UNIVERSITAT DE BARCELONA

Morphological structure and biodiversity in fish assemblages

Estructura morfològica i biodiversitat en comunitats de peixos

Marc Farré Foix

ADVERTIMENT. La consulta d’aquesta tesi queda condicionada a l’acceptació de les següents condicions d'ús: La difusió d’aquesta tesi per mitjà del servei TDX (**www.tdx.cat**) i a través del Dipòsit Digital de la UB (**diposit.ub.edu**) ha estat autoritzada pels titulars dels drets de propietat intel·lectual únicament per a usos privats emmarcats en activitats d’investigació i docència. No s’autoritza la seva reproducció amb finalitats de lucre ni la seva difusió i posada a disposició des d’un lloc aliè al servei TDX ni al Dipòsit Digital de la UB. No s’autoritza la presentació del seu contingut en una finestra o marc aliè a TDX o al Dipòsit Digital de la UB (framing). Aquesta reserva de drets afecta tant al resum de presentació de la tesi com als seus continguts. En la utilització o cita de parts de la tesi és obligat indicar el nom de la persona autora.

ADVERTENCIA. La consulta de esta tesis queda condicionada a la aceptación de las siguientes condiciones de uso: La difusión de esta tesis por medio del servicio TDR (**www.tdx.cat**) y a través del Repositorio Digital de la UB (**diposit.ub.edu**) ha sido autorizada por los titulares de los derechos de propiedad intelectual únicamente para usos privados enmarcados en actividades de investigación y docencia. No se autoriza su reproducción con finalidades de lucro ni su difusión y puesta a disposición desde un sitio ajeno al servicio TDR o al Repositorio Digital de la UB. No se autoriza la presentación de su contenido en una ventana o marco ajeno a TDR o al Repositorio Digital de la UB (framing). Esta reserva de derechos afecta tanto al resumen de presentación de la tesis como a sus contenidos. En la utilización o cita de partes de la tesis es obligado indicar el nombre de la persona autora.

WARNING. On having consulted this thesis you’re accepting the following use conditions: Spreading this thesis by the TDX (**www.tdx.cat**) service and by the UB Digital Repository (**diposit.ub.edu**) has been authorized by the titular of the intellectual property rights only for private uses placed in investigation and teaching activities. Reproduction with lucrative aims is not authorized nor its spreading and availability from a site foreign to the TDX service or to the UB Digital Repository. Introducing its content in a window or frame foreign to the TDX service or to the UB Digital Repository is not authorized (framing). Those rights affect to the presentation summary of the thesis as well as to its contents. In the using or citation of parts of the thesis it’s obliged to indicate the name of the author.

Morphological structure and biodiversity in fish assemblages

Estructura morfològica i biodiversitat en comunitats de peixos

Marc Farré Foix

Memòria presentada per Marc Farré Foix per optar al grau de doctor
per a la Universitat de Barcelona

Programa de Doctorat en Biodiversitat

Facultat de Biologia, Universitat de Barcelona

Tesi desenvolupada en el Departament de Recursos Marins Renovables
de l'Institut de Ciències del Mar (ICM-CSIC) de Barcelona

Director de la tesi:
Dr. Víctor Manuel Tuset Andújar
ICM-CSIC

Co-director de la tesi:
Dr. Antoni Lombarte Carrera
ICM-CSIC

Tutora de la tesi:
Dra. Cruz Palacín Cabañas
UB

Doctorand:
Marc Farré Foix
ICM-CSIC

Barcelona, Maig del 2016

The present thesis was conducted within the framework of the projects CONFLICT (Ref. CGL2008-00047) of the Spanish National Research Plans, ESCAL 1 (Ref. PCC30004/99), ESCAL 2 (Ref. 02P30015) of the DG Fisheries of the Government of Catalonia, EMPAFISH (E.U. DG MARE project Ref. 006539), IDEADOS (Ref. CTM2008-04489-C03-03) MAFIA (Ref. CTM2012-39587-C04-03), MEDER, financed by the Spanish Institute of Oceanography (IEO), and ANTROMARE (Ref. CTM2009-12214-C02-01-MAR), thanks to a pre-doctoral grant from the Government of Andorra (ATC010-AND, academic years 2012-2015).

AGRAÏMENTS/AGRADECIMIENTOS/AKNOWLEDGEMENTS

Exceptuant el darrer any (durant el qual sabia, ja sí que sí, que aquest moment arribaria tard o d'hora), mai m'hauria imaginat que em trobaria en aquesta situació. Qui m'anava a dir a mi al setembre del 2011, quan tot just entrava al Institut de Ciències del Mar de Barcelona per realitzar les pràctiques del màster de cap a la saleta del cafè, que acabaria immers en aquesta etapa que ara, casi cinc anys més tard, conclou. La realització d'aquesta tesi ha estat una etapa apassionant, intensa, dura, divertida i enriquidora a parts iguals. I també ha estat força llarga, en la qual han passat moltes coses i en la qual hi han estat directament involucrades moltes persones. Les coses son impossibles de resumir en aquest apartat. No obstant, sí que m'agradaria mencionar a les persones que han fet possible que aquesta tesi sigui un realitat. Probablement me'n oblidaré més d'una, intentaré que no sigui així. Aquí el meu breu i humil homenatge a totes elles.

En primer lloc, voldria agrair als meus directors, al Víctor i al Toni, per la oportunitat que em vau oferir, per la confiança que m'heu transmès des del primer dia i durant tot aquest temps, per la paciència que heu tingut, per tot el coneixement que m'heu ensenyat i sobretot per la llibertat que m'heu donat. A Víctor, gracias por tu espíritu de continua superación e innovación, por tu exigencia, por tus continuas ideas y por enseñarme a trabajar duro para conseguir los objetivos. Gracias por estar siempre disponible, por las continuas horas extra de soporte entre tus obligaciones, en forma de interminables sesiones por Skype, resolviendo dudas de todo tipo. I al Toni, gràcies per tot el coneixement ictiològic que m'has transmès, per tenir la porta del teu despatx sempre oberta per a qualsevol qüestió, pels múltiples consells i per guiar-me en tots els meus moviments dins el complex món de la investigació, així com també per les llargues xerrades informals mes enllà de la tesi. Moltes gràcies als dos, espero que el vostre balanç també hagi estat positiu. També m'agradaria agrair de manera especial a la Montserrat Solé, el meu primer contacte dins l'ICM, i que va actuar d'enllaç amb els que posteriorment serien els meus directors i contribuir a que aquesta historia comencés.

També m'agradaria donar les gràcies a tots els investigadors amb els que he tingut la sort de col·laborar i als que han estat sempre disposats a ajudar-me. Al Francesc Maynou, per tota la ajuda i els coneixements proporcionats quan el complex món de la estadística em feia anar de bòlit; a la Laura Recasens, pels seus consells i ajuda a l'hora de encarar i preparar els treballs; al Joan Cartes, per la seva paciència, disponibilitat i ajuda a l'hora d'entendre millor un món fins fa ben poc desconegut per mi com és el deep-sea; a la Pilar Olivar, per ajudar-me a resoldre tots els dubtes sobre mictòfids i el domini mesopelàgic en general, i al l'Enric Massutí, per l'ajuda i cessió de dades. També moltes gràcies al José Antonio, per la seva paciència i disponibilitat a l'hora de ajudar-me a resoldre problemes informàtics varis i a fer mapes, juntament amb l'Andrés Ospina. I a la resta de persones del Departament que han contribuït a que durant la meva estada al departament m'hagi sentit com a casa: a la Isabel Palomera, per haver-me donat la oportunitat d'embarcar-me en una campanya oceanogràfica i per la seva ajuda en qualsevol àmbit sempre amb un somriure; al Joan Baptista Company, per la valuosa informació quan vaig marxar d'estada a Santa Barbara; al Pere Abelló, al Francesc Sardà, a la Conchita Borruel…i a tothom qui em pugui estar oblidant, gràcies!

