que presentaven nombrosos inconvenients associats a problemes d'al·lometria i mida de les estructures, així com d'estandardització de les comparatives. Durant els anys 1980-1990, en el camp de la morfometria es van desenvolupar un conjunt d'avenços analítics en l'obtenció de les dades morfològiques que van suposar una revolució. La característiques geomètriques de les estructures (basades en coordenades cartesianes en l'espai) van esdevenir components essencials en l'anàlisi de la morfologia, i simultàniament es va desenvolupar un suport estadístic i multivariant molt potent i robust per al seu anàlisi. Aquesta nova disciplina revolucionària es va conèixer amb el nom de *morfometria geomètrica* (GM) (Bookstein, 1991; Rohlf and Marcus, 1993).

Des dels seus orígens, la GM dels objectes s'ha obtingut mitjançant nombrosos els mecanismes, incloent mesures de contorns (com els anàlisis de Fourier, escales de curvatura o "wavelets") o tècniques de definició de punts de coordenades fixos i homòlegs (*landmarks*) en estructures d'interès anatòmic. Aquesta darrera metodologia s'ha anat consolidant al llarg del temps com una de les més útils a l'hora de quantificar i analitzar la variació de la forma entre estructures, gràcies principalment al seu potent suport estadístic associat i a la facilitat, simplicitat i rapidesa en la obtenció de les dades de forma (Kendall, 1984, 1985; Adams et al., 2004; 2013). El mecanisme de funcionament del mètode consisteix en una definició i selecció de punts de coordenades homòlegs en estructures d'interès i el seu processat previ per tal de que siguin comparables entre ells. Durant aquest anàlisi, es poden obtenir els components individuals de la variació en la forma (*partial o relative warps*), que s'utilitzen en els anàlisis multivariants ja que poden ser interpretats com les variables de canvi en la forma entre estructures. Aquests resultats de variació de la forma poden ser representats gràficament en l'espai (*morfoespai*), on cadascuna de les estructures es localitza en funció de les seves característiques morfològiques. Aquest mètode gràfic permet una millor interpretació dels patrons de canvi en la forma de les estructures. A més, en les darreres dècades, la definició de les formes ha estat complementada mitjançant la incorporació d'un altre tipus de punts de coordenades (*semilandmarks*), capaços de desplaçar-se al llarg de les superfícies de les estructures permetent definir estructures



mòbils o no fixes, i que a més poden ser processats estadísticament de manera idèntica que els *landmarks*. Aquest descobriment ha suposat un avenç molt important dins la GM, ja que el fet de poder definir punts mòbils, com ara curvatures, contorns o estructures no fixes, permet obtenir una descripció més detallada de la forma dels objectes (Bookstein, 1997; Bookstein et al., 1999; Adams et al., 2004).

Gràcies a tots els seus avantatges metodològics en el l'estudi de la variació de la morfologia, la aplicació i utilitat de la GM s'ha estès, en les darreres dècades, a múltiples disciplines científiques, com ara la sistemàtica, la filogènia, la paleontologia, la taxonomia, la biologia evolutiva, la biologia del desenvolupament i la ecologia de comunitats (Zelditch et al., 2004). Els anàlisis han sigut aplicats en nombroses estructures corporals de diferents ordres taxonòmics, incloent vertebrats, invertebrats o fins i tot en el regne vegetal (botànica). No obstant, un dels grups zoològics tradicionalment més investigat han estat els peixos, donada la gran plasticitat morfològica que presenten. L'anàlisi de la seva variabilitat morfològica avarca des de l'estructura corporal sencera (Loy et al., 2001; Chakrabarty, 2005; Clabaut et al., 2007; Young et al., 2009; Claverie and Wainwright, 2014) fins a estructures més específiques com el crani o peces maxil·lars i mandibulars (Wainwright et al., 2002, 2004; Postl et al., 2008; Cooper and Westneat, 2009), aletes (Wainwright et al., 2002; Dornburg et al., 2011; Vergara-Solana et al., 2014), escates (Ibañez et al., 2007a) o otòlits (Monteiro et al., 2005 Lombarte et al., 2010, Tuset et al., 2016), entre altres.

Un altre camp científic on l'estudi de la variabilitat morfològica ha començat a utilitzar-se de manera freqüent ha estat el de la biodiversitat de comunitats. La biodiversitat es un concepte multidimensional complex, que inclou la variabilitat genètica i fenotípica, la riquesa d'espècies, les seves propietats funcionals i les seves relacions filogenètiques, i donada aquesta complexitat es impossible mesurar-la amb índexs simples (Purvis and Hector, 2000; Pavoine and Bonsall, 2011; Magurran, 2013; Loiseau and Gaertner, 2015). Estudis recents han organitzat el concepte general de biodiversitat com un conjunt de mesures ecològiques, taxonòmiques, filogenètiques i funcionals (Lyashevskaya and Farnsworth, 2012). Actualment, els índexs de diversitat funcional són els més utilitzats en estudis biològics, ja que tenen en compte el paper que exerceixen les espècies dins de les comunitats (Petchey and Gaston, 2002; Somerfield et al., 2008; Villéger et al., 2010; Mouillot et al., 2014). En el seu desenvolupament solen considerar-se caràcters que afecten als hàbits i *fitness* de les espècies, com ara la dieta,

els mètodes de locomoció, l'ús de l'hàbitat, la reproducció o la seva resiliència. No obstant, la manca d'informació en molts d'aquests caràcters funcionals (sobretot d'organismes que habiten ecosistemes inaccessibles) i la manca de consens dins de la comunitat científica a l'hora de seleccionar els trets funcionals adients a incloure provoquen cert grau de subjectivitat en la seva aplicació i dificultats a l'hora de comparar diferents mesures obtingudes (Petchey and Gaston, 2002, 2006; Villéger et al., 2008). Per aquest motiu, i seguint les premisses ecomorfològiques que relacionen la morfologia de les espècies amb les seves estratègies ecològiques i biològiques dins les comunitats, l'estudi de la morfologia ha començat a emprar-se en estudis d'avaluació de la biodiversitat. La quantificació de la variabilitat morfològica dins els sistemes pot ajudar a entendre la estructura i organització interna de les comunitats, especialment quan la informació ecològica o funcional dels ecosistemes es escassa o absent. De fet, mètodes de GM ja han estat utilitzats en propòsits de biodiversitat, generant mesures de diversitat quantitatives i qualitatives (Recasens et al., 2006; Lombarte et al., 2012).

### 12.2 Objectius de la tesi

L'objectiu principal d'aquesta tesi és descriure la variabilitat morfològica de diferents comunitats de peixos provinents del Nord-Oest del mar Mediterrani (costa catalana i Illes Balears) i del Nord-Est de l'oceà Atlàntic (Illes Canàries) a partir de mètodes de morfometria geomètrica (GM), així com destacar la importància de la morfologia de les espècies en estudis de biodiversitat i com a eina útil a l'hora intentar entendre les dinàmiques internes que ajudin a entendre la estructura i organització de les comunitats. Els objectius més específics són els següents:

1. Aplicar una metodologia específica de GM basada en *landmarks* i *semilandmarks*, incloent la forma corporal general i la forma i posició de les aletes i òrgans sensorials, per tal de demostrar la seva utilitat en estudis de estructura de comunitats.
2. Desenvolupar noves mesures de diversitat morfològica usant mètodes de GM, així com descriure la seva correlació amb altres índexs ja existents, per tal de proporcionar una alternativa que ajudi a complementar els estudis de diversitat en comunitats de peixos.

3. Caracteritzar morfològicament i determinar la diversitat de diferents comunitats de peixos: des de comunitats mesopelàgiques provinents de les Illes Canàries, fins a comunitats litorals a llarg de la costa catalana o comunitats demersals a llarg de la plataforma i talús continental de les Illes Balears.
4. Realitzar una comparativa dels morfoespais i dels índexs de biodiversitat obtinguts per les diferents comunitats estudiades, i així avaluar la habilitat del mètodes morfològics a l'hora de descriure la estructura i organització en comunitats de peixos.
5. Demostrar la capacitat de l'enfoc morfològic presentat en aquesta tesi com a eina descriptiva que permeti inferir en aspectes ecològics que determinen el funcionament de les comunitats, com ara l'efecte dels factors ambientals, la repartició de recursos, l'ús de l'hàbitat o relacions interespecífiques com la coexistència, la competència o la dominància.

### 12.3 Resultats

En el capítol 4, es va comparar la estructura d'una comunitat de peixos mitjançant diferents metodologies de definició de *landmarks* i *semilandmarks* comunament utilitzades en estudis previs, per tal d'identificar quina d'elles era capaç d'incloure una major quantitat d'informació morfològica sobre les espècies i per tal d'observar si l'esquema utilitzat influeix en la distribució de les mateixes en el morfoespai. Els resultats van mostrar que les diferents metodologies oferien distribucions diferents, i suggerien que la incorporació de punts en estructures corporals d'importància biològica, com aletes i òrgans sensorials, contribuïen a millorar la diferenciació entre espècies i la interpretació del morfoespai. A més, varis mètodes numèrics i gràfics es van utilitzar per analitzar la distribució interna dels morfoespais, i es va establir que el mètode d'agregació de punts són els més apropiats per davant dels índexs de disparitat morfològica. Els mètodes gràfics, com la densitat de Kernel o els gràfics de Gabriel, van resultar útils per analitzar i interpretar la ocupació del morfoespai (especialment en les zones amb més densitat d'espècies), i per tant la complexitat estructural de la comunitat.

No obstant, els mètodes numèrics també son necessaris per tal d'analitzar la distribució de les espècies en distàncies més curtes i la significança estadística dels resultats.

En el capítol 5, es va caracteritzar la diversitat morfològica de diverses comunitats de peixos litorals de la costa catalana utilitzant una metodologia de GM basada en *landmarks* que definia la forma corporal general de les espècies, així com altres estructures corporals com ara les aletes o diversos òrgans sensorials. Diferents mesures morfològiques (incloent un nou índex proposat en aquest treball, anomenat “riquesa morfològica”, *MR*) van ser calculades mitjançant dades qualitatives (presència/absència) i quantitatives (abundància) i també van ser comparades amb altres mesures de diversitat comunament utilitzades (de caire ecològic, taxonòmic i funcional) per tal d'avaluar la seva correlació. Els resultats van demostrar que els diferents índexs morfològics correlacionaven correctament amb les diferents dimensions de la diversitat: *MD* amb la diversitat taxonòmica, *EMI* amb la complexitat estructural i taxonòmica i *MR* amb les mesures de riquesa específica i diversitat funcional. A més, les mesures morfològiques calculades mitjançant dades qualitatives i quantitatives van obtenir resultats semblants, suggerint que per calcular aquestes mesures no son necessàries dades d'abundància. Aquest fet demostra que l'anàlisi de la diversitat pot ser realitzat únicament amb llistes faunístiques, permetent la possibilitat d'analitzar dades històriques i de determinar canvis en la estructura de les comunitats al llarg de grans períodes temporals.

En el capítol 6, es va analitzar la variabilitat morfològica en diferents comunitats de peixos mesopelàgics provinents de les Illes Canàries, per tal de diferenciar les estratègies biològiques que permeten la coexistència de les espècies dins els ecosistemes. De manera semblant al estudi realitzat en el capítol 4, es van fer servir diferents mètodes gràfics per analitzar la ocupació dels morfoespais. Els resultats van demostrar que els mètodes de “patterning” son més útils i vàlids a l'hora d'interpretar la distribució de les espècies dins els morfoespais que el “convex hull”, que només és interessant per identificar espècies amb morfologies més extremes i que es localitzen en la perifèria de l'espai. Aquests resultats representen un exemple més de que l'anàlisi del morfoespai és una eina útil per identificar i diferenciar els hàbits ecològics de les espècies, essencials per entendre la estructura i organització de les comunitats.

En el capítol 7, es va determinar i comparar la estructura ecològica i morfològica de varies comunitats de peixos del litoral català. Seguint la premissa de que actualment l'ús de caràcters morfològics i funcionals està creixent en importància a l'hora de descriure les comunitats, es va utilitzar una metodologia de GM basada en *landmarks* (la utilitzada al llarg de tota la tesi) per quantificar la diversitat morfològica d'aquestes comunitats. Les comunitats també es van definir ecològicament, a nivell de composició i abundància específica, per tal de comparar ambdues caracteritzacions. Finalment, també es va analitzar l'efecte d'alguns factors ambientals sobre la estructura ecològica de les comunitats mitjançant un anàlisi de CCA. Els resultats van determinar que la comparativa morfològica mostrava diferències més grans entre comunitats que la ecològica. La comparativa ecològica diferenciava les comunitats en funció de la abundància de les espècies més abundants, i generalment agrupava en funció de la proximitat geogràfica de les comunitats. En canvi, la comparativa morfològica va demostrar ser independent de la abundància i de la composició específica, i ajuntava les comunitats en funció de la distribució de les espècies en el morfoespai i de la complexitat estructural del hàbitat: les comunitats amb mescla de tipus de substrat mostraven més similitud entre elles, ja que contenien més riquesa de formes corporals gràcies a que la heterogeneïtat del hàbitat permetia l'aparició d'estils de vida més diversos. Paral·lelament, el CCA va indicar que el tipus de substrat i la localització geogràfica afectaven significativament a la composició de les comunitats. L'estudi suggeria de nou que la morfologia de les espècies aporta informació vàlida i alternativa als anàlisis ecològics més clàssics, i a més permet discutir el paper ecològic i funcional de les espècies en els ecosistemes, clau a l'hora d'examinar la seva estructura.

Finalment, en el capítol 8, es va investigar l'efecte que té la profunditat en la estructura morfològica i funcional de les comunitats de peixos, un dels gradients ambientals que afecta de manera més intensa a la composició, zonació, estructura i diversitat de les comunitats biològiques marines. Per tal d'avaluar aquest efecte, es van analitzar diverses comunitats de peixos demersals al llarg d'un fort gradient batimètric (plataforma i talús continental; 40-2200 m) provinents dels voltants de les Illes Balears (Mallorca i Menorca). Les comunitats es van caracteritzar des del punt de vista morfològic (utilitzant la metodologia de GM emprada durant tota la tesi), funcional i ecològic. Els anàlisis realitzats van revelar que tant la estructura morfològica com la funcional patien canvis significatius amb l'augment de profunditat, i que moltes

espècies, sobretot les més dominants, presentaven posicions semblants dins els dos espais. Els morfoespais presentaven menys riquesa de formes corporals a mesura que augmentava la profunditat (fruit de la reducció dràstica en el nombre de espècies). També es va poder observar una clara tendència cap al allargament de la forma corporal (reduint-se les formes arrodonides fins a la seva desaparició en els nivells més profunds) i una progressiva “migració” de les espècies cap a la perifèria del morfoespai, demostrant la proliferació de formes morfològiques més extremes i una reducció de la redundància morfològica. Per altra banda, la diversitat funcional va augmentar fins a fondàries mitjanes del talús (aproximadament 1400 m), a partir d’ on va decreixer notablement, tot i que la redundància va reduir-se fins els nivells més profunds. La interpretació dels resultats obtinguts per l’anàlisi morfo-funcional va permetre inferir ens alguns processos i dinàmiques que regeixen la estructura de les comunitats, com ara la repartició dels recursos, la diferenciació d’hàbitat, les interaccions tròfiques o relacions interespecífiques com la coexistència, la dominància o la competència.

### 12.4 Conclusions

1. El mètode específic de definició de *landmarks* afecta a la distribució de les espècies dins el morfoespai. La incorporació de *landmarks* i *semilandmarks* que defineixen estructures d’importància biològica, com aletes o òrgans sensorials, proporciona una diferenciació més clara de les espècies i contribueix a definir-les millor ecològicament.
2. La millor opció per avaluar la ocupació dels morfoespais es mitjançant una combinació de mètodes analítics gràfics i numèrics. La densitat de Kernel, els gràfics de Gabriel, els mètodes de patterning o les cel·les de Voronoi proporcionen un enfoc visualment més intuïtiu i gràfic. No obstant, els mètodes numèrics també son necessaris per comprovar la significança estadística dels resultats.
3. La aplicació de mètodes de GM en la forma corporal dels peixos permet la obtenció de índexs de diversitat morfològica (*MD*, *EMI* i *MR*), mesures vàlides i útils com a complements en estudis de biodiversitat de comunitats: proporcionen informació

sobre la variabilitat de morfologies (i per tant, de funcions, rols i estratègies) dins les comunitats.

