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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 toward the periphery, with a proliferation of more extreme body traits, demonstrating lower morphological redundancy. In addition, a trend toward 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 ecosystem such as coexistence and dominance.

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., 2009a; 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 cannot 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.,

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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 interspecific 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 toward 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 orient 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.

2. Materials and methods

2.1. Study area

The study was performed around the coasts of Mallorca and Menorca (Balearic Islands, north western Mediterranean Sea), including a small transect between the NW of Mallorca Island and the Catalan coast, along the Balearic Basin (Fig. 1). Sampling around the Balearic Islands covered both shelf and slope until 800 m, while in the Balearic Basin transect included only slope depths from 800 m to 2200 m. 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 neighboring 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