Òbviament, a tots els companys del Departament de Recursos Marins Renovables del ICM que he tingut durant tota la meva estada (becaris, tècnics, personal laboral, estudiants, etc.), per tots els moments viscuts, tant a nivell professional (intercanvi de consells, coneixements, informació, programes, lab meetings, etc.) com d'oci (cerveses i nits apoteòsiques, dinars indoor and outdoor, campanyes, calçotades, sortides o partits de volley platja amb els Chanclas, entre altres): Ainhoa, Alba, Alejandro, Alfredo, Amalia, Anabel, Anna M., Ariadna, Balbina, Carol, Catarina, Chiara, Claudio, Cristina, Dafni, Daniela, Federico, Fernando, Giulia, Guiomar, John, José Antonio, Laia, Marta, Nieves, Noelia, Paula, Raquel, Sonia, Susana, Tabita, Ulla, Valeria, Valerio, Vanesa, Xavi…part d'aquesta tesis també es vostra! Dins aquesta gran família, m'agradaria fer especial menció a la Anabel i la Amalia, les meves germanes grans en el Departament, pel seva calidesa des del primer dia i per la seva ajuda incondicional en múltiples àmbits...no se què hauria fet sense vosaltres! Y también a las componentes del despacho B-59, mi hogar durante gran parte de la tesis y el mejor despacho del departamento: Ari, Raquel y Ulla, por vuestro agradable recibimiento en mis épocas de novato, por haber cuidado al benjamín del grupo, así como por toda la ayuda, consejo y conocimiento que me habéis proporcionado, que es mucho. També als nous components del despatx durant la meva darrera etapa, Florence, Morane i Xavi, per l'aire nou i energia renovada que heu aportat quan aquest anava quedant buit. Y también me gustaría acordarme de mis compañeros, mayoritariamente del Departamento de Biología Marina, en mi primer despacho (el P-39) en mis inicios del doctorado: Caterina, Fran, Johannes, Maria, Marta T., Miguel, Teresa…gracias por el agradable ambiente de trabajo que creabais.

No puedo olvidarme de los distintos colaboradores y estudiantes que hemos tenido en nuestro grupo durante todos estos años: Anita, Carolina Siliprandi, Diana Catarino, José Luis Otero i Xènia. Muchas Gracias, también aprendí mucho a vuestro lado.

I would to thank you to my supervisor during my stay in the MSI in Santa Barbara, Dr. Milton Love, and all the remaining members of the Love Lab, Mary Nishimoto, Scott Clark and Merritt McCrea. Many thanks you for your kind assistance in all the aspects, for being always willing to listen and advice and for all the knowledge received about rockfishes. I hope to see you sometime in Andorra! Also to my team mates of the FC Real United, to allow me playing soccer during my stay and for the after-match beers; to the general manager of the Studio Plaza Apartments, Felipe Garcia, and their sons, Oscar and Diego; to my “amigos” at home, Daniel and Paul; to Unai, for his help during the first weeks, and to all the international people that I met during the stay.

També voldria agrair a la meva tutora de la UB, la Creu Palacín, per la seva disponibilitat i per haver acceptat tutelar aquesta tesi, i a la coordinadora del programa de doctorat de Biodiversitat, la Maria José López-Fuster, per la ajuda proporcionada.

Ja fora de l’àmbit de la feina, en primer lloc m’agradaria donar les gràcies als varis companys de pis que he tingut a Barcelona durant tota aquesta època, la gent amb que probablement he compartit més hores fora del ICM i que sempre han creat un clima de convivència i benestar ideal. En primer lloc, a l’Efrem i al Pepo, per accedir a acceptar-me en el seu pis de Xifré 64 (de manera un pèl clandestina, tot s’ha de dir…), per tots els riures que vam fer i els grans moments i records que vam viure, incloent parets pintades de manera “peculiar”, viatges a IKEA a comprar quadres i canvis regulars en la distribució del material culinari. I en segon lloc, a l’Anna i el Pau, per acollir-me sense dubtar i amb gran rapidesa en la fantàstica llar de Carme 106, pel vostre càlid acolliment desde bon principi en un pis creat anteriorment, per la vostra senzillesa i fàcil convivència, i per la vostra comprensió durant períodes d’absència o d’embogiment extrem de final de tesi, sempre envoltats de vermuts domingueros molons, constants problemes tècnics, orquídies hormonades, bèsties sarnoses, cuquis, shawarmas i gintònics nocturns, pastissets halal, humor, sarcasme i bon rotllo….sou tots collonuts!

A totes les amistats universitàries que hem sobreviscut a l’època post-llicenciatura i que durant aquests anys, afortunadament, encara ens hem anat veient amb regularitat a Barcelona per passar moments de qualitat i de desconnexió. Al grup de bionenes: Alba, Anna, Cris, Elisenda, Maria, Marina, Rut, Sandra Ba, Sandreta i Xell…per ser sempre tant actives (entre planazos i grups de watsap, ja he perdut el compte), autèntiques i divines, i per tenir-me tant mimat, que en el fons sabeu que m'agrada. També especial menció a la Georgina, per la seva hiperactivitat social, per tenir-me sempre informat i per comptar amb mi en molts dels seus plans; i al Guifré, pels farts de riure, plans molons, i debats, maquinacions i ennagenacions mentals que hem arribat a desenvolupar durant els necessaris parèntesis de feina en la nostra coincidència al CMIMA. I també al grup de sirènids, Anna, Ares, Guifré, i Toni, sovint preparats per capbussar-se i descobrir els fons marins, i sempre disposats a pegar-se unes bones juergues, marcar-se uns volleys i fer viatges d'immersió extraordinaris.

A la colla d'amics de tota la vida d'Andorra, que sempre han estat els meus confidents i que han actuat de com a vàlvules d'escapament i desconnexió durant els caps de setmana de tornada a casa, i que, tot i no saber ben bé el que he estat fent (sociologia de peixos, deien alguns…) i/o estar desperdigats pel món, sempre han estat i els he sentit al meu costat. Moltes gràcies Àlex, Ali, Ari, Efrem, Euli, Guille, Joanet, Manel, Maria Crespo, Maria Faus, Obon, Pep, Pepo, Santi, Sergi i Xell (i respectius/ves)…sou magnífics!

I finalment, als meus pares, Jordi i Dolors, per haver-me deixat sempre la opció i llibertat per triar, pels tots valors que m'han inculcat, pel seu amor i suport incondicional, pels seus constants ànims i savis consells…i que tot junt ha fet possible que aquest projecte s'hagi fet realitat. Al meu germà, Jordi, també pel seu suport, per la bona relació que hem tingut sempre, pel seu peculiar però talentós sentit de l'humor i per ser un referent en molts aspectes. A vosaltres si que us ho dec tot, i per aquest motiu aquesta tesi també és vostra. I també a la resta de la família, àvies, tiets, tieta i cosina.

I a tu, Marta, per ser la companya de viatge perfecta. Gràcies per la teva paciència, comprensió, alegria i amor, per donar-me estabilitat durant els moments difícils, per totes les experiències inoblidables que hem viscut i per les que ens queden per viure.

A tots i totes que l'heu fet possible…Moltes gràcies! ¡Muchas gracias! Thank you!

"First they ignore you, then they laugh at you, then they fight you, then you win"
Mahatma Gandhi

Barcelona, 03 de maig del 2016

TABLE OF CONTENTS

SECTION 2: APPLICATIVE PART

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 phylogenic purposes (Bock, 1990). The first references manifesting the relation between the morphology of species with their surrounding environment appeared at the beginning of the 20th 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 20th 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).

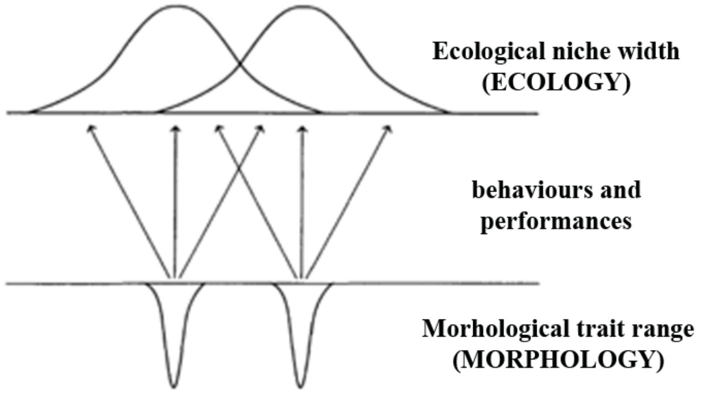


Figure 1. Graphic explaining the relationship between ecology and morphology. The bell-shape curves represent the width of an arbitrary ecological niche (above), and the phenotypic range of an arbitrary morphological trait (below). The arrows represent the acting mechanisms (behaviours) and their efficiency (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 20th 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.