4. Aquestes mesures morfològiques son independents entre elles i correlacionen significativament amb altres components de la biodiversitat, demostrant el seu encaixament dins la complexa xarxa de múltiples components de la diversitat i reforçant la seva habilitat com a eina complementaria en estudis de diversitat: *MD* està lligat a la diversitat taxonòmica, *EMI* defineix la complexitat estructural i taxonòmica de les comunitats i *MR* correlaciona amb mesures de riquesa específica i de diversitat funcional.
5. Els mètodes de GM permeten calcular mesures de diversitat de manera fàcil i ràpida en comparació a altre mètodes alternatius, i no requereixen d'un grau de coneixement excessivament alt sobre la morfologia de les espècies. A més, els índexs calculats amb dades qualitatives i quantitatives van proporcionar resultats equivalents.
6. Els resultats obtinguts confirmen que l'anàlisi de la forma corporal en peixos basada en mètodes de GM es útil i essencial per investigar la estructura de les comunitats, especialment quan la informació ecològica és escassa o absent. A més, permeten analitzar les comunitats a partir de dades qualitatives, fet que obre la possibilitat d'estudiar la evolució de comunitats al llarg de grans escales temporals a partir de llistes faunístiques qualitatives o comparar dades provinents de mostres heterogènies.
7. Els resultats de l'avaluació dels morfoespais de comunitats de peixos des del litoral fins el *deep-sea*, incloent-hi el domini mesopelàgic, provinents de la costa catalana, mar balear i de les Illes Canàries, demostren que l'anàlisi de la distribució interna dels morfoespais ajuda a entendre el funcionament i estructura de les comunitats de peixos.
8. La caracterització ecològica de les comunitats litorals de la costa catalana va agrupar les comunitats principalment en funció de la proximitat geogràfica i de la proporció d'espècies més dominants. En canvi, la comparativa morfològica va mostrar diferències més grans entre comunitats, era independent de la abundància i composició específica i va agrupar en base a la distribució de les espècies en el morfoespai.

9. La baixa similitud mostrada pels diferents morfoespais analitzats reforça la hipòtesis de que la morfologia dels peixos està relacionada amb la complexitat de l'hàbitat: comunitats que presenten major complexitat estructural (mescla de tipus de substrats o esculls artificials) contenen un nombre major de formes corporals ja que permeten suportar una major variabilitat de estratègies ecològiques.
10. El tipus de substrat i la localització geogràfica van afectar significativament a la composició ecològica de les comunitats. Comunitats amb mescla de substrats van presentar composicions més diverses, mentre que les de substrats tous eren ecològicament més simples i específicament menys riques. Les aportacions fluvials i els diferents règims pesquers també van contribuir a les diferències observades.
11. En l'anàlisi de la evolució dels morfoespais al llarg de la profunditat realitzat en comunitats de peixos demersals de les Illes Balears, es van observar varies tendències generals: 1) una reducció progressiva de la riquesa de formes corporals; 2) una proliferació de morfologies més extremes, causant una dispersió general de les espècies cap a la perifèria del morfoespai i una reducció progressiva de la redundància morfològica; 3) la distribució de la abundància específica va seguir una tendència semblant, amb les espècies més dominants prop de la perifèria; 4) un patró general cap a l'allargament de la forma corporal i una progressiva reducció de les formes arrodonides fins a la seva desaparició total en les comunitats més profundes.
12. El patró de distribució de les espècies en els espais morfològic i funcional va ser similar al llarg de la profunditat. Ambdós anàlisis van presentar canvis notables a mesura que la profunditat augmentava, provocades principalment per les restriccions ambientals, la substitució de espècies més dominant i la disponibilitat de recursos.
13. La diversitat funcional va augmentar amb la profunditat fins els 1400 m, a partir d'on va decreixer dràsticament. La forta reducció del nombre d'espècies va afectar a la diversitat funcional al llarg del gradient de profunditat, fet que va causar un empobriment de la funcionalitat del ecosistema (en termes de variabilitat de funcions) en els nivells més profunds del talús continental.
14. En canvi, la redundància morfològica i funcional va anar reduint-se constantment fins els nivells més profunds. Les condicions ambientals i la limitació de recursos en els ecosistemes del *deep-sea* seleccionen cap a adquirir estratègies particulars i



extremes per tal de superar les restriccions ambientals. Les espècies desenvolupen graus més alts d'especialització en l'ús dels recursos i en la diferenciació del nínxol, reduint així la competència interespecífica.

- 15.** Els resultats generals d'aquesta tesi reforcen la hipòtesi de que la morfologia de les espècies és una eina vàlida per tal d'indagar en els seus rols ecològics i funcionals dins els ecosistemes. L'anàlisi del morfoespai permet inferir en aspectes claus del funcionament de les comunitats, com la repartició de recursos, la diferenciació d'hàbitat o relacions interespecífiques com la coexistència, la competència o la dominància. Per tant, l'avaluació de la variabilitat morfològica ajuda a millorar el coneixement de la estructura, organització i funcionament de les comunitats de peixos.



# 13

## **Appendix 1**

### **Supplementary Material**



13.1 Supplementary material CHAPTER 6

**Supplementary Table S1.** Checklist data of mesopelagic fishes captured in the southeast Fuerteventura Island (North-eastern Atlantic). *EN*: epipelagic at night, *NN*: neritic at night, *UMD*: upper mesopelagic at daytime, *UMN*: upper mesopelagic at nighttime, *LMD*: lower mesopelagic at daytime, *LMN*: lower mesopelagic at nighttime.

Order	Family	Species	Daytime		Nighttime				
			UMD	LMD	NN	EN	UMN	LMN	
Anguilliformes	Derichthyidae	<i>Derichthys serpentinus</i>	0	0	0	0	1	0	
	Nemichthyidae	<i>Avocettina infans</i>	0	0	0	0	1	0	
		<i>Nemichthys curvirostris</i>	1	1	0	0	0	0	
		<i>Nemichthys scolopaceus</i>	1	0	0	0	0	0	
	Serrivomeridae	<i>Serrivomer beanii</i>	1	1	1	1	1	1	
		<i>Serrivomer lanceolatooides</i>	1	1	0	0	1	1	
Saccopharyngiformes	Saccopharyngidae	<i>Saccopharynx ampullaceus</i>	0	0	0	0	0	1	
Clupeiformes	Engraulidae	<i>Engraulis encrasicolus</i>	0	0	1	1	0	0	
	Cupleidae	<i>Sardina pilchardus</i>	0	0	1	1	0	0	
		<i>Sardinella aurita</i>	0	0	0	1	0	0	
		<i>Sardinella maderensis</i>	0	0	0	1	0	0	
Argentiniformes	Opisthoproctidae	<i>Bathylagichthys greyae</i>	0	1	0	1	1	0	
		<i>Dolichopteryx longipes</i>	1	0	0	0	0	0	
		<i>Opisthoproctus grimaldii</i>	0	0	0	0	1	0	
		<i>Opisthoproctus soleatus</i>	1	0	0	0	1	0	
	Microstomatidae	<i>Dolicholagus longirostris</i>	0	1	0	0	1	0	
		<i>Melanolagus bericoides</i>	0	0	0	0	1	0	
		<i>Nansenia groenlandica</i>	1	0	0	0	1	0	
	Platyroctidae	<i>Holtbyrnia macrops</i>	0	1	0	0	1	1	
		<i>Maulisia maui</i>	0	1	0	0	0	0	
		<i>Searsia koefoedi</i>	0	1	0	0	0	1	
		Alepocephalidae	<i>Xenodermichthys copei</i>	0	1	0	0	1	1
	Stomiiformes	Gonostomatidae	<i>Bonapartia pedaliota</i>	1	0	0	0	1	0
<i>Cyclothone braueri</i>			1	1	0	0	1	1	
<i>Cyclothone microdon</i>			1	1	0	0	0	1	
<i>Cyclothone pallida</i>			1	0	0	0	0	0	
<i>Cyclothone pseudopallida</i>			1	1	0	0	1	1	
<i>Manducus maderensis</i>			0	0	0	1	0	0	
<i>Diplophos taenia</i>			0	0	0	1	0	0	
<i>Gonostoma denudatum</i>			1	1	0	0	1	0	
<i>Gonostoma elongatum</i>			1	1	0	0	1	1	
<i>Margrethia obtusirostra</i>			1	1	0	0	1	1	
Sternoptychidae		<i>Argyropelecus aculeatus</i>	1	0	0	0	1	1	
		<i>Argyropelecus gigas</i>	1	1	0	0	1	0	
		<i>Argyropelecus hemigymnus</i>	1	1	0	1	1	1	
		<i>Mauroliticus muelleri</i>	0	0	0	1	0	0	

### 13. Appendix 1. Supplementary Material

Order	Family	Species	Daytime		Nighttime			
			UMD	LMD	NN	EN	UMN	LMN
		<i>Sternoptyx diaphana</i>	1	1	0	1	1	1
		<i>Valenciennellus tripunctulatus</i>	1	1	0	0	1	1
	Phosichthyidae	<i>Ichthyococcus ovatus</i>	1	1	0	0	1	0
		<i>Vinciguerria attenuata</i>	1	1	0	1	1	1
		<i>Vinciguerria nimbaria</i>	1	1	0	1	1	0
		<i>Vinciguerria poweriae</i>	1	0	0	0	0	1
	Stomiidae	<i>Astronesthes gemmifer</i>	1	1	0	0	0	0
		<i>Astronesthes indicus</i>	0	1	0	1	1	0
		<i>Astronesthes leucopogon</i>	0	0	0	1	0	0
		<i>Astronesthes macropogon</i>	0	0	0	1	0	0
		<i>Astronesthes micropogon</i>	0	1	0	1	1	0
		<i>Astronesthes neopogon</i>	0	0	0	0	1	0
		<i>Bathophilus brevis</i>	1	0	0	0	0	0
		<i>Bathophilus digitatus</i>	1	0	0	0	0	0
		<i>Bathophilus vaillanti</i>	1	1	0	1	1	1
		<i>Borostomias mononema</i>	1	0	0	0	0	0
		<i>Chauliodus danae</i>	1	1	0	1	1	1
		<i>Chauliodus sloani</i>	1	1	0	1	1	1
		<i>Eustomias braueri</i>	1	0	0	0	0	0
		<i>Eustomias obscurus</i>	0	0	0	1	1	0
		<i>Flagellostomias boureei</i>	0	0	0	1	0	0
		<i>Idiacanthus fasciola</i>	1	1	0	1	1	1
		<i>Leptostomias gladiator</i>	0	0	0	0	1	0
		<i>Leptostomias longibarba</i>	0	1	0	0	0	0
		<i>Malacosteus niger</i>	0	1	0	0	0	1
		<i>Melanostomias tentaculatus</i>	1	0	0	0	0	0
		<i>Photonectes braueri</i>	1	0	0	0	0	0
		<i>Photostomias guernei</i>	0	1	0	0	1	1
		<i>Rhadinesthes decimus</i>	0	0	0	0	1	1
		<i>Stomias boa</i>	1	1	0	1	0	1
		<i>Stomias longibarbus</i>	1	0	0	0	0	0
Aulopiformes	Scopelarchidae	<i>Benthalbella infans</i>	1	0	0	0	0	0
		<i>Rosenblattichthys hubbsi</i>	0	0	0	0	0	1
		<i>Scopelarchus analis</i>	0	0	0	0	1	0
	Evermannellidae	<i>Evermannella indica</i>	0	0	0	0	1	0
	Alepisauridae	<i>Omosudis lowii</i>	0	0	0	0	0	1
	Paralepididae	<i>Lestidiops sphyrenoides</i>	1	0	0	0	0	0
		<i>Macroparalepis affinis</i>	0	0	0	0	0	1
		<i>Macroparalepis brevis</i>	0	0	0	0	1	0
		<i>Magnisudis atlantica</i>	0	0	0	0	1	0
		<i>Paralepis brevirostris</i>	1	0	0	0	0	0
		<i>Sudis hyalina</i>	0	0	0	0	1	0

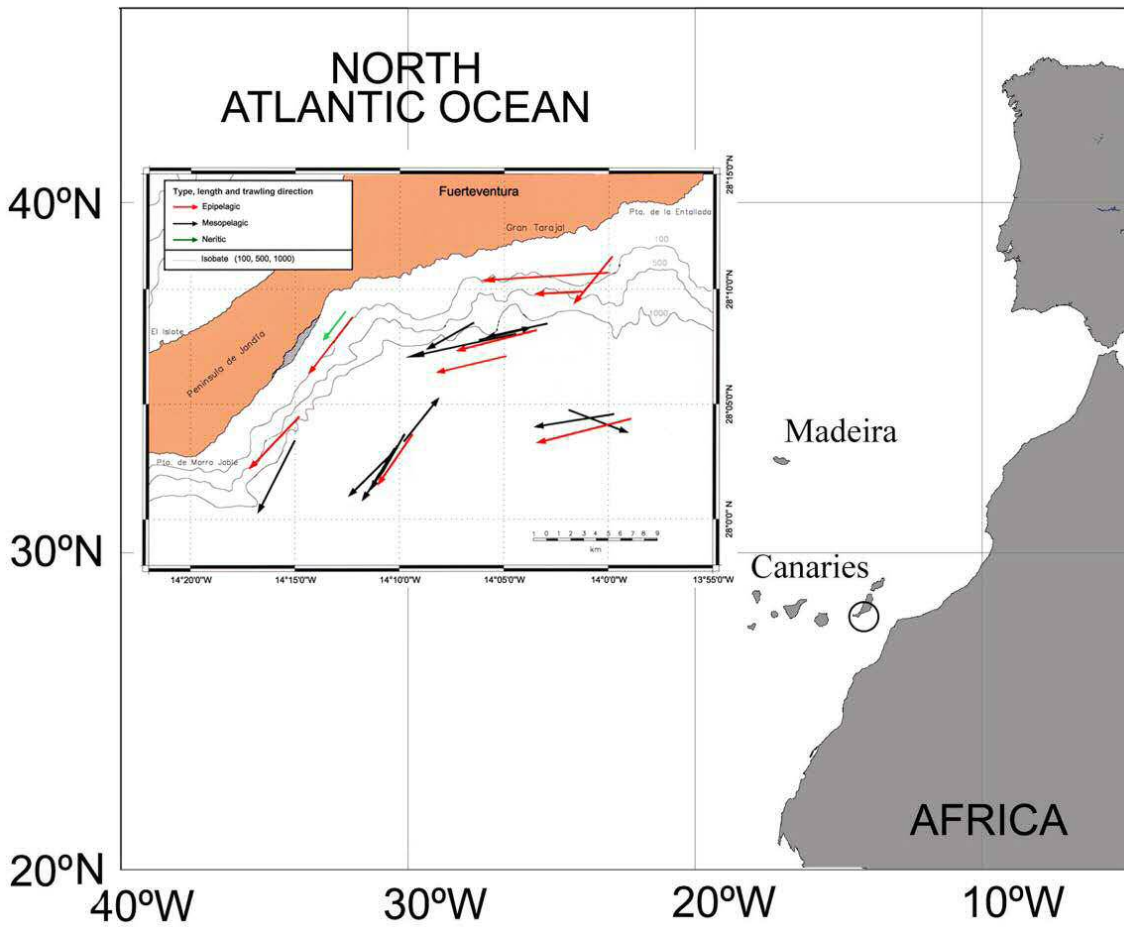
13. Appendix 1. Supplementary Material

Order	Family	Species	Daytime		Nighttime			
			UMD	LMD	NN	EN	UMN	LMN
Myctophiformes	Myctophidae	<i>Benthoosema suborbitale</i>	1	1	0	1	1	1
		<i>Bolinichthys indicus</i>	1	1	0	1	1	1
		<i>Bolinichthys supralateralis</i>	0	0	0	0	0	1
		<i>Ceratoscopelus maderensis</i>	1	1	1	1	1	1
		<i>Ceratoscopelus warmingii</i>	0	1	0	1	0	1
		<i>Diaphus adenomus</i>	1	0	0	0	0	0
		<i>Diaphus dumerilii</i>	1	0	1	1	1	0
		<i>Diaphus effulgens</i>	1	0	0	0	0	0
		<i>Diaphus holti</i>	1	1	0	1	1	1
		<i>Diaphus lucidus</i>	0	0	0	1	1	0
		<i>Diaphus metopoclampus</i>	1	0	0	0	1	0
		<i>Diaphus mollis</i>	1	1	0	1	1	1
		<i>Diaphus perspicillatus</i>	1	0	0	1	1	0
		<i>Diaphus rafinesquii</i>	1	1	0	1	1	1
		<i>Diaphus termophilus</i>	1	0	0	0	0	0
		<i>Diogenichthys atlanticus</i>	1	1	0	1	1	1
		<i>Gonichthys cocco</i>	1	1	0	0	1	1
		<i>Hygophum benoitii</i>	1	0	0	1	1	1
		<i>Hygophum hygomii</i>	1	1	1	1	1	1
		<i>Hygophum reinhardtii</i>	0	1	0	1	1	1
		<i>Hygophum taaningi</i>	0	0	0	1	1	1
		<i>Lampadena chavesi</i>	1	1	0	0	0	0
		<i>Lampanyctus alatus</i>	1	1	0	1	1	1
		<i>Lampanyctus crocodilus</i>	0	0	0	1	0	1
		<i>Lampanyctus festivus</i>	1	1	0	1	1	1
		<i>Lampanyctus nobilis</i>	1	0	0	1	0	0
		<i>Lampanyctus photonotus</i>	0	1	0	1	1	0
		<i>Lampanyctus pusillus</i>	1	1	0	1	1	1
		<i>Lepidophanes gaussi</i>	0	1	0	1	1	1
		<i>Lepidophanes guentheri</i>	0	0	0	1	0	0
		<i>Lobianchia dofleini</i>	1	1	1	1	1	1
		<i>Lobianchia gemellarii</i>	1	1	0	1	1	1
		<i>Myctophum nitidulum</i>	0	0	0	1	0	0
		<i>Myctophum punctatum</i>	1	0	0	1	1	0
		<i>Myctophum selenops</i>	1	0	0	0	1	1
		<i>Nannobranchium atrum</i>	0	1	0	1	1	1
		<i>Nannobranchium cuprarium</i>	0	1	0	0	0	1
		<i>Notolychnus valdiviae</i>	1	0	0	1	1	1
		<i>Notoscopelus bolini</i>	0	0	1	1	1	1
		<i>Notoscopelus caudispinosus</i>	0	0	0	1	0	0
		<i>Notoscopelus elongatus</i>	0	0	0	1	0	0
		<i>Notoscopelus resplendens</i>	1	1	1	1	1	1

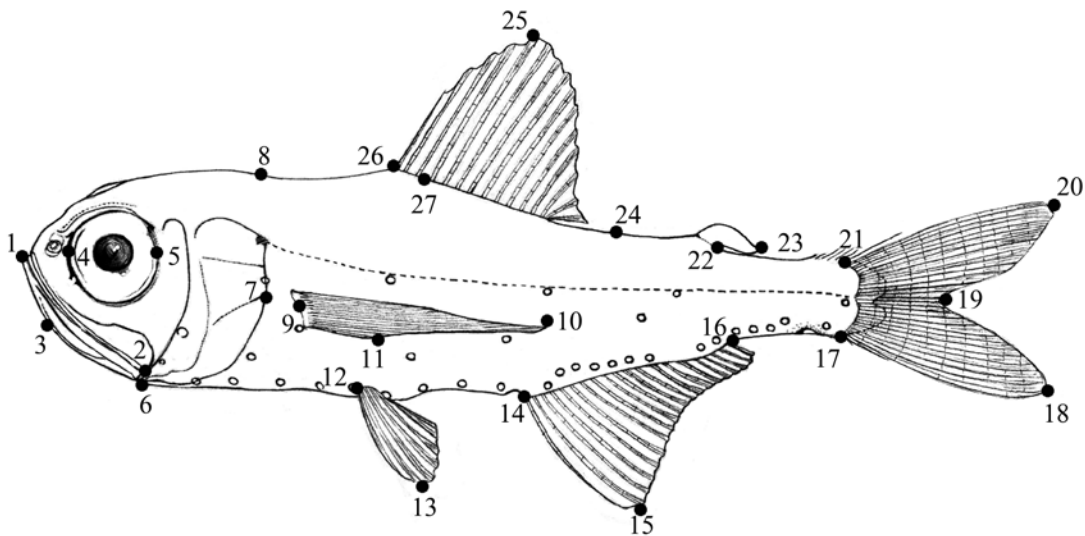
### 13. Appendix 1. Supplementary Material

Order	Family	Species	Daytime		Nighttime			
			UMD	LMD	NN	EN	UMN	LMN
		<i>Symbolophorus veranyi</i>	0	0	1	1	0	0
Lampriformes	Stylephoridae	<i>Stylephorus chordatus</i>	0	0	0	0	0	1
	Regalecidae	<i>Regalecus glesne</i>	0	0	0	1	0	0
Gadiformes	Melanonidae	<i>Melanonus zugmayeri</i>	0	0	0	0	0	1
Lophiiformes	Oneirodidae	<i>Oneirodes anisacanthus</i>	0	1	0	0	0	0
	Ceratiidae	<i>Cerantias holboelli</i>	0	1	0	0	0	0
Beloniformes	Scomberesocidae	<i>Scomberesox saurus</i>	0	0	0	0	1	0
Stephanoberyciformes	Melamphaidae	<i>Melamphaes typhlops</i>	1	0	0	0	1	1
		<i>Poromitra capito</i>	0	0	0	0	1	0
		<i>Poromitra megalops</i>	0	1	0	0	0	1
		<i>Scopelogadus beanii</i>	0	1	0	0	1	1
Beryciformes	Anoplogastridae	<i>Anoplogaster cornuta</i>	0	0	0	0	1	0
	Diretmidae	<i>Diretmus argenteus</i>	1	0	0	0	1	1
Gasterosteiformes	Macrorhamphosidae	<i>Macroramphosus scolopax</i>	1	0	0	1	0	0
Perciformes	Carangidae	<i>Trachurus picturatus</i>	0	0	1	1	0	0
		<i>Trachurus trachurus</i>	0	0	1	0	0	0
	Sparidae	<i>Boops boops</i>	0	0	0	1	0	0
	Gempylidae	<i>Diplospinus multistriatus</i>	1	1	0	1	1	0
	Trichiuridae	<i>Benthodesmus simonyi</i>	1	0	0	1	0	0
		<i>Lepidopus caudatus</i>	1	1	0	1	1	0
	Scombridae	<i>Scomber colias</i>	0	0	0	1	0	0
	Nomeidae	<i>Cubiceps gracilis</i>	0	0	0	1	0	0
	Caproidae	<i>Capros aper</i>	1	0	0	0	0	0
<i>Number of species</i>			74	61	12	67	79	61

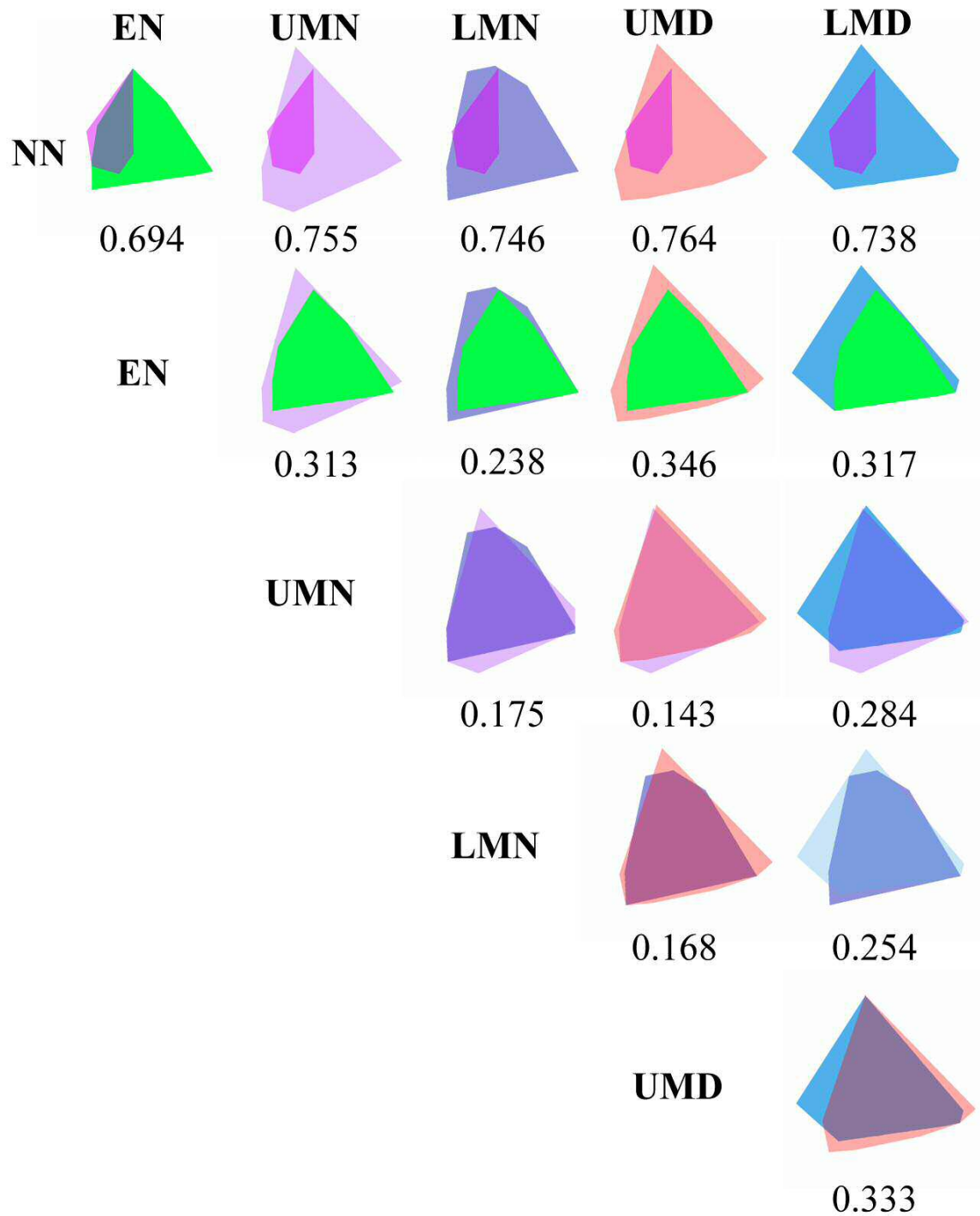




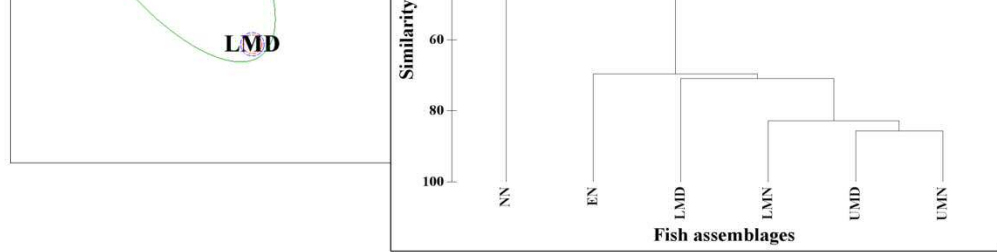
**Figure S1.** Localization of the study area and trawl tows.



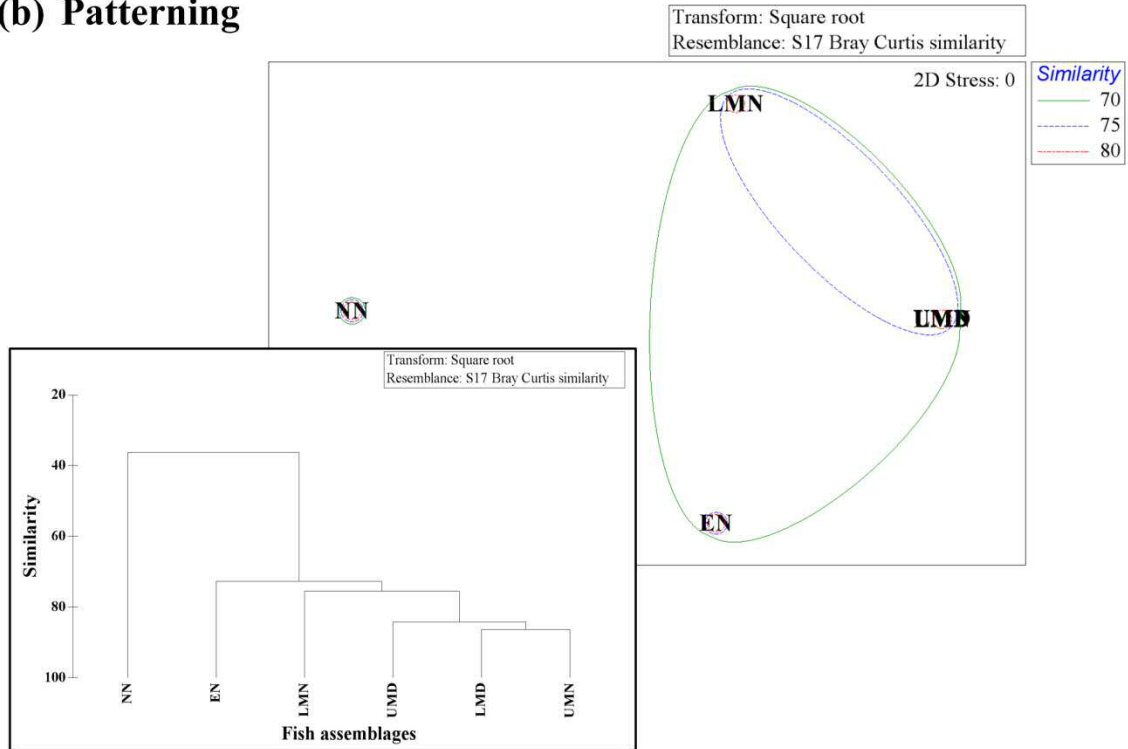
**Figure S2.** Scheme of a mesopelagic fish showing the landmarks used in the study. Drawn by Mrs. Isabel Bordes.



**Figure S3.** Graphical illustration showing the dissimilarity in the convex hull between the studied fish assemblages.



## (b) Patterning



**Figure S4.** Cluster dendrogram and MDS plot representing the similarity among fish assemblages according to convex hull (a) and patterning (b) of morphospace. *NN* neritic assemblage at nighttime, *EN* epipelagic assemblage at nighttime, *UMN* upper mesopelagic assemblage at nighttime, *LMN* lower mesopelagic assemblage at nighttime, *UMD* upper mesopelagic assemblage at daytime, *LMD* lower mesopelagic assemblage at daytime.

13.2 Supplementary material CHAPTER 7

**Supplementary Table S1.** Abundance data (N) of total captured species of the different assemblages defined in the Central zone (Vilanova i la Geltrú-Calafell) and in the Northern zone (L'Estartit), and the number of individuals and species for each assemblage. The table also includes the taxonomic classification of species (order, family, specie). Bold and underlined values indicate the species with >10 % of abundance in the assemblage.