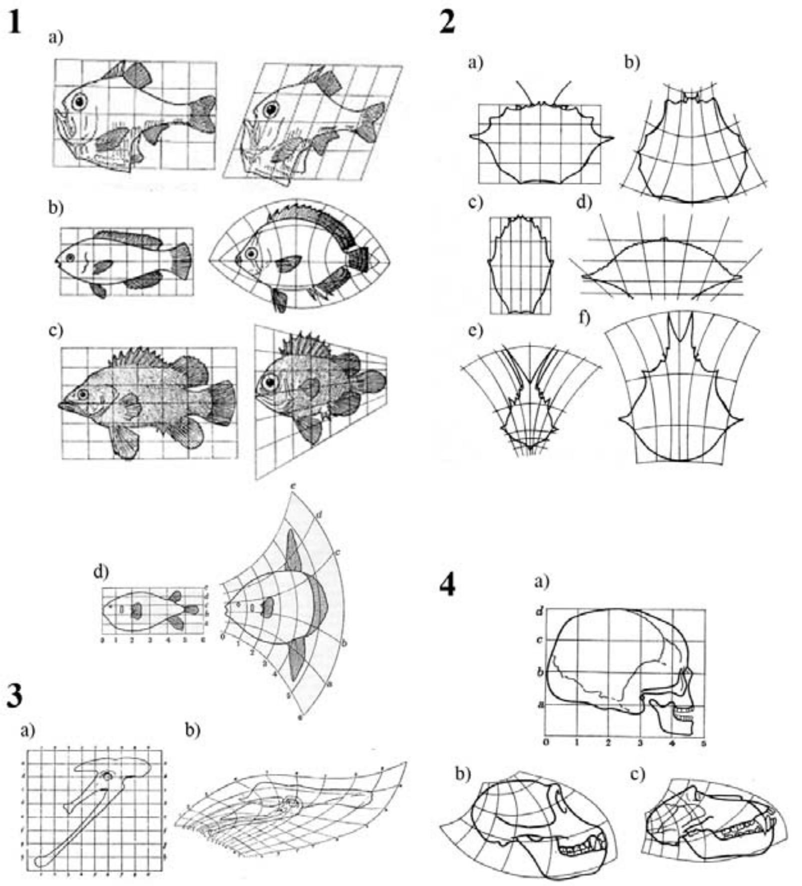


Figure 2. Examples of differences in morphology and shape in several groups of organisms proposed by Thompson (1917). Method of Cartesian transformations in (1) fishes (body of a) *Argyropelecus olfersi* to *Sternoptyx diaphana,* b) *Scarus* sp. to *Pomacanthus* sp., c) *Polyprion* sp. to *Pseudopriacanthus* sp., and d) *Diodon* sp. to *Orthagoriscus* 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 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 (Lleonart 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.

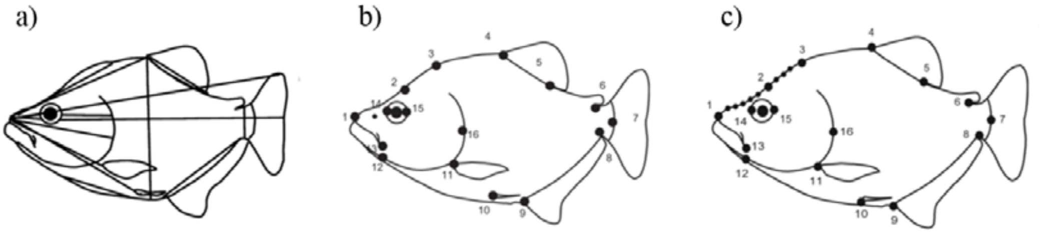


Figure 3. Evolution of methods of morphometric measurements: (a) traditional linear measurements of the external morphology of a teleost, (b) landmark-based GM measurements (homologous coordinate points in anatomical structures of interest, defining the geometric shape of the object) of the external 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 Zeldtich 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 de 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; Zeldtich et al., 2003). Finally, the results of all these statistical treatments can be plotted in space (the morphospace), providing a graphical 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).

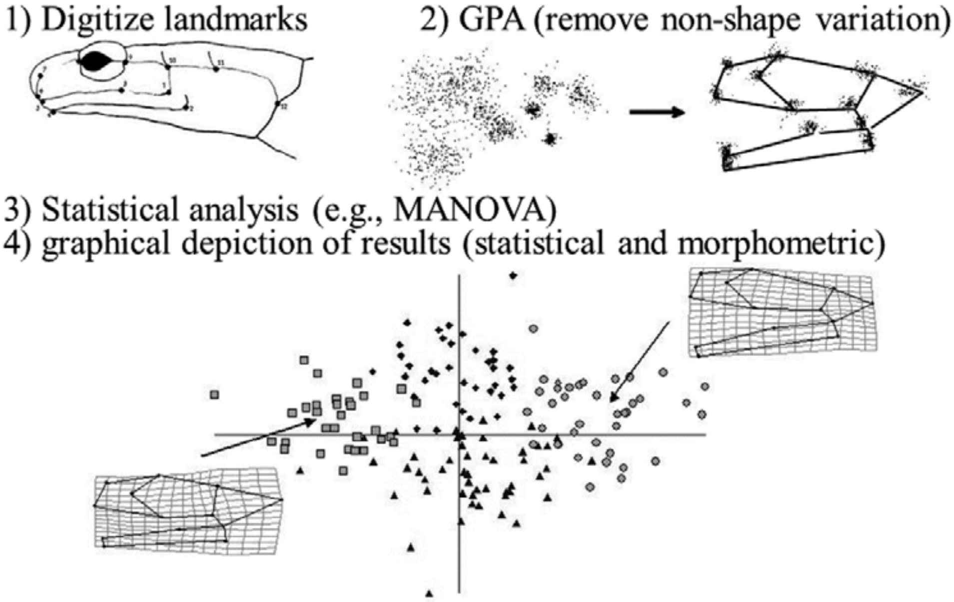


Figure 4. Explanatory diagram of the different steps during a landmark-based geometric morphometric procedure. 1) Selection and digitization of the landmarks on the anatomical points of interest (in this case, head of *Plethodon salamander*), 2) Representation before and after the application of the 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 21st 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, 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; Klingenber 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; Zeldtich et al., 2000; 2004; Bastir and Rosas, 2004; Crespi-Abril et al., 2009).

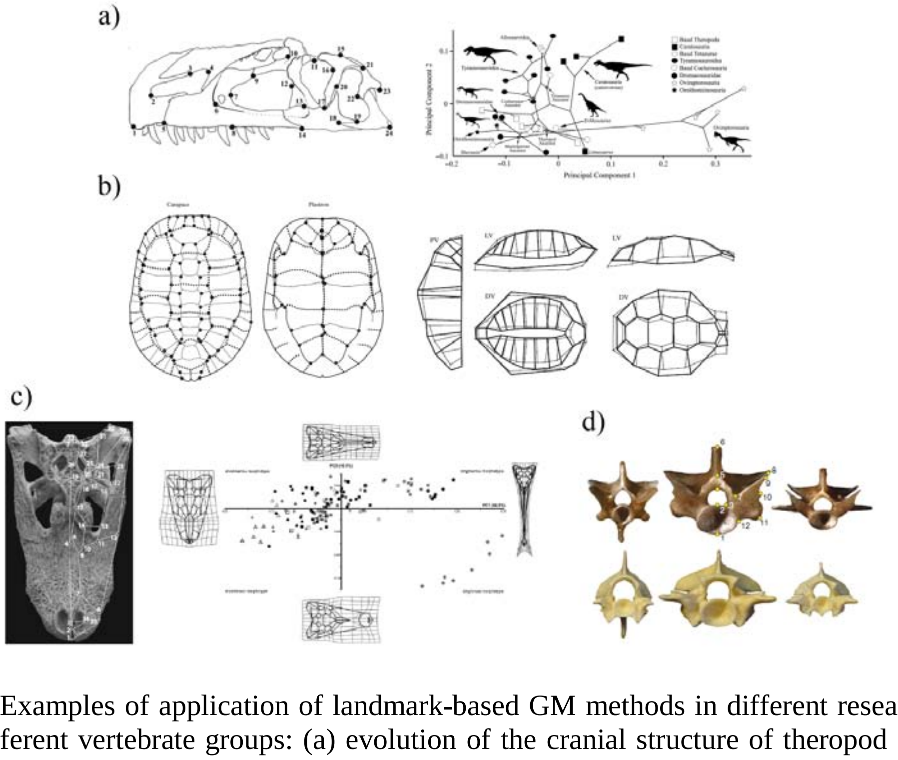


Figure 5. Examples of application of landmark-based GM methods in different research fields and on different vertebrate groups: (a) evolution of the cranial structure of theropod dinosaurs (from Brusatte et al., 2012); (b) effects of environment in the evolution of turtle shells (from Claude et al., 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).