Order	Family	Specie	Acronym	Number of individuals													
				Central Zone						Northern zone							
				CS10	CSEA15	CS15	CS20	CA15	CR15	NG20	NR15	NS10	NS15	NS20	NSM20	NM20	
Aulopiformes	Synodontidae	<i>Synodus saurus</i>	<i>Ssau</i>		1								1				
Anguilliformes	Congridae	<i>Conger conger</i>	<i>Ccon</i>					1									
Beloniformes	Belonidae	<i>Belone belone</i>	<i>Bbel</i>		1												
Clupeiformes	Clupeidae	<i>Sardina pilchardus</i>	<i>Spil</i>										6				
Clupeiformes	Clupeidae	<i>Sardinella aurita</i>	<i>Saur</i>		3												
Clupeiformes	Clupeidae	<i>Sprattus sprattus</i>	<i>Sspr</i>													20	
Gadiformes	Merlucciidae	<i>Merluccius merluccius</i>	<i>Mmer</i>				1	6								<b>35</b>	1
Gadiformes	Phycidae	<i>Phycis phycis</i>	<i>Pphy</i>					18	5	6	2	3					4
Gadiformes	Gadidae	<i>Trisopterus minutus</i>	<i>Tmin</i>														
Lophiiformes	Lophiidae	<i>Lophius piscatorius</i>	<i>Lpis</i>				3	10									1
Mugiliformes	Mugilidae	<i>Chelon labrosus</i>	<i>Clab</i>			4		3	3			42	1				
Mugiliformes	Mugilidae	<i>Liza aurata</i>	<i>Laur</i>	3		2		1	2								
Mugiliformes	Mugilidae	<i>Mugil cephalus</i>	<i>Mcep</i>					1	1			<b>47</b>	16			1	
Mugiliformes	Mugilidae	<i>Liza ramada</i>	<i>Lram</i>			1		2									
Mugiliformes	Mugilidae	<i>Oedalechilus labeo</i>	<i>Olab</i>	1													
Ophidiiformes	Ophidiidae	<i>Ophidion rochei</i>	<i>Oroc</i>									1					
Perciformes	Moronidae	<i>Dicentrarchus labrax</i>	<i>Dlab</i>			1	1	1				26		1	2	1	
Perciformes	Serranidae	<i>Serranus cabrilla</i>	<i>Scab</i>		82			10	10	3							

Order	Family	Specie	Acronym	Number of individuals												
				Central Zone						Northern zone						
				CS10	CSEA15	CS15	CS20	CA15	CR15	NG20	NR15	NS10	NS15	NS20	NSM20	NM20
Perciformes	Serranidae	<i>Serranus scriba</i>	<i>Sescr</i>		105	1										
Perciformes	Pomatomidae	<i>Pomatomus saltator</i>	<i>Psal</i>	1												
Perciformes	Carangidae	<i>Caranx rhonchus</i>	<i>Crho</i>	24	5	1										
Perciformes	Carangidae	<i>Seriola dumerili</i>	<i>Sdum</i>	21	9	51	<b>15</b>	5					1	1	2	
Perciformes	Carangidae	<i>Trachinotus ovatus</i>	<i>Tova</i>	1												
Perciformes	Carangidae	<i>Trachurus mediterraneus</i>	<i>Tmed</i>	14	159	<b>62</b>	1		7			1	3	2	15	1
Perciformes	Haemulidae	<i>Pomadasys incisus</i>	<i>Pinc</i>		15	1		9	2							
Perciformes	Sparidae	<i>Boops boops</i>	<i>Bboo</i>		4			4	2	1	1	3		4	6	
Perciformes	Sparidae	<i>Dentex dentex</i>	<i>Dden</i>	16	7	47	3	2							1	2
Perciformes	Sparidae	<i>Diplodus annularis</i>	<i>Dann</i>		120	12		5	4	5	2					
Perciformes	Sparidae	<i>Diplodus cervinus</i>	<i>Dcer</i>			4		1								
Perciformes	Sparidae	<i>Diplodus puntazzo</i>	<i>Dpun</i>	2	1	3	1		1	1						
Perciformes	Sparidae	<i>Diplodus sargus</i>	<i>Dsar</i>	28		5	3	15	18	7		6	11			3
Perciformes	Sparidae	<i>Diplodus vulgaris</i>	<i>Dvul</i>	4	51	19	4	4	2	3	1	6		6	2	
Perciformes	Sparidae	<i>Lithognathus mormyrus</i>	<i>Lmor</i>	<b>105</b>	8	4		5	11	2		24	<b>62</b>	5		
Perciformes	Sparidae	<i>Oblada melanura</i>	<i>Omel</i>	1	4					1		4				
Perciformes	Sparidae	<i>Pagellus acarne</i>	<i>Paca</i>		201	12	1	<b>65</b>	<b>44</b>	29	<b>49</b>	11	7	<b>162</b>		
Perciformes	Sparidae	<i>Pagellus bogaraveo</i>	<i>Pbog</i>					1		8					<b>26</b>	2
Perciformes	Sparidae	<i>Pagellus erythrinus</i>	<i>Pery</i>	22	67	<b>63</b>	4	40	31	<b>48</b>	13	23	<b>27</b>	43	<b>37</b>	<b>17</b>
Perciformes	Sparidae	<i>Pagrus auriga</i>	<i>Paur</i>				1									
Perciformes	Sparidae	<i>Pagrus pagrus</i>	<i>Ppag</i>	2	35	30	6	20	1				3	8		2
Perciformes	Sparidae	<i>Sarpa salpa</i>	<i>Ssal</i>	11		1				1		<b>61</b>	3	7		
Perciformes	Sparidae	<i>Sparus aurata</i>	<i>Spaur</i>	6		19	<b>24</b>	2	1			8				<b>29</b>
Perciformes	Sparidae	<i>Spondyliosoma cantharus</i>	<i>Scan</i>		4	2		3		1			4			2
Perciformes	Centracanthidae	<i>Spicara maena</i>	<i>Smae</i>		4					<b>59</b>		3		1	3	

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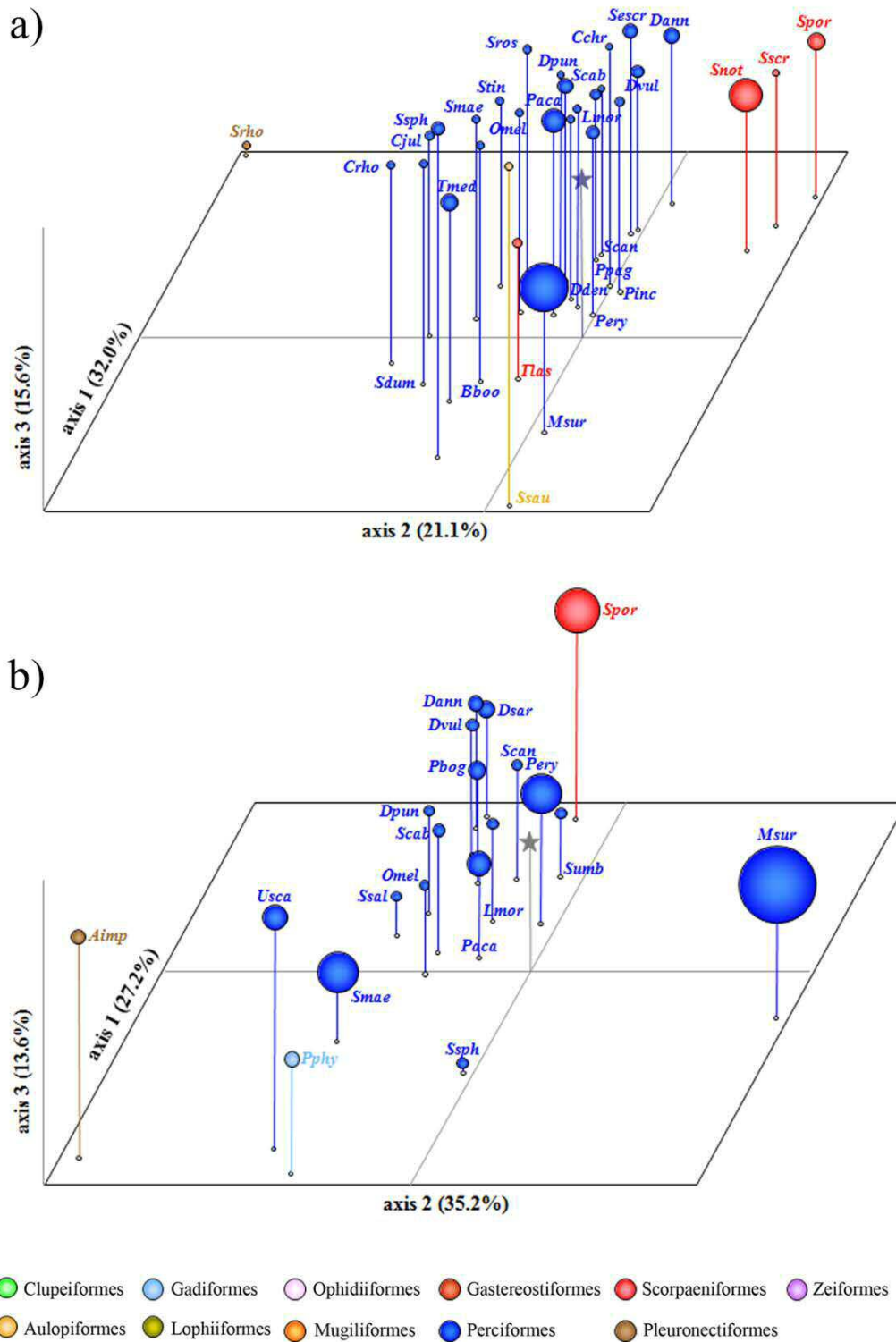
Order	Family	Specie	Acronym	Number of individuals												
				Central Zone						Northern zone						
				CS10	CSEA15	CS15	CS20	CA15	CR15	NG20	NR15	NS10	NS15	NS20	NSM20	NM20
Perciformes	Sciaenidae	<i>Sciaena umbra</i>	<i>Sumb</i>	1		11	6	3	11		2					3
Perciformes	Sciaenidae	<i>Umbrina canariensis</i>	<i>Ucan</i>				1	2	4							
Perciformes	Sciaenidae	<i>Umbrina cirrosa</i>	<i>Ucir</i>	2				1								
Perciformes	Mullidae	<i>Mullus barbatus</i>	<i>Mbar</i>		3			5	4					3		
Perciformes	Mullidae	<i>Mullus surmuletus</i>	<i>Msur</i>		<b>965</b>	4	2	6	4	<b>171</b>	<b>76</b>	27	<b>68</b>	<b>217</b>		1
Perciformes	Pomacentridae	<i>Chromis chromis</i>	<i>Cchr</i>		9			4	1							
Perciformes	Labridae	<i>Coris julis</i>	<i>Cjul</i>		10			1	1							
Perciformes	Labridae	<i>Labrus merula</i>	<i>Lmer</i>			4		1	1							
Perciformes	Labridae	<i>Labrus viridis</i>	<i>Lvir</i>		1											
Perciformes	Labridae	<i>Symphodus cinereus</i>	<i>Scin</i>		1											
Perciformes	Labridae	<i>Symphodus mediterraneus</i>	<i>Smed</i>		2											
Perciformes	Labridae	<i>Symphodus roissali</i>	<i>Sroi</i>		1											
Perciformes	Labridae	<i>Symphodus rostratus</i>	<i>Sros</i>		13											
Perciformes	Labridae	<i>Symphodus tinca</i>	<i>Stin</i>	1	5	1			3							
Perciformes	Labridae	<i>Xyrichtys novacula</i>	<i>Xnov</i>		4								1			
Perciformes	Trachinidae	<i>Trachinus araneus</i>	<i>Tara</i>	2		2										
Perciformes	Trachinidae	<i>Trachinus draco</i>	<i>Tdra</i>								2	8	8		6	
Perciformes	Trachinidae	<i>Trachinus radiatus</i>	<i>Trad</i>				1									
Perciformes	Uranoscopidae	<i>Uranoscopus scaber</i>	<i>Usca</i>			1	6	1	4	25	6	2	11	3	5	5
Perciformes	Sphyraenidae	<i>Sphyraena sphyraena</i>	<i>Ssph</i>		68	1				2	1			2		
Perciformes	Sphyraenidae	<i>Sphyraena viridensis</i>	<i>Svir</i>	2	1											
Perciformes	Scombridae	<i>Auxis rochei</i>	<i>Aroc</i>												1	
Perciformes	Scombridae	<i>Euthynnus alletteratus</i>	<i>Eall</i>	1												
Perciformes	Scombridae	<i>Sarda sarda</i>	<i>Ssar</i>	7	1	6	7									<b>43</b>
Perciformes	Scombridae	<i>Scomber colias</i>	<i>Scol</i>			<b>111</b>									17	

Order	Family	Specie	Acronym	Number of individuals												
				Central Zone						Northern zone						
				CS10	CSEA15	CS15	CS20	CA15	CR15	NG20	NR15	NS10	NS15	NS20	NSM20	NM20
Perciformes	Scombridae	<i>Scomber scombrus</i>	<i>Ssco</i>			1						1		16	2	
Pleuronectiformes	Scophthalmidae	<i>Scophthalmus rhombus</i>	<i>Srho</i>	1	2		12	31	24				7	1		
Pleuronectiformes	Scophthalmidae	<i>Psetta maxima</i>	<i>Pmax</i>					6	1				3		1	
Pleuronectiformes	Bothidae	<i>Arnoglossus imperialis</i>	<i>Aimp</i>								4					
Pleuronectiformes	Bothidae	<i>Arnoglossus laterna</i>	<i>Alat</i>					1								
Pleuronectiformes	Bothidae	<i>Arnoglossus thori</i>	<i>Atho</i>		1											
Pleuronectiformes	Bothidae	<i>Bothus podas</i>	<i>Bpod</i>	1		1		29	<b>56</b>	1	2	8	4			
Pleuronectiformes	Citharidae	<i>Citharus linguatula</i>	<i>Clin</i>					3						4	<b>50</b>	
Pleuronectiformes	Soleidae	<i>Microchirus variegatus</i>	<i>Mvar</i>					1								
Pleuronectiformes	Soleidae	<i>Solea lascaris</i>	<i>Slas</i>					1								
Pleuronectiformes	Soleidae	<i>Solea senegalensis</i>	<i>Ssen</i>				7	32	8							
Pleuronectiformes	Soleidae	<i>Solea solea</i>	<i>Ssol</i>			1	3	15	11			<b>126</b>	16	4	3	
Pleuronectiformes	Soleidae	<i>Synaptura lusitanica</i>	<i>Slus</i>					1								
Pleuronectiformes	Soleidae	<i>Synapturichthys kleinii</i>	<i>Skle</i>				1									
Scorpaeniformes	Dactylopteridae	<i>Dactylopterus volitans</i>	<i>Dvol</i>	<b>54</b>	1	15			5				1		1	
Scorpaeniformes	Scorpaenidae	<i>Scorpaena notata</i>	<i>Snot</i>	1	<b>353</b>	2		<b>166</b>	<b>39</b>		1		6	3		
Scorpaeniformes	Scorpaenidae	<i>Scorpaena porcus</i>	<i>Spor</i>	7	155	23	4	<b>69</b>	20	<b>76</b>	2	5	5	6		
Scorpaeniformes	Scorpaenidae	<i>Scorpaena scrofa</i>	<i>Sscr</i>	1	6	3		7	12		1		3	1		
Scorpaeniformes	Triglidae	<i>Aspitrigla cuculus</i>	<i>Acuc</i>								8			4		
Scorpaeniformes	Triglidae	<i>Aspitrigla obscura</i>	<i>Aobs</i>			1			1							
Scorpaeniformes	Triglidae	<i>Trigla lucerna</i>	<i>Tluc</i>		3		2	9	1			4		4	5	
Scorpaeniformes	Triglidae	<i>Trigloporus lastoviza</i>	<i>Tlas</i>		10	6									3	
Syngnathiformes	Syngnathidae	<i>Syngnathus acus</i>	<i>Sacu</i>									2				
Zeiformes	Zeidae	<i>Zeus faber</i>	<i>Zfab</i>				1									

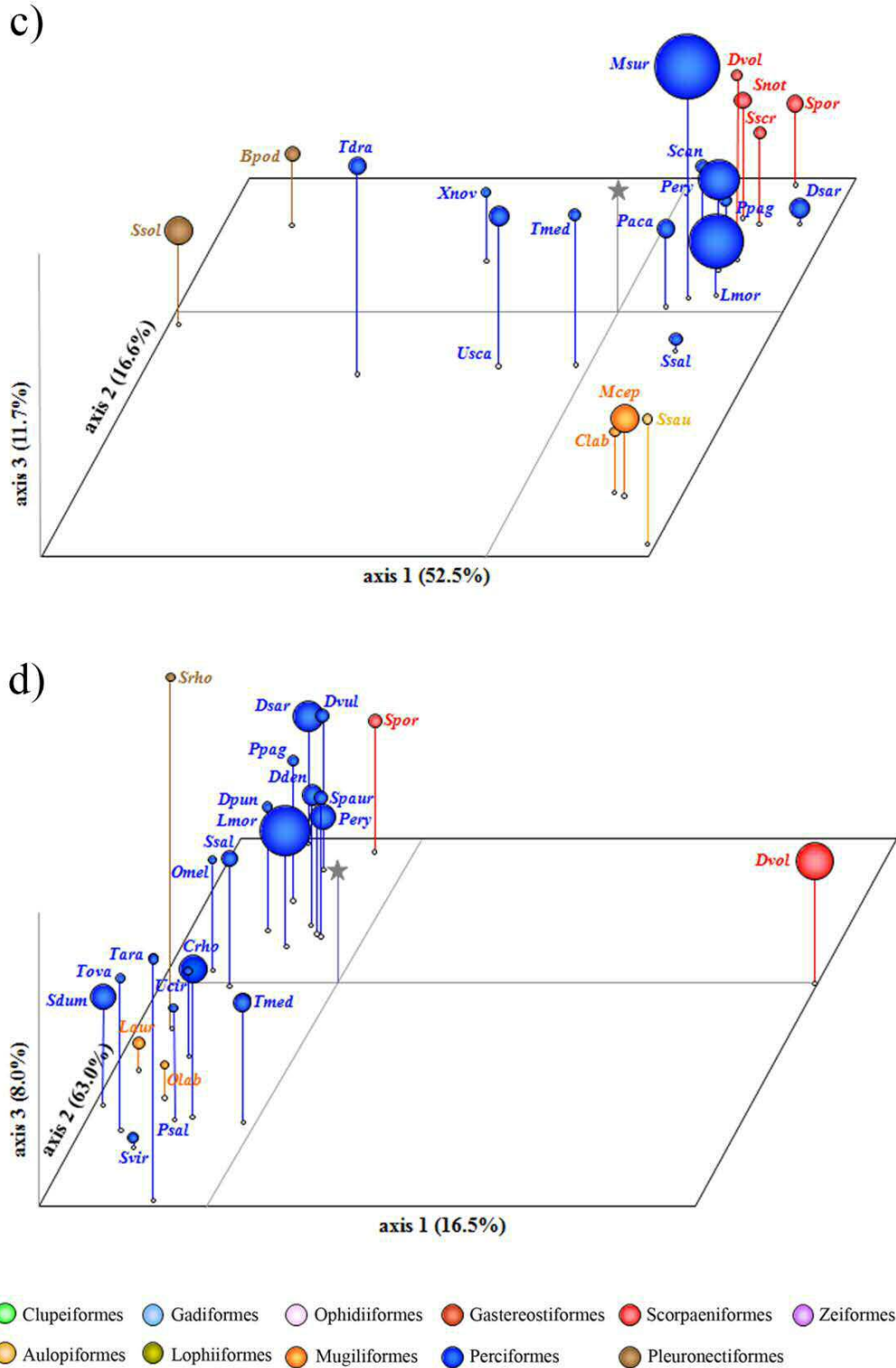
### 13. Appendix 1. Supplementary Material

Order	Family	Specie	Acronym	Number of individ						
				Central Zone						
				CS10	CSEA15	CS15	CS20	CA15	CR15	NG20
		Individuals		343	2501	539	121	629	356	456
		Specific richness		30	43	40	27	48	37	22

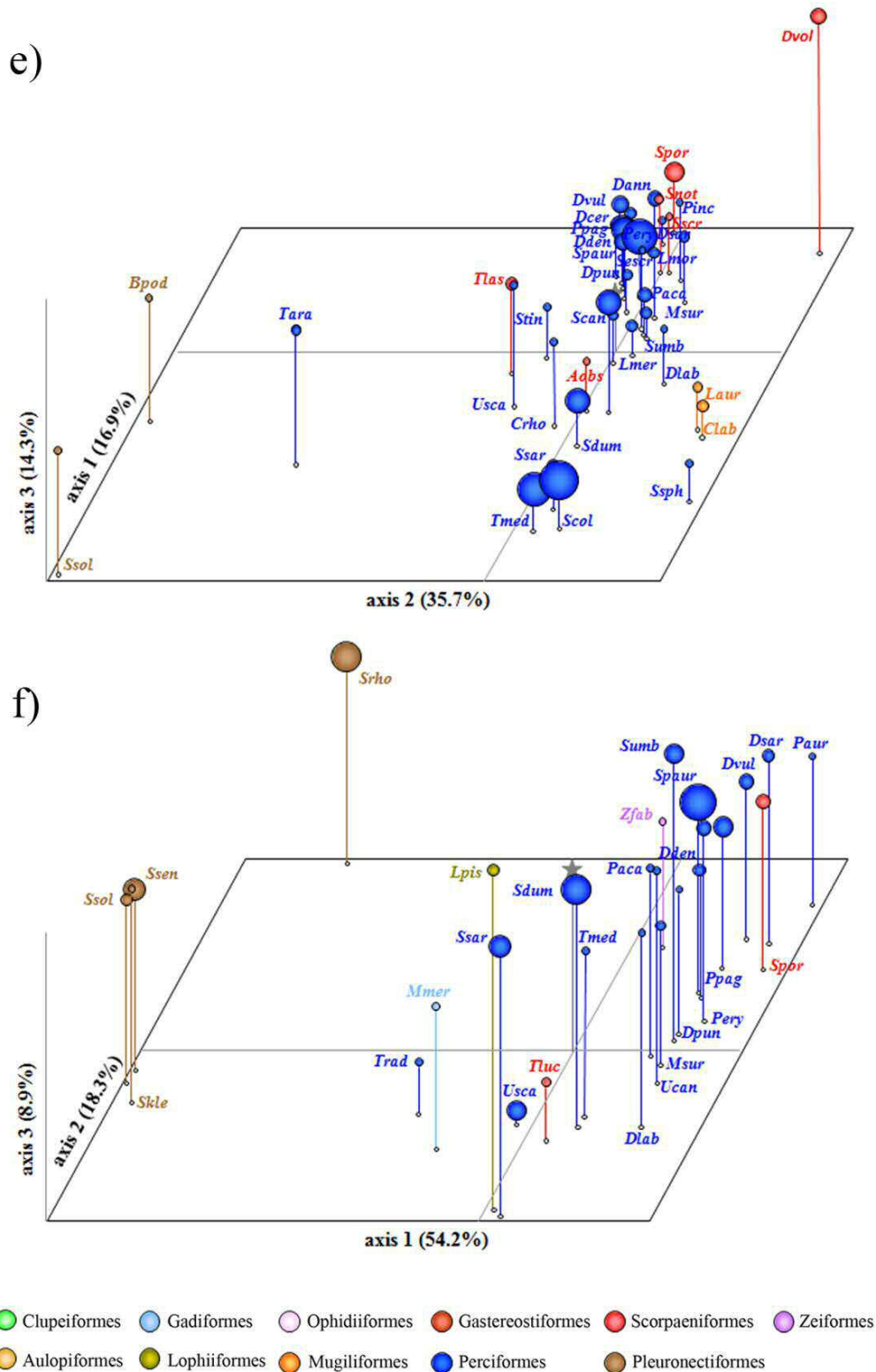




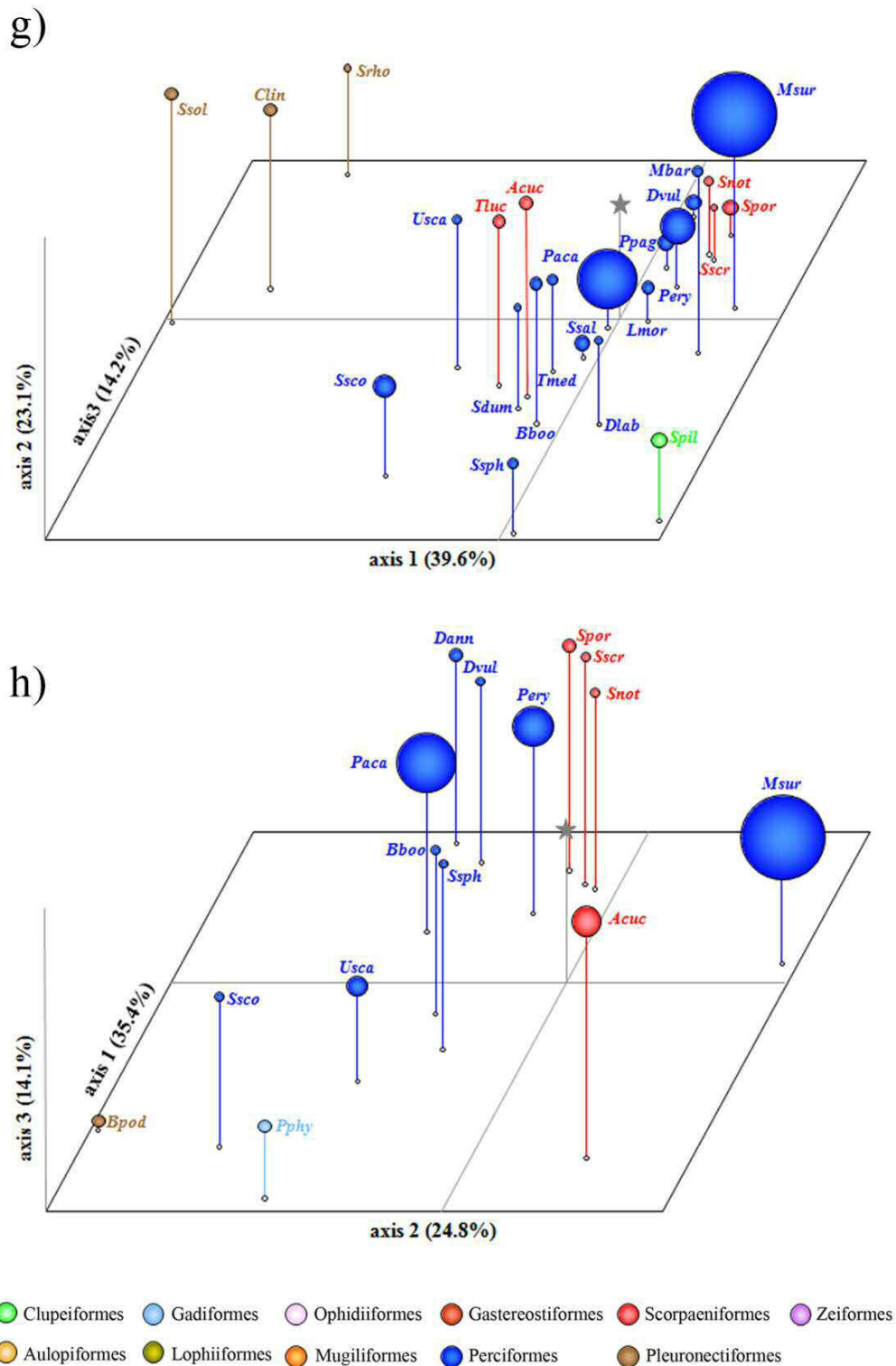
**Figure S1.** Representation of the fish morphospaces of rocky-seagrasses (*CSEA15*) (a) and gravel (*NG20*) (b) assemblages. The first three relative warps represent the three axis of the morphospace, providing each of them the corresponding percentage of total morphological variability. The size point of each species represents its specific abundance within the assemblage, and the colour represents the taxonomical order to which it belongs.



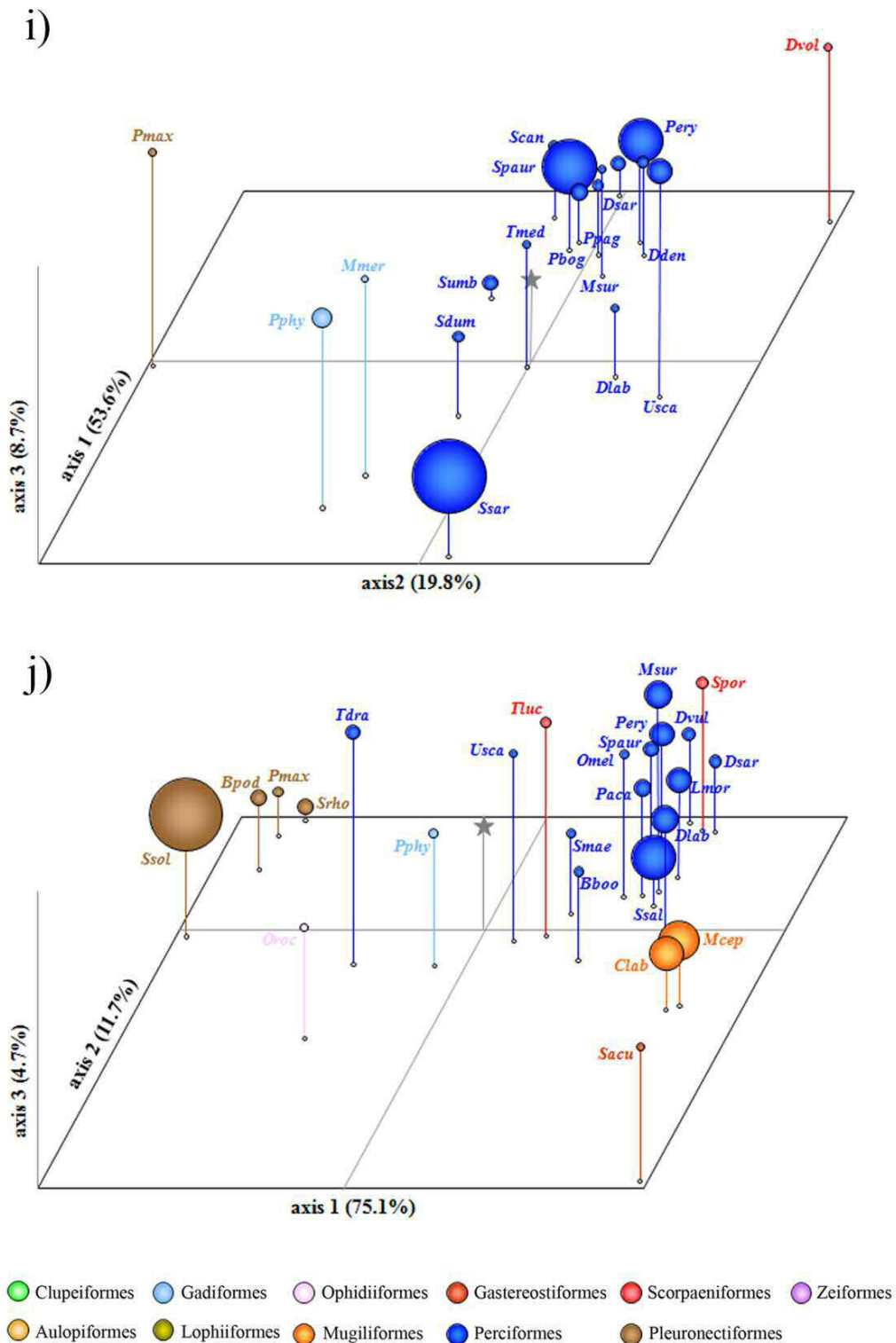
**Figure S2.** Representation of the fish morphospaces of sandy 10-20 m (NS15) (c) and sandy <10 m (CS10) (d) assemblages. The first three relative warps represent the three axis of the morphospace, providing each of them the corresponding percentage of total morphological variability. The size point of each species represents its specific abundance within the assemblage, and the colour represents the taxonomical order to which it belongs.



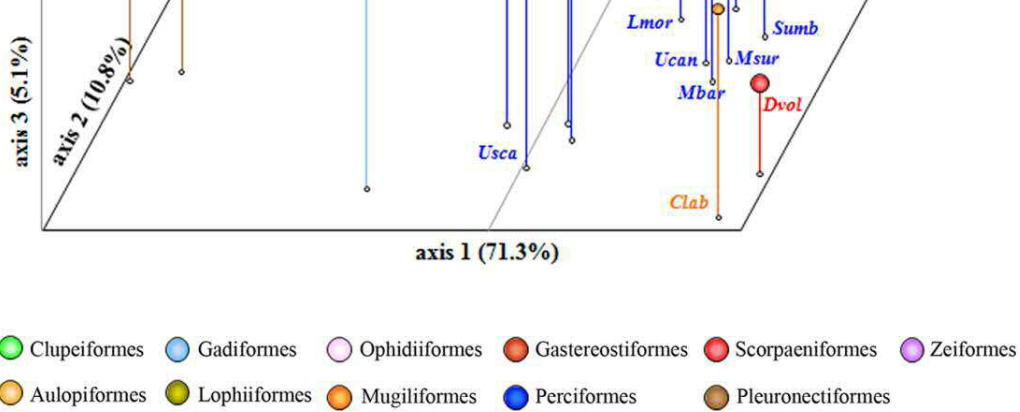
**Figure S3.** Representation of the fish morphospaces of sandy-rocky (*CS15*) (e) and sandy >20 m (*CS20*) (f) assemblages. The first three relative warps represent the three axis of the morphospace, providing each of them the corresponding percentage of total morphological variability. The size point of each species represents its specific abundance within the assemblage, and the colour represents the taxonomical order to which it belongs.



**Figure S4.** Representation of the fish morphospace of sandy-rocky >20 m (NS20) (g) and rocky (NR15) (h) assemblages. The first three relative warps represent the three axis of the morphospace, providing each of them the corresponding percentage of total morphological variability. The size point of each species represents its specific abundance within the assemblage, and the colour represents the taxonomical order to which it belongs



**Figure S5.** Representation of the fish morphospaces of muddy (NM20) (i) and sandy <10 m (NS10) (j) assemblages. The first three relative warps represent the three axis of the morphospace, providing each of them the corresponding percentage of total morphological variability. The size point of each species represents its specific abundance within the assemblage, and the colour represents the taxonomical order to which it belongs.