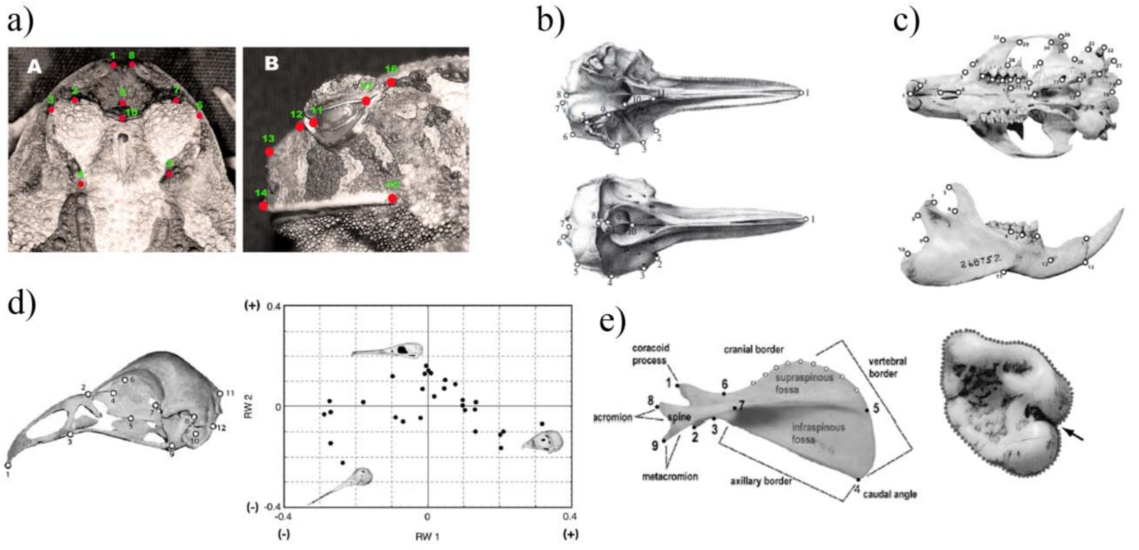


Figure 6. Examples of application of landmark-based GM methods in different research fields and on different vertebrate groups: (a) variations in head shape of neotropical toad populations (*Proceratophrys cristiceps*) (from Vieira et al., 2008); (b) cranial shape differentiation between different cetacean 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).

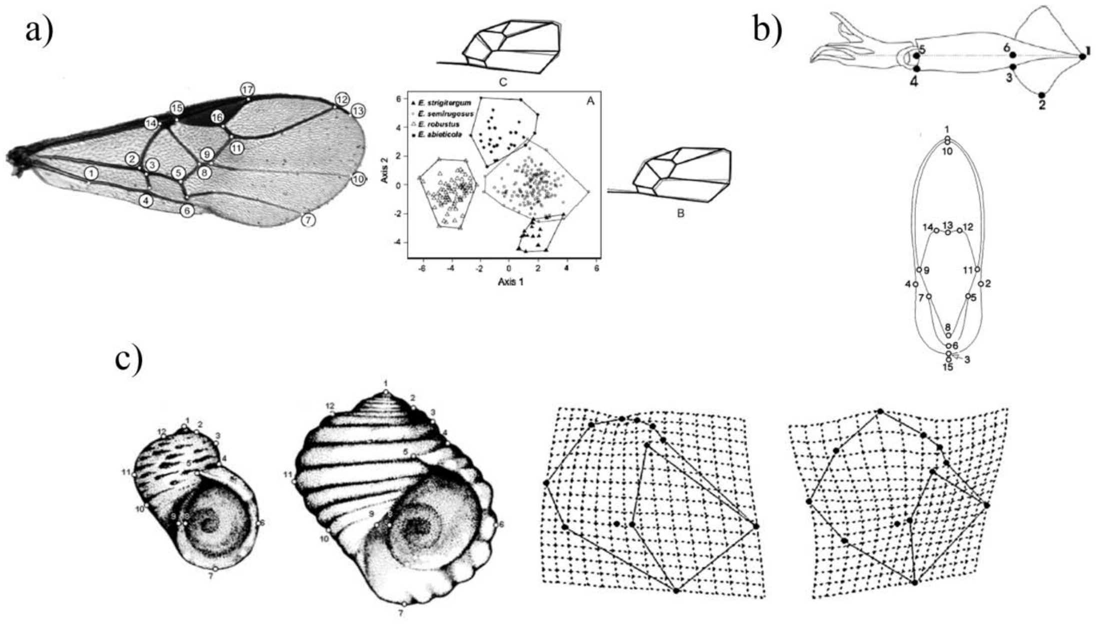


Figure 7. Examples of application of landmark-based GM methods in different research fields and on different invertebrate groups: (a) morphological differentiation of wing venation in species of hymenopters (*Eubazus* sp.) (from Villemant et al., 2007); (b) Onthogenetic variation on body shape of *Illex 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 polinitzation and flowering (Gómez et al., 2008).