**Figure S6.** Representation of the fish morphospaces of rocky-sandy (*CR15*) (k) assemblage. The first three relative warps represent the three axis of the morphospace, providing each of them the corresponding percentage of total morphological variability. The size point of each species represents its specific abundance within the assemblage, and the colour represents the taxonomical order to which it belongs.

## 13.3 Supplementary Material CHAPTER 8

**Supplementary Table S1.** List of species with taxonomic classification (order, family, species), used acronym for each species, abundance data (N/km<sup>2</sup>) and number of total captured species for the different defined assamblages. Orders are listed alphabetically.

Order	Family	Specie	Acronym	Assemblages					
				A (40-80m)	B (80-250m)	C (250-500m)	D (500-800m)	E (800-1400m)	F (1400-2200m)
Albuliformes	Notacanthidae	<i>Notacanthus bonaparte</i>	Notbon				959.65	4462.79	209.79
Albuliformes	Notacanthidae	<i>Polyacanthonotus rissoanus</i>	Polris				50.62	352.53	633.27
Anguilliformes	Chlopsidae	<i>Chlopsis bicolor</i>	Chlbic		23.7				
Anguilliformes	Congridae	<i>Conger conger</i>	Concon	95.17		11.53	217.64		
Anguilliformes	Congridae	<i>Gnathophis mystax</i>	Gnamys			11.53			
Anguilliformes	Congridae	<i>Pseudophichthys splendens</i>	Psespl				81.5		
Anguilliformes	Nemichthyidae	<i>Nemichthys scolopaceus</i>	Nemsco				25.31		
Anguilliformes	Nettastomatidae	<i>Nettastoma melanurum</i>	Netmel					108.64	
Anguilliformes	Ophichthidae	<i>Ophisurus serpens</i>	Ophser		23.25				
Anguilliformes	Synaphobranchidae	<i>Dysomma brevirostre</i>	Dysbre			12.22			
Argentiniiformes	Alepocephalidae	<i>Alepocephalus rostratus</i>	Aleros					2725.15	756.29
Argentiniiformes	Argentinidae	<i>Argentina sphyraena</i>	Argsph		449581.32	62990.61			
Argentiniiformes	Argentinidae	<i>Glossanodon leioglossus</i>	Glolei		20569.79	38.48			
Aulopiformes	Aulopidae	<i>Aulopus filamentosus</i>	Aulfil	996.1	62.97				
Aulopiformes	Chlorophthalmidae	<i>Chlorophthalmus agassizi</i>	Chlaga			81187.52	49.2		
Aulopiformes	Evermannellidae	<i>Evermannella balbo</i>	Evebal				12.71	26.32	43.47
Aulopiformes	Ipnopidae	<i>Bathypterois mediterraneus</i>	Batmed					364.67	10577.30
Aulopiformes	Paralepididae	<i>Arctozenus risso</i>	Arcris				35.35	26.32	
Aulopiformes	Synodontidae	<i>Synodus saurus</i>	Synsau	140.92					
Beryciformes	Trachichthyidae	<i>Hoplostethus mediterraneus</i>	Hopmed			2230.26	553.21		
Gadiformes	Gadidae	<i>Gadiculus argenteus</i>	Gadarg			234871.95			

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Order	Family	Specie	Acronym	Assemblages					
				A (40-80m)	B (80-250m)	C (250-500m)	D (500-800m)	E (800-1400m)	F (1400-2200m)
Gadiformes	Gadidae	<i>Micromesistius poutassou</i>	Micpou		23.25	13240.92	49.31		
Gadiformes	Gadidae	<i>Molva dypterygia</i>	Moldyp		31.73	1094.75	51.24		
Gadiformes	Gadidae	<i>Trisopterus capelanus</i>	Tricap	61594.18	3990.75				
Gadiformes	Macrouridae	<i>Coelorinchus caelorhincus</i>	Coecae			20648.01	12.9		
Gadiformes	Macrouridae	<i>Coelorinnchus mediterraneus</i>	Coemed					698.97	1549.96
Gadiformes	Macrouridae	<i>Coryphaenoides guentheri</i>	Corgue					25.38	5610.74
Gadiformes	Macrouridae	<i>Coryphaenoides mediterraneus</i>	Cormed						636.32
Gadiformes	Macrouridae	<i>Hymenocephalus italicus</i>	Hymita			9653.38	2787.21		
Gadiformes	Macrouridae	<i>Nezumia aequalis</i>	Nezaeq			26.22	4301.94	2047.28	
Gadiformes	Macrouridae	<i>Trachyrincus scabrus</i>	Trasca			36.66	148	1598.26	
Gadiformes	Merluccidae	<i>Merluccius merluccius</i>	Mermer	664.69	17671.64	962.77	86.18		
Gadiformes	Moridae	<i>Eretmophorus kleinenbergi</i>	Erekle						13.89
Gadiformes	Moridae	<i>Lepidion guentheri</i>	Lepgue						42.15
Gadiformes	Moridae	<i>Lepidion lepidion</i>	Leplep				1738.89	15506.40	2408.57
Gadiformes	Moridae	<i>Mora moro</i>	Mormor				250.45	1412.19	
Gadiformes	Phycidae	<i>Gaidropsarus biscayensis</i>	Gaibis			25.33		14.71	
Gadiformes	Phycidae	<i>Phycis blennoides</i>	Phyble		674.16	7515.77	8482.62	371.90	
Gadiformes	Phycidae	<i>Phycis phycis</i>	Phyphy	29.56	23.17				
Gasterosteiformes	Macroramposidae	<i>Macroramphosus scolopax</i>	Macscsco	103.05	10541.76	41.29	12.5		
Gasterosteiformes	Syngnathidae	<i>Syngnathus acus</i>	Synacu	895.21					
Lophiiformes	Lophiidae	<i>Lophius budegassa</i>	Lopbud	134.47	1530.99	853.59			
Lophiiformes	Lophiidae	<i>Lophius piscatorius</i>	Loppis	467.78	96.32	87.49	11.53		
Myctophiformes	Myctophidae	<i>Ceratoscopelus maderensis</i>	Cermad			382.49	61.78	23.26	
Myctophiformes	Myctophidae	<i>Lampanyctus crocodilus</i>	Lamcro			4452.7	35461.27	1644.87	226.23
Myctophiformes	Myctophidae	<i>Notoscopelus elongatus</i>	Notelo			379.95	23.06		48.64
Ophidiiformes	Bythitidae	<i>Cataetyx alleni</i>	Catall				13.06	695.16	153.90



Order	Family	Specie	Acronym	Assemblages					
				A (40-80m)	B (80-250m)	C (250-500m)	D (500-800m)	E (800-1400m)	F (1400-2200m)
Ophidiiformes	Bythitidae	<i>Cataetyx laticeps</i>	Catlat					23.26	150.19
Ophidiiformes	Carapidae	<i>Carapus acus</i>	Caracu	802.24	628.89				
Perciformes	Blenniidae	<i>Blennius ocellaris</i>	Bleoce	1592.43	964.45				
Perciformes	Blenniidae	<i>Parablennius tentacularis</i>	Parten	31.31					
Perciformes	Callanthiidae	<i>Callanthias ruber</i>	Calrub	333.19	4466.5				
Perciformes	Callionymidae	<i>Callionymus maculatus</i>	Calmac		114.84				
Perciformes	Callionymidae	<i>Synchiropus phaeton</i>	Synpha	31.31	5890.39	19575.18	76.01		
Perciformes	Caproidae	<i>Capros aper</i>	Capape		13627.83	24459.03	24.83		
Perciformes	Carangidae	<i>Trachurus mediterraneus</i>	Tramed	34209.4	34535.17	35.81			
Perciformes	Carangidae	<i>Trachurus picturatus</i>	Trapic	206.52	1276.37				
Perciformes	Carangidae	<i>Trachurus trachurus</i>	Tratra	860.85	7726.6	579.22			
Perciformes	Centracanthidae	<i>Centracanthus cirrus</i>	Cencir	1830.54	359019.06				
Perciformes	Centracanthidae	<i>Spicara maena</i>	Spimae	2694.94	89.16				
Perciformes	Centracanthidae	<i>Spicara smaris</i>	Spisma	165356.94	7470.95				
Perciformes	Centrolophidae	<i>Centrolophus niger</i>	Cennig				24.58		
Perciformes	Centrolophidae	<i>Schedophilus medusophagus</i>	Schmed			12.22	26.11	28.65	
Perciformes	Cepolidae	<i>Cepola macrophthalma</i>	Cepmac		851.81				
Perciformes	Epigonidae	<i>Epigonus denticulatus</i>	Epiden			1082.2	38.74		
Perciformes	Epigonidae	<i>Epigonus telescopus</i>	Epitel			107.72	191.4		
Perciformes	Gobiesocidae	<i>Diplecogaster bimaculata</i>	Dipbim	33.18					
Perciformes	Gobiidae	<i>Deltentosteus quadrimaculatus</i>	Delqua	29.56	5163.95				
Perciformes	Gobiidae	<i>Gobiidae spp.</i>	Gob	32.27					
Perciformes	Gobiidae	<i>Lesueurigobius friesii</i>	Lesfri		23.17				
Perciformes	Gobiidae	<i>Lesueurigobius sanzi</i>	Lessan		124.64				
Perciformes	Gobiidae	<i>Odondebuena balearica</i>	Odobal	35.88					

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Order	Family	Specie	Acronym	Assemblages					
				A (40-80m)	B (80-250m)	C (250-500m)	D (500-800m)	E (800-1400m)	F (1400-2200m)
Perciformes	Gobiidae	<i>Pomatoschistus marmoratus</i>	Pommar		21.46				
Perciformes	Labridae	<i>Coris julis</i>	Corjul	2690.36					
Perciformes	Mullidae	<i>Mullus barbatus</i>	Mulbar	13209.12	6312.97				
Perciformes	Mullidae	<i>Mullus surmuletus</i>	Mulsur	33328.23	15313.46	622.01			
Perciformes	Serranidae	<i>Serranus cabrilla</i>	Sercab	33740.94	9827.62				
Perciformes	Serranidae	<i>Serranus hepatus</i>	Serhep	29018.13	135367.46				
Perciformes	Sparidae	<i>Boops boops</i>	Booboo	82330.42	26359.65	17.89			
Perciformes	Sparidae	<i>Diplodus annularis</i>	Dipann	707.22					
Perciformes	Sparidae	<i>Diplodus puntazzo</i>	Dippun	99.96					
Perciformes	Sparidae	<i>Diplodus vulgaris</i>	Dipvul	516.04					
Perciformes	Sparidae	<i>Pagellus acarne</i>	Pagaca	8807.2	1006.45				
Perciformes	Sparidae	<i>Pagellus bogaraveo</i>	Pagbog	1883.29	303.63	76.25	13.06		
Perciformes	Sparidae	<i>Pagellus erythrinus</i>	Pagery	4697.14	314.38				
Perciformes	Sparidae	<i>Pagrus pagrus</i>	Pagpag	512.44					
Perciformes	Sparidae	<i>Spondyliosoma cantharus</i>	Spocan	357.15					
Perciformes	Trachinidae	<i>Trachinus draco</i>	Tradra	4211.99	15852.74				
Perciformes	Trachinidae	<i>Trachinus radiatus</i>	Trarad	424.8	66.23				
Perciformes	Trichiuridae	<i>Lepidopus caudatus</i>	Lepcau			488.29			
Perciformes	Uranoscopidae	<i>Uranoscopus scaber</i>	Urasca	509.29	540.24				
Perciformes	Zoarcidae	<i>Melanostigma atlanticum</i>	Melatl					79.33	11.10
Pleuronectiformes	Bothidae	<i>Arnoglossus imperialis</i>	Arnimp	3019.94	1056.33				
Pleuronectiformes	Bothidae	<i>Arnoglossus laterna</i>	Arnlat	65.81	691.24				
Pleuronectiformes	Bothidae	<i>Arnoglossus rueppelii</i>	Arnroe		15612.36	36.29			
Pleuronectiformes	Bothidae	<i>Arnoglossus thori</i>	Arntho	7325.88	944.4				
Pleuronectiformes	Bothidae	<i>Bothus podas</i>	Botpod	176.33					

Order	Family	Specie	Acronym	Assemblages					
				A (40-80m)	B (80-250m)	C (250-500m)	D (500-800m)	E (800-1400m)	F (1400-2200m)
Pleuronectiformes	Citharidae	<i>Citharus linguatula</i>	Citlin	29.56	5550.67				
Pleuronectiformes	Cynoglossidae	<i>Symphurus ligulatus</i>	Symlig			63.33	722.68		
Pleuronectiformes	Cynoglossidae	<i>Symphurus nigrescens</i>	Symnig		193.68	800.84	153.29		
Pleuronectiformes	Scophthalmidae	<i>Lepidorhombus boscii</i>	Lepbos		2022.76	3871.9			
Pleuronectiformes	Scophthalmidae	<i>Lepidorhombus whiffiagonis</i>	Lepwhi		325.76	903.51			
Pleuronectiformes	Soleidae	<i>Bathysolea profundicola</i>	Batpro			52.44			
Pleuronectiformes	Soleidae	<i>Microchirus ocellatus</i>	Micoce	101.56					
Pleuronectiformes	Soleidae	<i>Microchirus variegatus</i>	Micvar	159.97	33.86	35.81			
Pleuronectiformes	Soleidae	<i>Monochirus hispidus</i>	Monhis	35.88	118.82				
Pleuronectiformes	Soleidae	<i>Pegusa impar</i>	Pegimp	199.83					
Pleuronectiformes	Soleidae	<i>Synapturichthys kleinii</i>	Synkle	631.36					
Scorpaeniformes	Dactylopteridae	<i>Dactylopterus volitans</i>	Dacvol	2771.66					
Scorpaeniformes	Peristediidae	<i>Peristedion cataphractum</i>	Percat		605.76	7673.3	12.9		
Scorpaeniformes	Scorpaenidae	<i>Helicolenus dactylopterus</i>	Heldac		4147.29	56825.38	37.7		
Scorpaeniformes	Scorpaenidae	<i>Scorpaena elongata</i>	Scoelo		22.32	406.41			
Scorpaeniformes	Scorpaenidae	<i>Scorpaena notata</i>	Sconot	6995.04	2704.23				
Scorpaeniformes	Scorpaenidae	<i>Scorpaena porcus</i>	Scopor	233					
Scorpaeniformes	Scorpaenidae	<i>Scorpaena scrofa</i>	Scoscr	2680.43	964.77	13.11			
Scorpaeniformes	Triglidae	<i>Chelidonichthys cuculus</i>	Checuc		42793.33				
Scorpaeniformes	Triglidae	<i>Chelidonichthys lucerna</i>	Cheluc	33.44	30.73				
Scorpaeniformes	Triglidae	<i>Lepidotrigla cavillone</i>	Lepcav	4014.7	50842.04				
Scorpaeniformes	Triglidae	<i>Trigla lyra</i>	Trilyr		1101.32	869.17			
Scorpaeniformes	Triglidae	<i>Trigloporus lastoviza</i>	Trilas	27414.35	492.01				
Stomiiformes	Stomiidae	<i>Chauliodus sloani</i>	Chaslo			12.22	38.32	48.01	57.74
Stomiiformes	Stomiidae	<i>Stomias boa boa</i>	Stoboa			257.19	348.54	52.63	

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Order	Family	Specie	Acronym	Assemblages						
				A (40-80m)	B (80-250m)	C (250-500m)	D (500-800m)	E (800-1400m)	F (1400-2200m)	
Zeiformes	Zeidae	<i>Zeus faber</i>	Zeufab	363.07	494.07					
		Number of species		60	63	48	38	23	17	

**Supplementary Table S2.** Functional-trait matrix with the categorization for each species (definition of the different categories in Table 1), including the taxonomical classification of species (order, family, specie) and the used acronym for each species. Species are listed alphabetically.