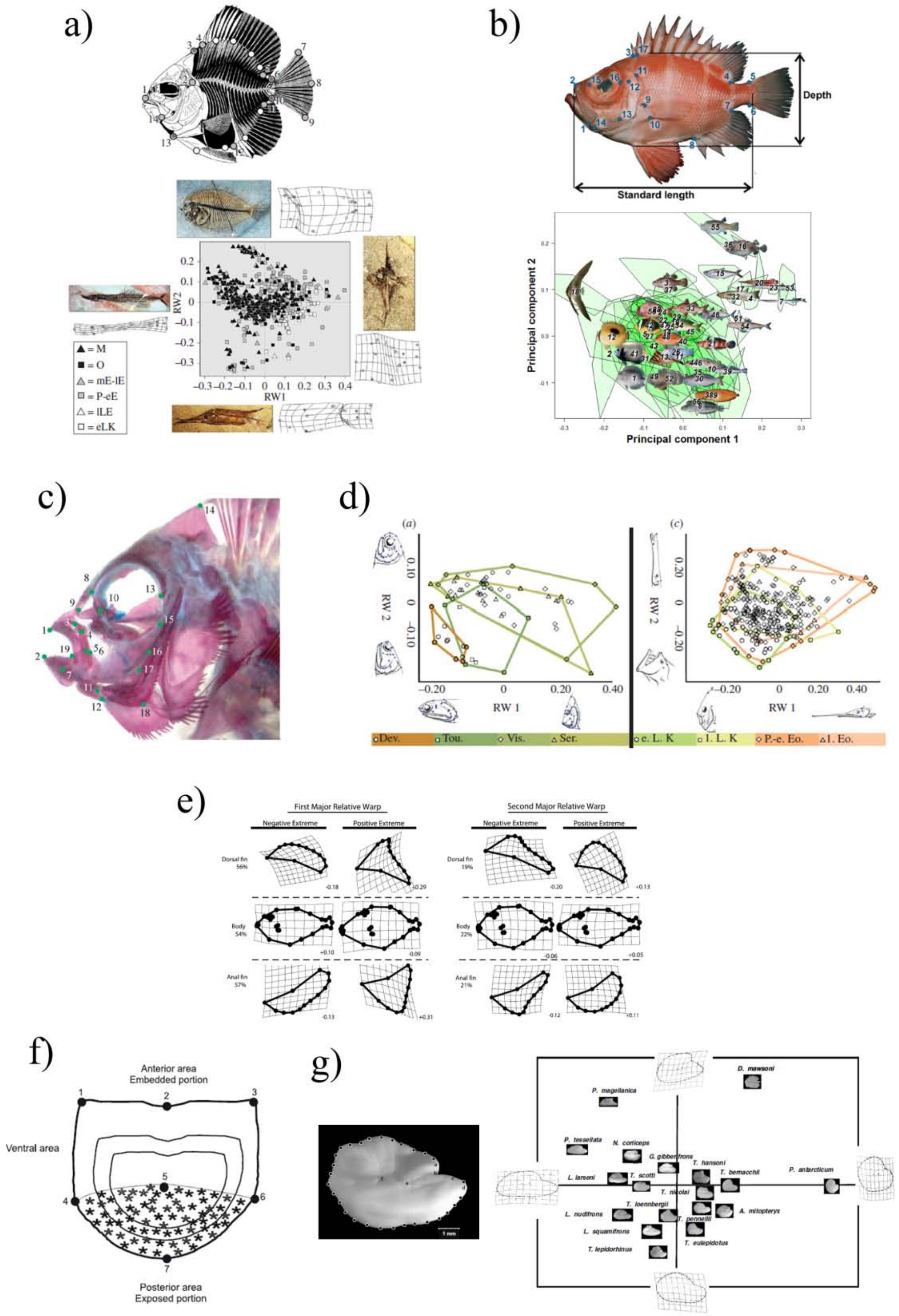


Figure 8. Examples of application of landmark-based GM methods on fishes in different research fields: landmark and semilandmark scheme and morphospace representation from (a) spinny-finned teleosts after the end-Createceous extinction (from Friedman, 2010) and from (b) 2939 Indo-Pacific reef fishes (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) interespecific 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; Lyashevska 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 began to be questioned as appropriate biodiversity descriptors because they present some limitations: i) they are simple α-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 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. 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.

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., Massutí, 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 no used, implicitly or explicitly, these articles for the elaboration of other doctoral thesis.

Barcelona, May 2016.

Dr. Víctor Manuel Tuset Andújar	Dr. Antoni Lombarte Carrera
PhD supervisor	PhD co-supervisor
Institut de Ciències del Mar (ICM-CSIC)	Institut de Ciències del Mar (ICM-CSIC)

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

Marc Farré [1], Víctor M. Tuset [1], Francesc Maynou [1], Laura Recasens [1],
Antoni Lombarte [1]

[1] Institut de Ciències del Mar, CSIC, Passeig Marítim de la Barceloneta 37-49, 08003,
Barcelona, Catalonia, Spain.

Accepted in *Scientia Marina* (February 2016)

DOI: http://dx.doi.org/10.3989/scimar.04280.15A

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 especies. Les tres opcions van proporcionar resultats diferents en relació a la distribució de les especies 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 especies, com ara aletes modificades o òrgans sensorials, contribueix a una diferenciació més clara de les especies 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 especies dins el morfoespai. Els resultats van demostrar que el mètodes d'agregació de punts, incloent anàlisis basats en quadrants o distancies, 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 especies 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 especies 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; Klingenber, 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 (40.5º - 42.5ºN, 0.30º - 3.25ºE) was used for this study. In particular, an artificial reef-sandy assemblage of the central coast (41º10.52'N; 1º35.16'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	*Conger conger*	Ccon
Gadiformes	Merlucciidae	*Merluccius merluccius*	Mmer
Gadiformes	Phycidae	*Phycis phycis*	Pphy
Lophiiformes	Lophiidae	*Lophius piscatorius*	Lpis
Mugiliformes	Mugilidae	*Chelon labrosus*	Clab
Mugiliformes	Mugilidae	*Liza aurata*	Laur
Mugiliformes	Mugilidae	*Mugil cephalus*	Mcep
Mugiliformes	Mugilidae	*Liza ramada*	Lram
Perciformes	Moronidae	*Dicentrarchus labrax*	Dlab
Perciformes	Serranidae	*Serranus cabrilla*	Scab
Perciformes	Carangidae	*Seriola dumerili*	Sdum
Perciformes	Haemulidae	*Pomadasys incisus*	Pinc
Perciformes	Sparidae	*Boops boops*	Bboo
Perciformes	Sparidae	*Dentex dentex*	Dden
Perciformes	Sparidae	*Diplodus annularis*	Dann
Perciformes	Sparidae	*Diplodus cervinus*	Dcer
Perciformes	Sparidae	*Diplodus sargus*	Dsar
Perciformes	Sparidae	*Diplodus vulgaris*	Dvul
Perciformes	Sparidae	*Lithognathus mormyrus*	Lmor
Perciformes	Sparidae	*Pagellus acarne*	Paca
Perciformes	Sparidae	*Pagellus bogaraveo*	Pbog
Perciformes	Sparidae	*Pagellus erythrinus*	Pery
Perciformes	Sparidae	*Pagrus pagrus*	Ppag
Perciformes	Sparidae	*Sparus aurata*	Saur
Perciformes	Sparidae	*Spondyliosoma cantharus*	Scan
Perciformes	Sciaenidae	*Sciaena umbra*	Sumb
Perciformes	Sciaenidae	*Umbrina canariensis*	Ucan
Perciformes	Sciaenidae	*Umbrina cirrosa*	Ucir
Perciformes	Mullidae	*Mullus barbatus*	Mbar
Perciformes	Mullidae	*Mullus surmuletus*	Msur
Perciformes	Pomacentridae	*Chromis chromis*	Cchr
Perciformes	Labridae	*Coris julis*	Cjul
Perciformes	Labridae	*Labrus merula*	Lmer
Perciformes	Uranoscopidae	*Uranoscopus scaber*	Usca
Pleuronectiformes	Scophthalmidae	*Scophthalmus rhombus*	Srho
Pleuronectiformes	Scophthalmidae	*Psetta maxima*	Pmax
Pleuronectiformes	Bothidae	*Arnoglossus laterna*	Alat
Pleuronectiformes	Bothidae	*Bothus podas*	Bpod
Pleuronectiformes	Citharidae	*Citharus linguatula*	Clin
Pleuronectiformes	Soleidae	*Microchirus variegatus*	Mvar
Pleuronectiformes	Soleidae	*Solea lascaris*	Slas

Pleuronectiformes	Soleidae	*Solea senegalensis*	Ssen
Pleuronectiformes	Soleidae	*Solea solea*	Ssol
Pleuronectiformes	Soleidae	*Synaptura lusitanica*	Slus
Scorpaeniformes	Scorpaenidae	*Scorpaena notata*	Snot
Scorpaeniformes	Scorpaenidae	*Scorpaena porcus*	Spor
Scorpaeniformes	Scorpaenidae	*Scorpaena scrofa*	Sscr
Scorpaeniformes	Triglidae	*Trigla lucerna*	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 wether 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.

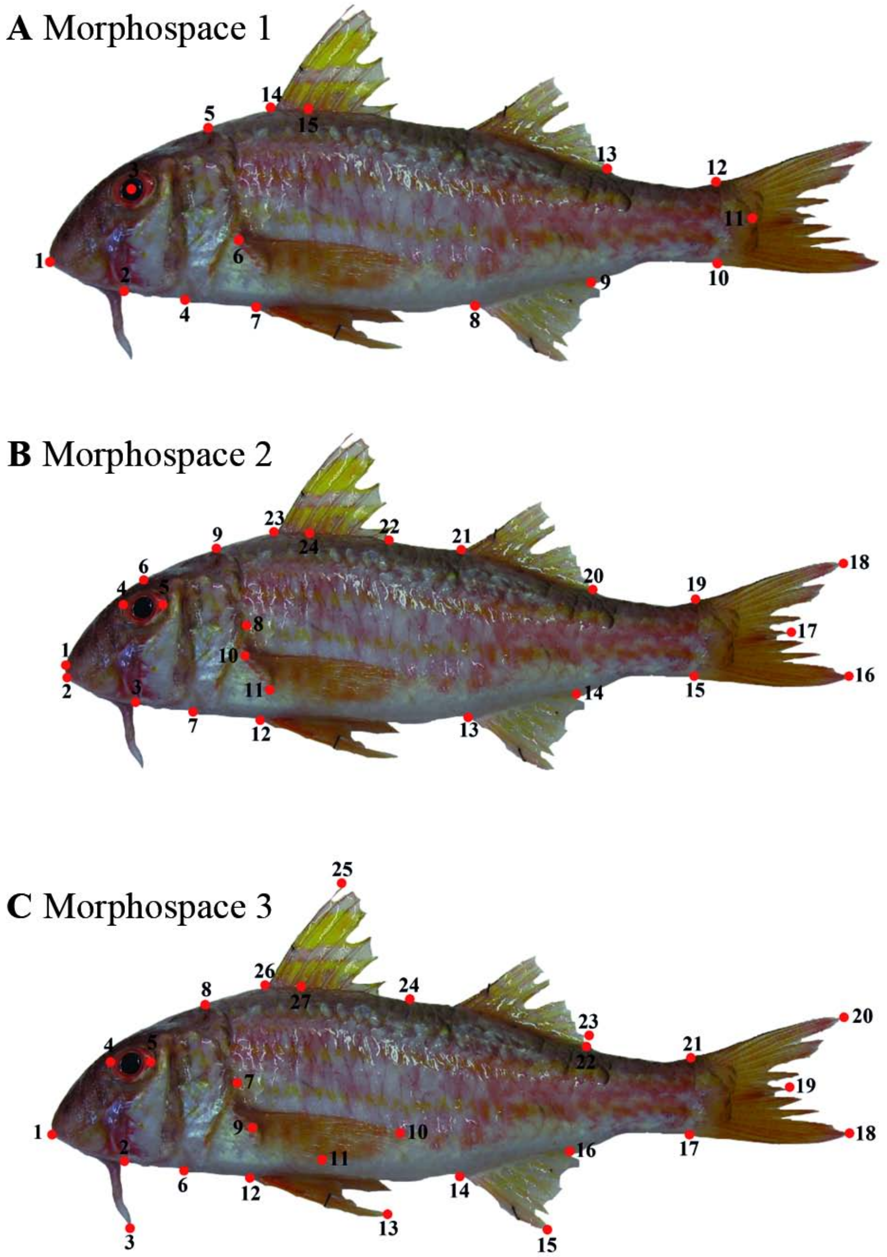


Figure 1. Location of the selected landmarks and semilandmarks in the left side of standardised images for the three different used methods (morphospace 1, 2 and 3). The description of the meaning of landmarks for each method is detailed in Table 2. In method 1 (A, morphospace 1), landmark 15 is a semilandmark; 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. Specie 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	**Anterior tip of the snout bone**	Anterior tip of the mouth
2	Posterior tip of the mouth	Anterior tip of the mouth	Posterior tip of the mouth
3	**Central point in the midline through the eye**	Posterior tip of the mouth	**Distal tip of the barbel, placed at 80º of the body margin (or projection in the lower jaw inferior margin of the position of the hyomandibular insertion, when no barbels)**
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	**Dorsal margin of the head exactly above the centre of the eye**	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	**Central point in the baseline of the pectoral fin**
10	Ventral insertion of the caudal fin	Dorsal insertion of the pectoral fin	**Posterior tip of the pectoral fin when the fin is in position of maximum extension**
11	**Posterior margin of the caudal peduncle**	**Ventral insertion of the pectoral fin**	**Ventral margin of the pectoral fin when the fin is in position of maximum extension**
12	Dorsal insertion of the caudal fin	Insertion of the pelvic fin	Insertion of the pelvic fin

13	Posterior insertion of the dorsal fin (second dorsal fin if exists)	Anterior insertion of the anal fin	**Distal tip of the pelvic fin when the fin is in position of maximum extension**
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	**Distal tip from the anterior insertion of the anal fin when the fin is in position of maximum extension**
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	-	**Anterior insertion of the second dorsal fin (if exists)**	Dorsal insertion of the caudal fin
22	-	**Posterior insertion of the first dorsal fin (if second dorsal fin exists)**	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)	**Posterior tip of the dorsal fin (second dorsal fin if exists) when the fin is in position of maximum extension**

24	-	Point of maximum body height in the body margin	**Transition point between spines and soft rays in the dorsal fin (if only one dorsal fin exists) or central point in the gap between the two dorsal fins on the dorsal margin of the body (if second dorsal fin exists)**
25	-	-	**Distal tip of the first spine of the dorsal fin (first dorsal fin if second fin exists) when the fin is in position of maximum extension**
26	-	-	Anterior insertion of the dorsal fin (first dorsal fin if second fin exists)
27	-	-	Point of maximum body height in the body margin

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*≈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:

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

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:

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

where d_{ij} is the Euclidean distance between the i^{th} and j^{th} points in a data set of n points, and λ 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.

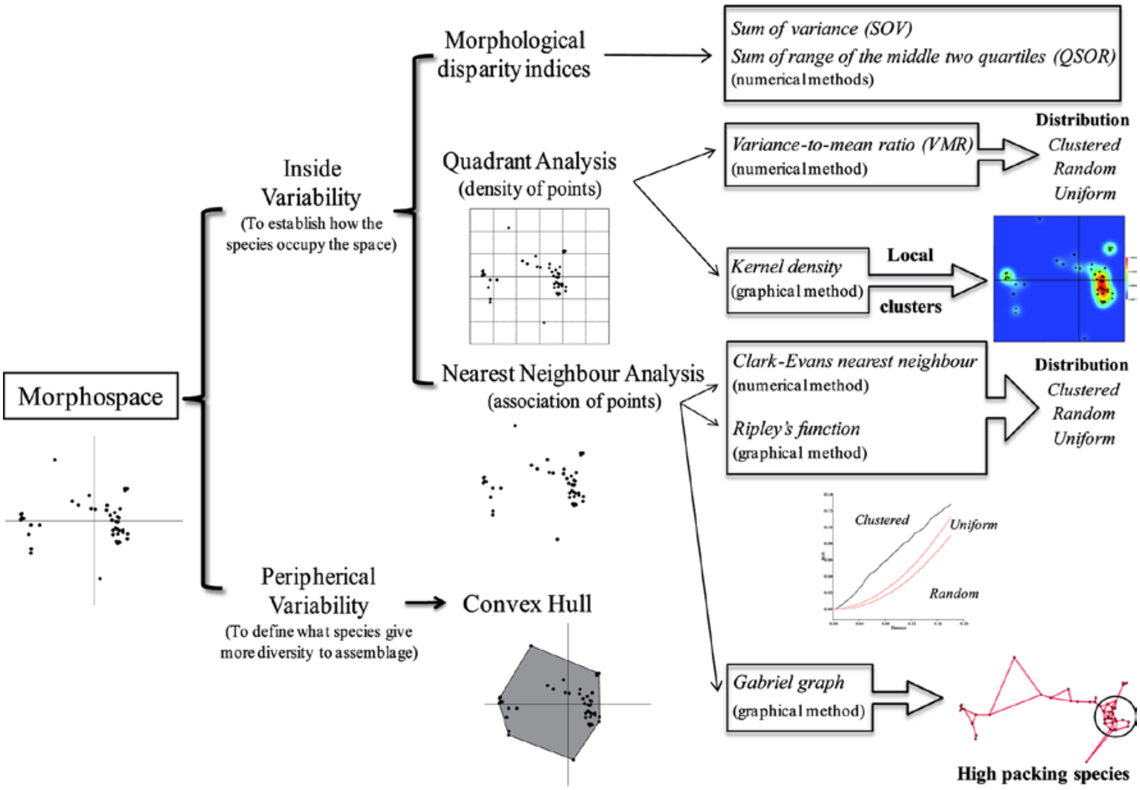


Figure 2. Explanatory scheme for the procedure of analysis of morphospaces, including all the used analyses and methods.

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).