Order	Family	Specie	Acronym	Body shape	Swimming Type	Motility	Size	Vertical distribution	Diet
Argentiniiformes	Alepocephalidae	<i>Alepocephalus rostratus</i>	Aleros	Elo	Car	H	ML	BENTP	nmM
Aulopiformes	Paralepididae	<i>Arctozenus risso</i>	Arcris	Elo	Car	H	SM	MESP	mM
Argentiniiformes	Argentinidae	<i>Argentina sphyraena</i>	Argsph	Elo	Car	R	SM	BENTP	nmM
Pleuronectiformes	Bothidae	<i>Arnoglossus imperialis</i>	Arnimp	Asy	Ang	S	SM	ENDB	NS
Pleuronectiformes	Bothidae	<i>Arnoglossus laterna</i>	Arnlat	Asy	Ang	S	S	ENDB	NS
Pleuronectiformes	Bothidae	<i>Arnoglossus rueppelii</i>	Arn rue	Asy	Ang	S	SM	ENDB	NS
Pleuronectiformes	Bothidae	<i>Arnoglossus thori</i>	Arntho	Asy	Ang	S	SM	ENDB	NS
Aulopiformes	Aulopidae	<i>Aulopus filamentosus</i>	Aulfil	Fus	Sub	R	M	EPIB	NS
Aulopiformes	Ipnopidae	<i>Bathypterois mediterraneus</i>	Batmed	Elo	Bat	S	SM	EPIB	NS
Pleuronectiformes	Soleidae	<i>Bathysolea profundicola</i>	Batpro	Asy	Ang	S	SM	ENDB	NS
Perciformes	Blenniidae	<i>Blennius ocellaris</i>	Bleoce	Obl	Dio	S	SM	EPIB	EPIB
Perciformes	Sparidae	<i>Boops boops</i>	Booboo	Fus	Car	H	SM	BENTP	nmM
Pleuronectiformes	Bothidae	<i>Bothus podas</i>	Botpod	Asy	Ang	S	SM	ENDB	EPIB
Perciformes	Callanthiidae	<i>Callanthias ruber</i>	Calrub	Fus	Car	R	SM	BENTP	nmM
Perciformes	Callionymidae	<i>Callionymus maculatus</i>	Calmac	Elo	Sub	S	SM	EPIB	EPIB
Perciformes	Caproidae	<i>Capros aper</i>	Capape	Ova	Bal	H	S	BENTP	nmM
Ophidiiformes	Carapidae	<i>Carapus acus</i>	Caracu	Ang	Ang	S	SM	EPIB	EPIB
Ophidiiformes	Bythitidae	<i>Cataetyx alleni</i>	Catall	Elo	Ang	R	SM	BENTP	NS
Ophidiiformes	Bythitidae	<i>Cataetyx laticeps</i>	Catlat	Elo	Ang	R	M	BENTP	NS
Perciformes	Centracanthidae	<i>Centracanthus cirrus</i>	Cencir	Fus	Car	H	SM	BENTP	nmM
Perciformes	Centrolophidae	<i>Centrolophus niger</i>	Cennig	Fus	Car	H	M	BENTP	nmM

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Order	Family	Specie	Acronym	Body shape	Swimming Type	Motility	Size	Vertical distribution	Diet
Perciformes	Cepolidae	<i>Cepola macrophthalma</i>	Cepmac	Ang	Ang	S	M	BENTP	nmM
Myctophiformes	Myctophidae	<i>Ceratoscopelus maderensis</i>	Cermad	Obl	Car	H	S	MESP	mM
Stomiiformes	Stomiidae	<i>Chauliodus sloani</i>	Chaslo	Elo	Car	R	SM	BATHYP	mM
Scorpaeniformes	Triglidae	<i>Chelidonichthys cuculus</i>	Checuc	Obl	Sub	S	SM	EPIB	EPIB
Scorpaeniformes	Triglidae	<i>Chelidonichthys lucerna</i>	Cheluc	Obl	Sub	S	M	EPIB	EPIB
Anguilliformes	Chlopsidae	<i>Chlopsis bicolor</i>	Chlbic	Ang	Ang	S	ML	ENDB	EPIB
Aulopiformes	Chlorophthalmidae	<i>Chlorophthalmus agassizi</i>	Chlaga	Fus	Sub	R	SM	BENTP	nmM
Pleuronectiformes	Citharidae	<i>Citharus linguatula</i>	Citlin	Asy	Ang	S	SM	ENDB	NS
Gadiformes	Macrouridae	<i>Coelorinchus caelorhincus</i>	Coecae	Elo	Sub	R	M	BENTP	INF
Gadiformes	Macrouridae	<i>Coelorinchus mediterraneus</i>	Coemed	Elo	Sub	R	M	BENTP	NS
Anguilliformes	Congridae	<i>Conger conger</i>	Concon	Ang	Ang	S	L	BENTP	NS
Perciformes	Labridae	<i>Coris julis</i>	Corjul	Fus	Lab	R	SM	BENTP	EPIB
Gadiformes	Macrouridae	<i>Coryphaenoides guentheri</i>	Corgue	Elo	Sub	R	SM	BENTP	NS
Gadiformes	Macrouridae	<i>Coryphaenoides mediterraneus</i>	Cormed	Elo	Sub	R	SM	BENTP	NS
Scorpaeniformes	Dactylopteridae	<i>Dactylopterus volitans</i>	Dacvol	Obl	Sub	S	M	EPIP	EPIP
Perciformes	Gobiidae	<i>Deltentosteus quadrimaculatus</i>	Delqua	Obl	Sub	S	S	EPIB	EPIB
Perciformes	Gobiesocidae	<i>Diplecogaster bimaculata</i>	Dipbim	Obl	Sub	S	S	EPIB	EPIB
Perciformes	Sparidae	<i>Diplodus annularis</i>	Dipann	Ova	Car	R	SM	BENTP	EPIB
Perciformes	Sparidae	<i>Diplodus puntazzo</i>	Dippun	Ova	Car	R	M	BENTP	EPIB
Perciformes	Sparidae	<i>Diplodus vulgaris</i>	Dipvul	Ova	Car	R	SM	BENTP	INF
Anguilliformes	Synphobranchidae	<i>Dysomma brevirostre</i>	Dysbre	Ang	Ang	R	M	BENTP	NS
Perciformes	Epigonidae	<i>Epigonus denticulatus</i>	Epiden	Fus	Car	R	SM	BENTP	nmM
Perciformes	Epigonidae	<i>Epigonus telescopus</i>	Epitel	Fus	Car	R	M	BENTP	nmM
Gadiformes	Moridae	<i>Eretmophorus kleinenbergi</i>	Erekle	Elo	Sub	S	SM	BENTP	nmM
Aulopiformes	Evermannellidae	<i>Evermannella balbo</i>	Evebal	Obl	Sub	H	S	MESP	mM
Gadiformes	Gadidae	<i>Gadiculus argenteus</i>	Gadarg	Fus	Sub	R	S	BENTP	nmM

Order	Family	Specie	Acronym	Body shape	Swimming Type	Motility	Size	Vertical distribution	Diet
Gadiformes	Phycidae	<i>Gaidropsarus biscayensis</i>	Gaibis	Elo	Sub	R	SM	BENTP	INF
Argentiniiformes	Argentiniidae	<i>Glossanodon leioglossus</i>	Glolei	Elo	Car	R	SM	BENTP	nmM
Anguilliformes	Congridae	<i>Gnathophis mystax</i>	Gnamys	Ang	Ang	S	M	ENDB	NS
Perciformes	Gobiidae	<i>Gobiidae sp.</i>	Gob	Obl	Dio	S	S	EPIB	NS
Scorpaeniformes	Scorpaenidae	<i>Helicolenus dactylopterus</i>	Heldac	Obl	Sub	S	SM	EPIB	EPIB
Beryciformes	Trachichthyidae	<i>Hoplostethus mediterraneus</i>	Hopmed	Ova	Car	H	SM	BENTP	nmM
Gadiformes	Macrouridae	<i>Hymenocephalus italicus</i>	Hymita	Elo	Sub	R	SM	BENTP	NS
Myctophiformes	Myctophidae	<i>Lampanyctus crocodilus</i>	Lamcro	Obl	Car	H	SM	MESP	nmM
Gadiformes	Moridae	<i>Lepidion guentheri</i>	Lepgue	Fus	Sub	R	M	BENTP	NS
Gadiformes	Moridae	<i>Lepidion lepidion</i>	Leplep	Fus	Sub	R	SM	BENTP	NS
Perciformes	Trichiuridae	<i>Lepidopus caudatus</i>	Lepcau	Elo	Sub	H	ML	BENTP	nmM
Pleuronectiformes	Scophthalmidae	<i>Lepidorhombus boscii</i>	Lepbos	Asy	Ang	S	SM	ENDB	NS
Pleuronectiformes	Scophthalmidae	<i>Lepidorhombus whiffiagonis</i>	Lepwhi	Asy	Ang	S	M	ENDB	NS
Scorpaeniformes	Triglidae	<i>Lepidotrigla cavillone</i>	Lepcav	Obl	Sub	S	SM	EPIB	EPIB
Perciformes	Gobiidae	<i>Lesueurigobius friesii</i>	Lesfri	Obl	Dio	S	S	EPIB	EPIB
Perciformes	Gobiidae	<i>Lesueurigobius sanzi</i>	Lessan	Obl	Dio	S	S	EPIB	EPIB
Lophiiformes	Lophiidae	<i>Lophius budegassa</i>	Lopbud	Sym	Sub	S	ML	EPIB	NS
Lophiiformes	Lophiidae	<i>Lophius piscatorius</i>	Loppis	Sym	Sub	S	ML	EPIB	NS
Gasterosteiformes	Macroramposidae	<i>Macroramphosus scolopax</i>	Macscso	Ova	Bal	H	S	BENTP	nmM
Perciformes	Zoarcidae	<i>Melanostigma atlanticum</i>	Melatl	Ang	Ang	S	S	BENTP	nmM
Gadiformes	Merlucciidae	<i>Merluccius merluccius</i>	Mermer	Fus	Sub	R	ML	BENTP	nmM
Pleuronectiformes	Soleidae	<i>Microchirus ocellatus</i>	Micoce	Asy	Ang	S	SM	EPIB	EPIB
Pleuronectiformes	Soleidae	<i>Microchirus variegatus</i>	Micvar	Asy	Ang	S	SM	EPIB	EPIB
Gadiformes	Gadidae	<i>Micromesistius poutassou</i>	Micpou	Fus	Sub	R	M	BENTP	nmM
Gadiformes	Gadidae	<i>Molva dypterygia</i>	Moldyp	Elo	Sub	R	ML	BENTP	NS
Pleuronectiformes	Soleidae	<i>Monochirus hispidus</i>	Monhis	Asy	Ang	S	S	EPIB	EPIB

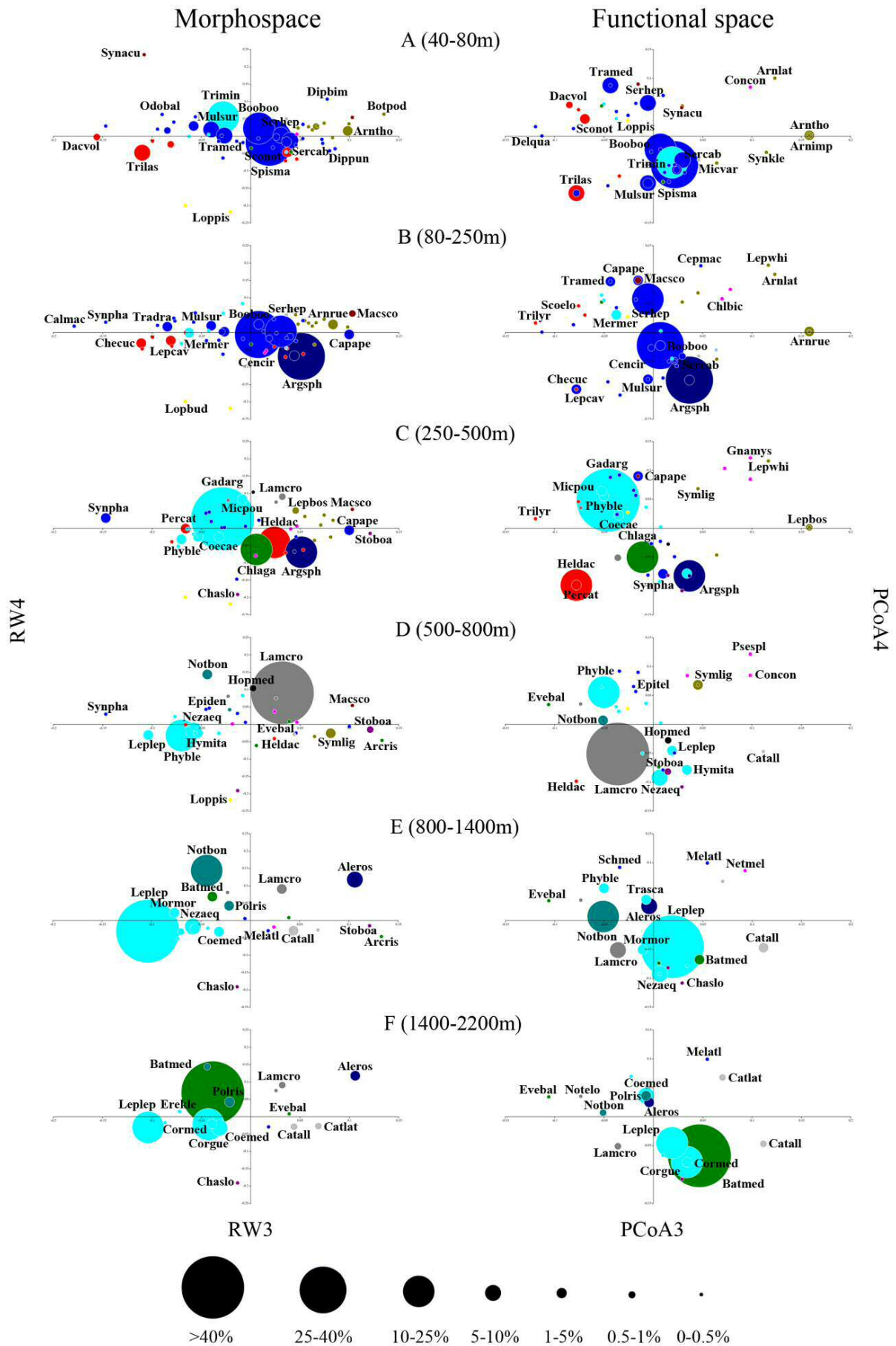
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Order	Family	Specie	Acronym	Body shape	Swimming Type	Motility	Size	Vertical distribution	Diet
Gadiformes	Moridae	<i>Mora moro</i>	Mormor	Fus	Sub	R	SM	BENTP	nmM
Perciformes	Mullidae	<i>Mullus barbatus</i>	Mulbar	Obl	Car	R	SM	BENTP	INF
Perciformes	Mullidae	<i>Mullus surmuletus</i>	Mulsur	Obl	Car	R	SM	BENTP	INF
Anguilliformes	Nemichthyidae	<i>Nemichthys scolopaceus</i>	Nemsco	Ang	Ang	H	L	MESP	nmM
Anguilliformes	Nettastomatidae	<i>Nettastoma melanurum</i>	Netmel	Ang	Ang	S	ML	BENTP	NS
Gadiformes	Macrouridae	<i>Nezumia aequalis</i>	Nezaeq	Elo	Sub	R	SM	BENTP	INF
Albuliformes	Notacanthidae	<i>Notacanthus bonaparte</i>	Notbon	Elo	Sub	R	M	BENTP	EPIB
Myctophiformes	Myctophidae	<i>Notoscopelus elongatus</i>	Notelo	Obl	Car	H	S	MESP	mM
Perciformes	Gobiidae	<i>Odondebuena balearica</i>	Odobal	Obl	Dio	S	S	EPIB	NS
Anguilliformes	Ophichthidae	<i>Ophisurus serpens</i>	Ophser	Ang	Bal	S	L	ENDB	NS
Perciformes	Sparidae	<i>Pagellus acarne</i>	Pagaca	Fus	Car	R	SM	BENTP	INF
Perciformes	Sparidae	<i>Pagellus bogaraveo</i>	Pagbog	Fus	Car	R	M	BENTP	INF
Perciformes	Sparidae	<i>Pagellus erythrinus</i>	Pagery	Fus	Car	R	SM	BENTP	INF
Perciformes	Sparidae	<i>Pagrus pagrus</i>	Pagpag	Fus	Car	R	M	BENTP	NS
Perciformes	Blenniidae	<i>Parablennius tentacularis</i>	Parten	Obl	Dio	S	S	EPIB	EPIB
Pleuronectiformes	Soleidae	<i>Pegusa impar</i>	Pegimp	Asy	Ang	S	SM	ENDB	EPIB
Scorpaeniformes	Peristediidae	<i>Peristedion cataphractum</i>	Percat	Obl	Sub	S	SM	EPIB	EPIB
Gadiformes	Phycidae	<i>Phycis blennoides</i>	Phyble	Fus	Sub	R	M	BENTP	INF
Gadiformes	Phycidae	<i>Phycis phycis</i>	Phyphy	Fus	Sub	R	M	BENTP	INF
Albuliformes	Notacanthidae	<i>Polyacanthonotus rissoanus</i>	Polris	Elo	Sub	R	M	BENTP	NS
Perciformes	Gobiidae	<i>Pomatoschistus marmoratus</i>	Pommar	Obl	Dio	S	S	EPIB	NS
Anguilliformes	Congridae	<i>Pseudophichthys splendens</i>	Psespl	Ang	Ang	S	M	ENDB	NS
Perciformes	Centrolophidae	<i>Schedophilus medusophagus</i>	Schmed	Fus	Car	H	M	BENTP	nmM
Scorpaeniformes	Scorpaenidae	<i>Scorpaena elongata</i>	Scoelo	Obl	Sub	S	M	EPIB	NS
Scorpaeniformes	Scorpaenidae	<i>Scorpaena notata</i>	Sconot	Obl	Sub	S	S	EPIB	NS
Scorpaeniformes	Scorpaenidae	<i>Scorpaena porcus</i>	Scopor	Obl	Sub	S	SM	EPIB	NS