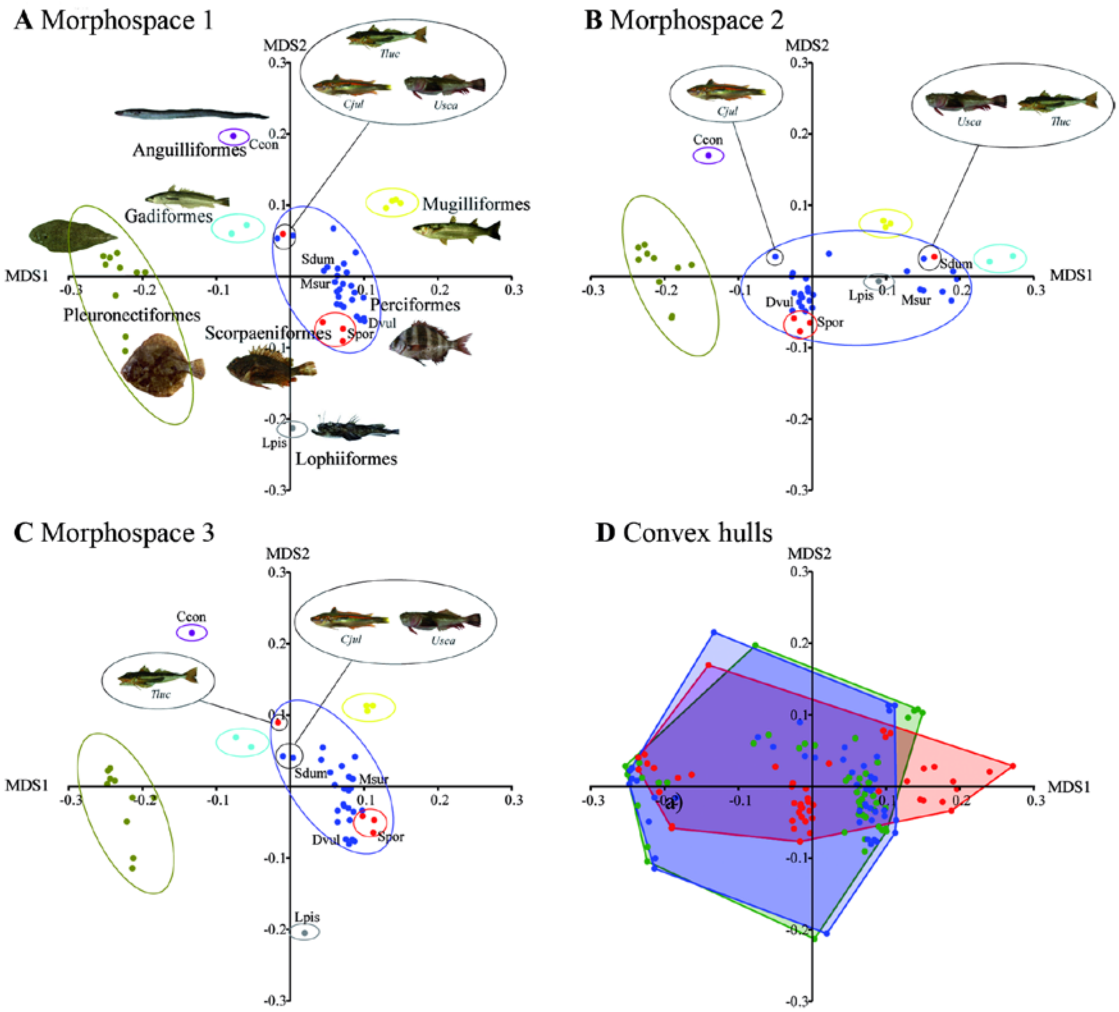


Figure 3. Representation of the morphospace for the A) first, B) second and C) third method showing the main differentiated groups of species. Ccon = *Conger conger*; Cjul = *Coris julis*; Dvul = *Diplodus vulgaris*; Lpis = *Lophius piscatorius*; Msur = *Mullus surmuletus*; Sdum = *Seriola dumerili*; Spor = *Scorpaena porcus*; Tluc = *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.

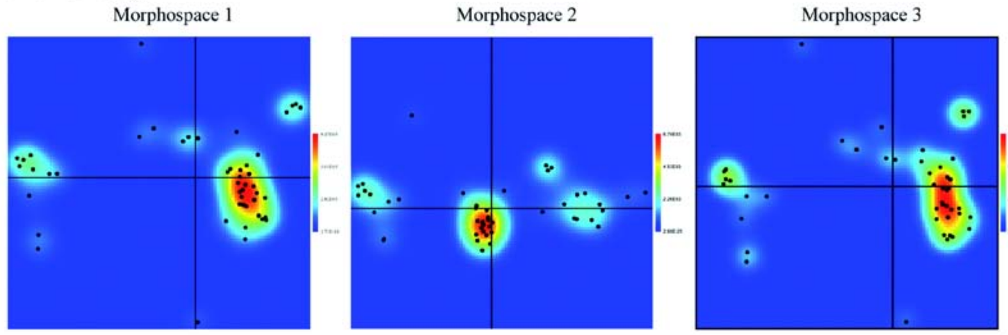
The second axis mainly distinguished between elongated (positive values) or rounded (negative values) body shapes in all of the morphospaces (Figs. 3A and 3C), although in morphospace 2 this distinction was less evident because species were more compacted along the axis (Fig. 3B). However, the axis also 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

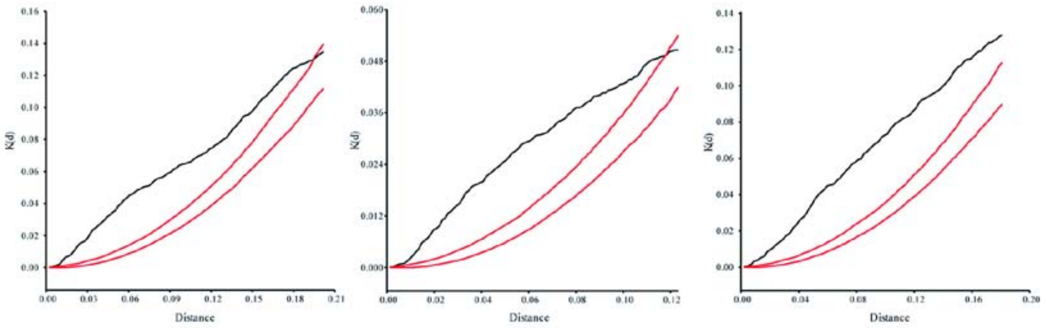
The *SOV* showed no differences among morphospaces, reaching similar values of variance (0.021) in the three cases. By contrast, the *QSOR* revealed greater disparity, attaining the highest value (0.028) in morphospace 2, which demonstrated a more dispersed distribution of points compared with the remaining 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

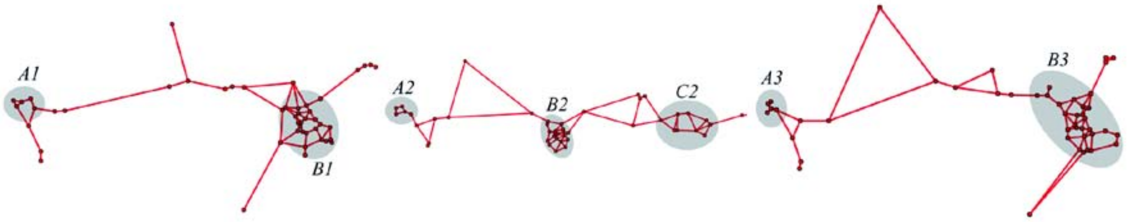


Figure 4. Representation of A) the Kernel density, B) the graphic of the Ripley's function and C) the Gabriel graphs for the three analysed methods. In the kernel graphics, colour legend indicates the degree of density of species (maximum density in red, minimum density in dark blue). In the graphic of the Ripley's function, the two red curves represent the 95% confidence envelops 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 eveni 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.

Acknowledgements

Data of this study were financed by project “ESCAL 1” (Ref. PCC30004/99), “ESCAL 2” (Ref. 02P30015) of the DG Fisheries of the Government of Catalonia, and “CONFLICT” (Ref. CGL2008-00047) of the Spanish National Research. Marc Farré Foix acknowledges a pre-doctoral grant and a third cycle tuition fee grant from the Government of Andorra, ATC-010-AND and AMTC010-AND/2013, academic years: 2013-2014 and 2014-2015.

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

Marc Farré [1], Víctor M. Tuset [1], Francesc Maynou [1], Laura Recasens [1],
Antoni Lombarte [1]

[1] Institut de Ciències del Mar (ICM-CSIC), Passeig Marítim de la Barceloneta 37-49,
08003, Barcelona, Catalonia, Spain

Published in *Ecological Indicators 29: 159-166* (2013)

DOI: http://dx.doi.org/10.1016/j.ecolind.2012.12.005

See the original publication in the Appendix 2 section

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 (Lyashevska and Farnswoth, 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 ‘bathypteroiform’ 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 (Echeinidae) 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), haddocks 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).