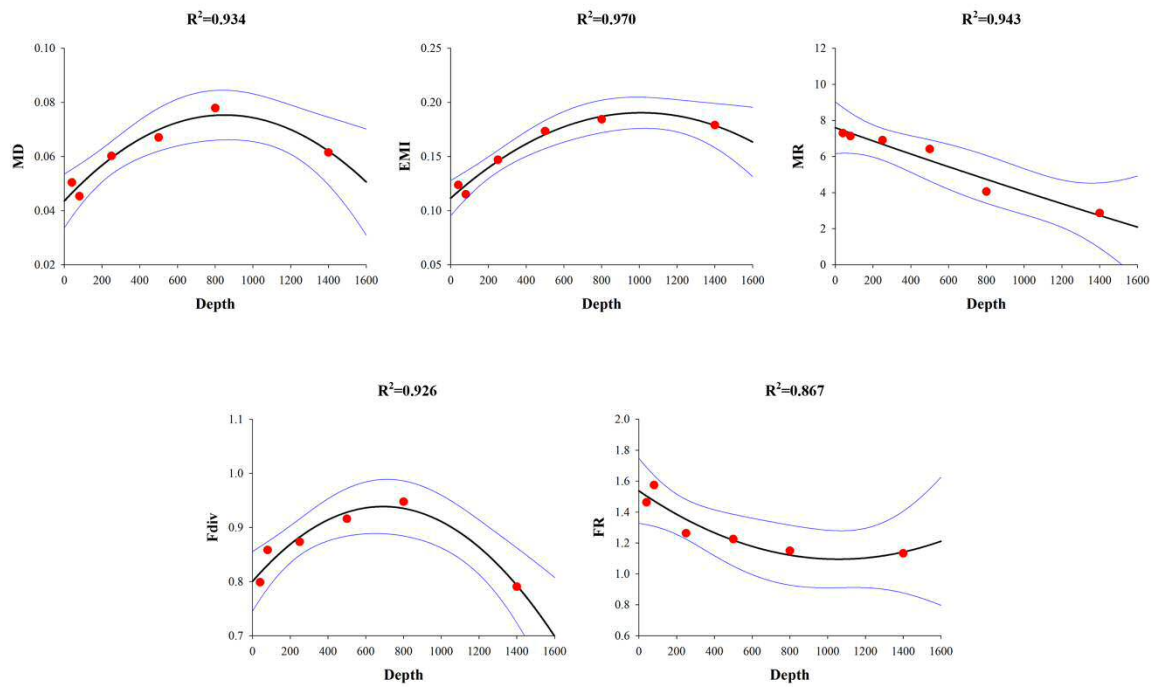


Order	Family	Specie	Acronym	Body shape	Swimming Type	Motility	Si
Scorpaeniformes	Scorpaenidae	<i>Scorpaena scrofa</i>	Scoscr	Obl	Sub	S	M
Perciformes	Serranidae	<i>Serranus cabrilla</i>	Sercab	Fus	Car	S	SH
Perciformes	Serranidae	<i>Serranus hepatus</i>	Serhep	Fus	Car	S	S
Perciformes	Centracanthidae	<i>Spicara maena</i>	Spimae	Fus	Car	R	SH
Perciformes	Centracanthidae	<i>Spicara smaris</i>	Spisma	Fus	Car	R	SH
Perciformes	Sparidae	<i>Spondyliosoma cantharus</i>	Spocan	Ova	Car	R	M
Stomiiformes	Stomiidae	<i>Stomias boa boa</i>	Stoboa	Elo	Car	H	SH
Pleuronectiformes	Cynoglossidae	<i>Symphurus ligulatus</i>	Symlig	Asy	Ang	S	S
Pleuronectiformes	Cynoglossidae	<i>Symphurus nigrescens</i>	Symnig	Asy	Ang	S	S
Pleuronectiformes	Soleidae	<i>Synapturichthys kleinii</i>	Synkle	Asy	Ang	S	SH
Perciformes	Callionymidae	<i>Synchiropus phaeton</i>	Synpha	Elo	Sub	S	SH
Gasterosteiformes	Syngnathidae	<i>Syngnathus acus</i>	Synacu	Elo	Ami	R	M
Aulopiformes	Synodontidae	<i>Synodus saurus</i>	Synsau	Elo	Sub	S	SH
Perciformes	Trachinidae	<i>Trachinus draco</i>	Tradra	Obl	Sub	S	SH
Perciformes	Trachinidae	<i>Trachinus radiatus</i>	Trarad	Obl	Sub	S	M
Perciformes	Carangidae	<i>Trachurus mediterraneus</i>	Tramed	Fus	Car	H	M
Perciformes	Carangidae	<i>Trachurus picturatus</i>	Trapic	Fus	Car	H	M
Perciformes	Carangidae	<i>Trachurus trachurus</i>	Tratra	Fus	Car	H	SH
Gadiformes	Macrouridae	<i>Trachyrincus scabrus</i>	Trasca	Elo	Sub	R	M
Scorpaeniformes	Triglidae	<i>Trigla lyra</i>	Trilyr	Obl	Sub	S	M
Scorpaeniformes	Triglidae	<i>Trigloporus lastoviza</i>	Trilas	Obl	Sub	S	SH
Gadiformes	Gadidae	<i>Trisopterus capelanus</i>	Tricap	Fus	Sub	R	SH
Perciformes	Uranoscopidae	<i>Uranoscopus scaber</i>	Urasca	Obl	Sub	S	SH
Zeiformes	Zeidae	<i>Zeus faber</i>	Zeufab	Ova	Bal	R	SH

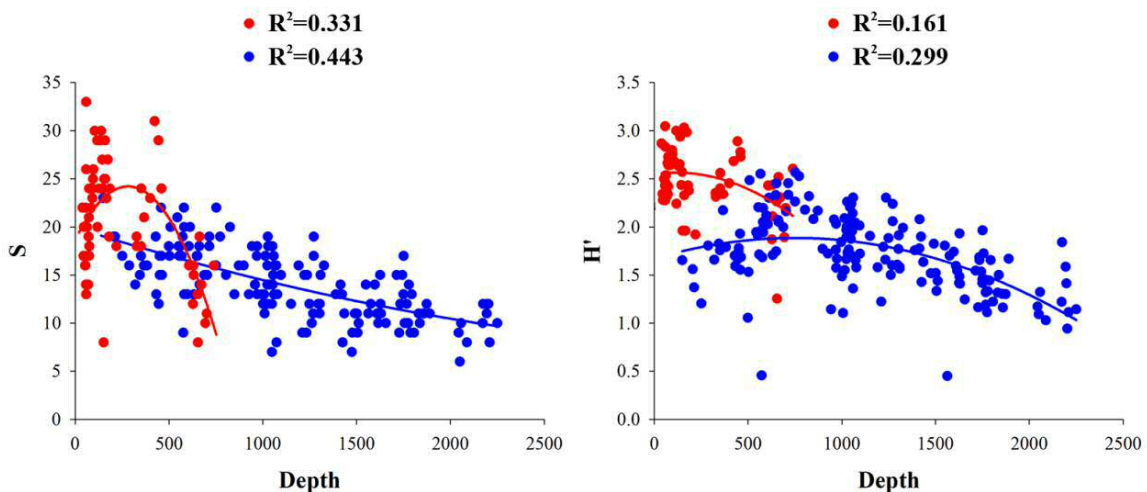
**Figure S1.** Representation of the morphospace (first column) and functional space (second column) for each assemblage along the bathymetric gradient. In the morphospaces, axes were represented by the third (RW3) and fourth (RW4) relative warp, and in the functional space by the third (PCoA3) and fourth (PCoA4) PCoA values. The size of point represents the relative abundance of species (%) within the assemblage, and the colour represents the order to it belongs: Albuliformes (turquoise), Anguilliformes (pink), Argentiniiformes (dark blue), Aulopiformes (green), Beryciformes (black), Gadiformes (light blue), Gasterosteiformes (maroon), Lophiiformes (yellow), Myctophiformes (dark grey), Ophidiiformes (light grey), Perciformes (blue), Pleuronectiformes (brown), Scorpaeniformes (red), Stomiiformes (violet), Zeiformes (sky blue). The acronyms of each species are defined in Supplementary Table S1.



### 13. Appendix 1. Supplementary Material



**Figure S2.** Bathymetric trends of the morphological and functional indices, with their respective second order polynomial regressions, of the different considered fish assemblages. Only the indices that followed a significant correlation with depth are shown (*MD*, *EMI*, *MR*, *Fdiv* and *FR*). In each plot, the two blue lines indicate the 95% confidence intervals; the black line is the obtained tendency. The value of  $R^2$  is provided.



**Figure S3.** Bathymetric trends of the ecological diversity indices ( $S$  and  $H'$ ), with their respective second order polynomial regressions, of the considered GOC73 (red points) and OTSB-14 hauls (blue points) separately. The blue and red lines represent the obtained tendency with depth. The value of  $R^2$  is provided.

**14**

**Appendix 2**

**Publications**

# 15

## **Glossary**



**15.1 General concepts**

<b>DOI</b>	Digital Object Identifier
<b>DSL</b>	Deep-Scattering Layer
<b>DVM</b>	Diel Vertical Migration
<b>GM</b>	Geometric Morphometrics
<b>GOC73</b>	Gear type commonly used in bottom trawling along the Mediterranean Sea
<b>ISI</b>	Institute for Scientific Information
<b>MPA</b>	Marine Protected Area
<b>NTZ</b>	No-Take Zone
<b>OTSB-14</b>	Trawl gear type commonly used for the analysis of deep-sea megafauna along the Mediterranean Sea



## 15.2 Biodiversity concepts

<b>CC</b>	Cluster Coefficients
<b><i>d</i></b>	Margalef's richness index
<b><i>EMI</i></b>	Morpho-geometric diversity index
<b><i>EMI2</i></b>	Morpho-geometric diversity index computed with qualitative data
<b><i>FD</i></b>	Functional Diversity index
<b><i>Fdis</i></b>	Functional Dispersion diversity index
<b><i>Fdiv</i></b>	Functional Divergence diversity index
<b><i>Feve</i></b>	Functional Evenness diversity index
<b><i>FR</i></b>	Functional Redundancy diversity index
<b><i>H'</i></b>	Shannon's diversity index
<b><i>J'</i></b>	Pielou's evenness index
<b><i>MD</i></b>	Morphological Disparity index
<b><i>MD2</i></b>	Morphological Disparity index computed using qualitative data
<b><i>MR</i></b>	Morphological Richness index
<b><i>MR2</i></b>	Morphological Richness index computed using qualitative data
<b><i>RW</i></b>	Relative Warp
<b><i>S</i></b>	Species richness index
<b><i>S'</i></b>	Simpson's dominance index
<b><math>\Delta</math> or <i>DELT</i></b>	Taxonomic diversity index
<b><math>\Delta^*</math> or <i>DSTR</i></b>	Taxonomic distinctness index
<b><math>\Delta^+</math> or <i>AvTD</i></b>	Average taxonomic distinctness index
<b><math>\Delta^+</math> or <i>VarTD</i></b>	Variation in taxonomic distinctness index

### 15.3 Fish assemblages

<b>A assemblage</b>	Fish assemblage from the Upper continental shelf, 40-80 m
<b>B assemblage</b>	Fish assemblage from the Lower continental shelf, 80-250 m
<b>C assemblage</b>	Fish assemblage from the Upper slope, 250-500 m
<b>CA15</b>	Fish assemblage from the Central zone, Artificial Reef, 15-19 m
<b>CR15</b>	Fish assemblage from the Central zone, Rocky-Sandy, 15-19 m
<b>CS10</b>	Fish assemblage from the Central zone, Sandy, <10 m depth
<b>CS15</b>	Fish assemblage from the Central zone, Sandy-Rocky, 15-19 m
<b>CS20</b>	Fish assemblage from the Central zone, Sandy, >20 m depth
<b>CSEA15</b>	Fish assemblage from the Central zone, Rocky-Seagrass, 10-14 m
<b>D assemblage</b>	Fish assemblage from the Upper-middle slope, 500-800 m
<b>E assemblage</b>	Fish assemblage from the Lower-middle slope 800-1400 m
<b>EN</b>	Fish assemblage Epipelagic-Night
<b>F assemblage</b>	Fish assemblage from the Lower slope, 1400-2200 m
<b>LMD</b>	Fish assemblage Lower Mesopelagic-Day
<b>LMN</b>	Fish assemblage Lower Mesopelagic-Night
<b>NG20</b>	Fish assemblage from the North zone, Gravel, 25-32 m
<b>NM20</b>	Fish assemblage from the North zone, Muddy, 30-33 m
<b>NN</b>	Fish assemblage Neritic-Night
<b>NR15</b>	Fish assemblage from the North zone, Rocky, 10-22 m
<b>NS10</b>	Fish assemblage from the North zone, Sandy, <10 m depth
<b>NS15</b>	Fish assemblage from the North zone, Sandy, 10-20 m
<b>NS20</b>	Fish assemblage from the North zone, Sandy-Rocky with higher proportion of rocky bottom, >20 m depth
<b>NSM20</b>	Fish assemblage from the North zone, Sandy-Muddy, 26-50 m
<b>UMD</b>	Fish assemblage Upper Mesopelagic-Day
<b>UMN</b>	Fish assemblage Upper Mesopelagic-Night

**15.4 Statistical and analytical methods**

<b>CCA</b>	Correspondence Canonical Analysis
<b>GPA / GLS</b>	General Procrustes Analyses / General Least-square Superimposition procedure
<b>K-S test</b>	Kolmogorov-Smirnov test
<b>MANOVA</b>	Multivariate ANalysis of VAriance
<b>nMDS</b>	non-metric MultiDimensional Scaling analysis
<b>OLS</b>	Ordinary Least Square method
<b>PCA</b>	Principal Components Analysis
<b>PCoA</b>	Principal Coordinates Analysis
<b>PCoA1</b>	Axis n° 1 of the PCoA
<b>PCoA2</b>	Axis n° 2 of the PCoA
<b>PCoA3</b>	Axis n° 3 of the PCoA
<b>PCoA4</b>	Axis n° 4 of the PCoA
<b>PCoAx</b>	Axis n° x of the PCoA
<b>PLS</b>	Partial Least Square method
<b>QSQR</b>	Sum of range of the middle two quartiles
<b>r</b>	Clark-Evans nearest neighbor
<b>R<sup>2</sup></b>	Coefficient of determination
<b>RDA</b>	Redundancy Analysis
<b>RDA1</b>	Axis n° 1 of the RDA
<b>RDA2</b>	Axis n° 2 of the RDA
<b>RW1</b>	Axis represented by the Relative Warp n° 1
<b>RW2</b>	Axis represented by the Relative Warp n° 2
<b>RW3</b>	Axis represented by the Relative Warp n° 3
<b>RW4</b>	Axis represented by the Relative Warp n° 4
<b>SOV</b>	Sum of Variance
<b>UPGMA</b>	Unweighted Pair Group Method with Arithmetic mean
<b>VMR</b>	Variance-to-Mean Ratio