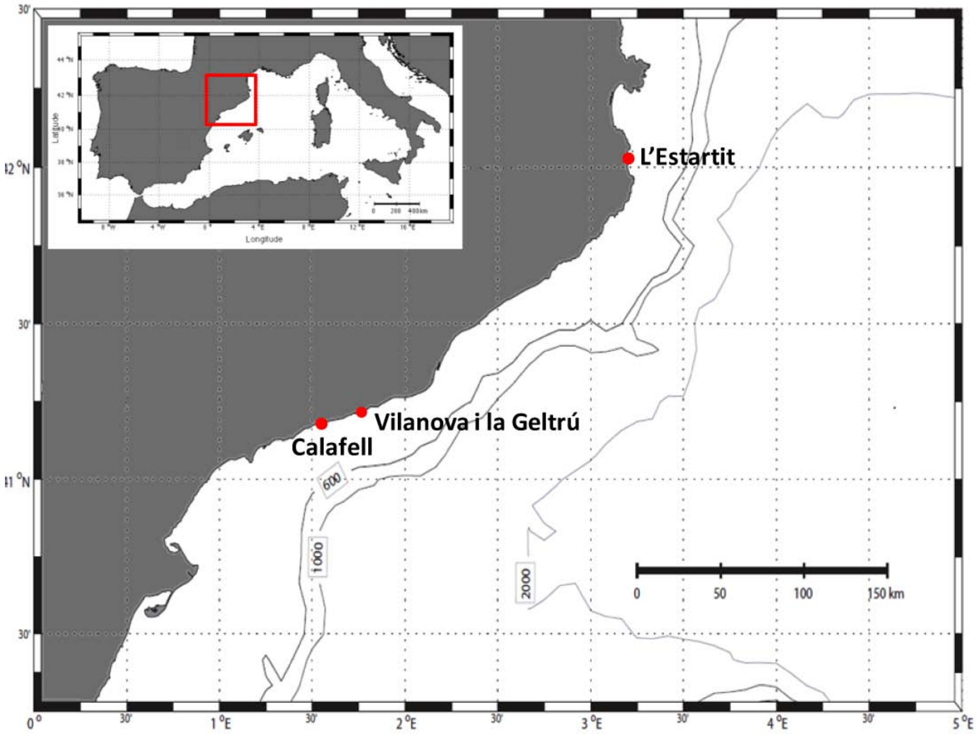


Figure 1. Geographical localization of sampling.

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 *DELT* (Δ), taxonomic distinctness *DSTR* (Δ^*), average taxonomic distinctness *AvTD* (Δ^+) and variation in taxonomic distinctness *VarTD* (Λ^+).

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

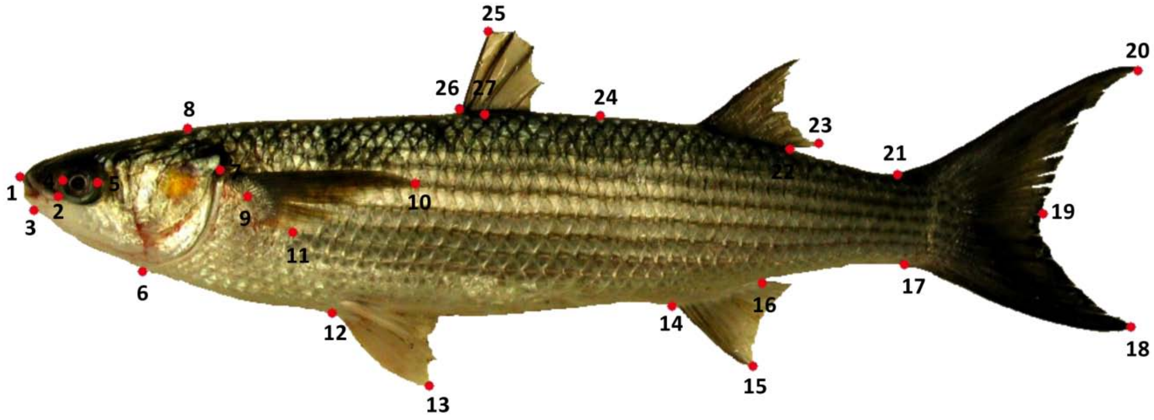


Figure 2. Identification of 27 landmarks and semilandmarks used in the geometric morphological analysis.

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

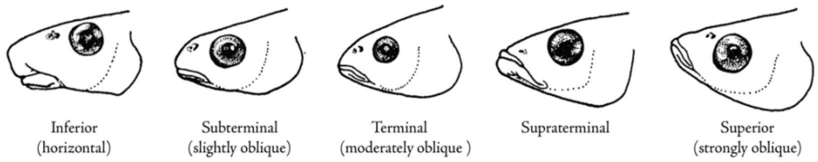
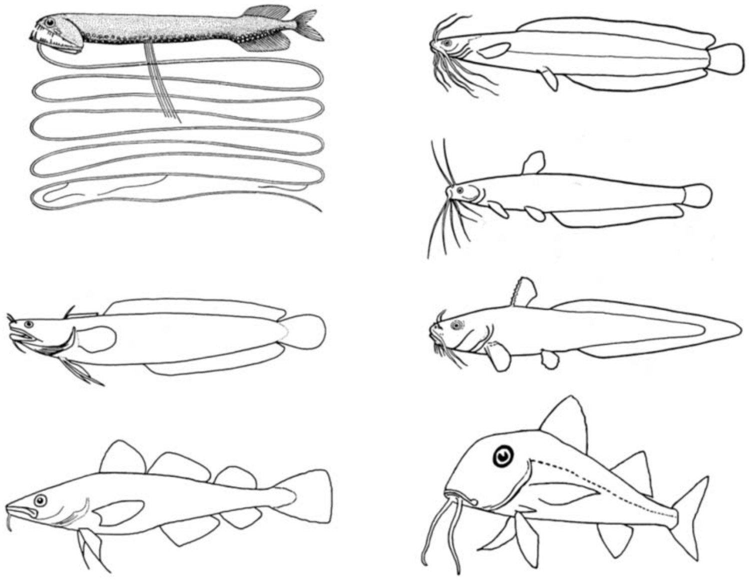
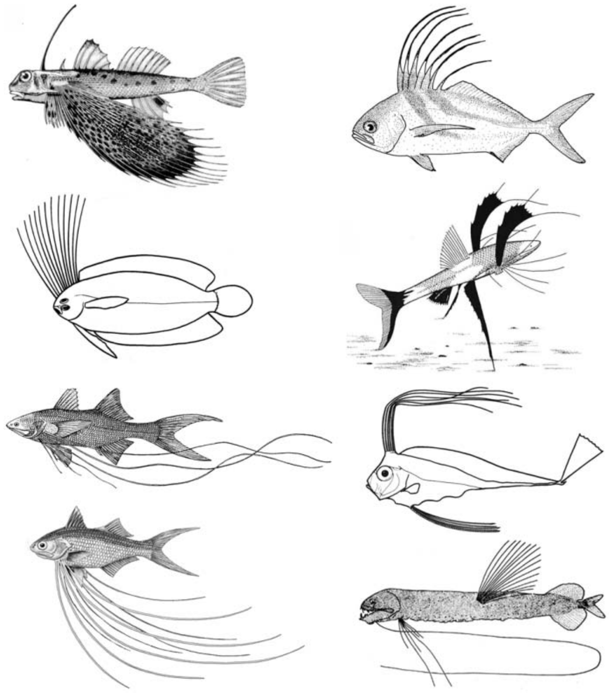
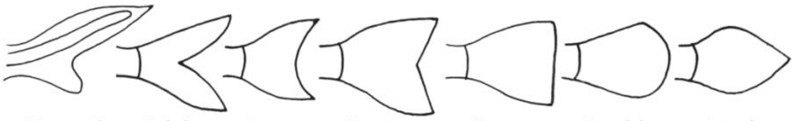
Points	Morphological meaning	Importance
1-2	Position and relative size of the mouth length respect to head and body size (from Jenkins and Burkhead, 1993)	*Ecological meaning*: related to food acquisition
		
3	Differentiates among fishes with or without sensorial barbels on chin, and position and relative size of barbels (from Kasumyan, 2011)	*Ecological meaning*: extremely diverse, related to mode of life, behaviour and feeding strategies. *Taxonomic value*
		
4-5	Position and relative size of eye and its position respect to head and body size	*Ecological meaning*: related to food acquisition and life strategies
6-8	Indicates the relative height and width of head respect to the body size	*Ecological meaning*: related to food acquisition and life strategies
24	Indicates the presence/absence of one or two dorsal fins	*Taxonomic value*
27	Defines the point of maximum height of the body shape	*Ecological meaning*: 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) 	*Ecological meaning*: related to swimming or walking over bottom, feeding and defensive strategies. *Taxonomic value*
12-13	Indicates pelvic fin shape and its relative position (see scheme before)	*Ecological meaning*: 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)	*Ecological meaning*: related to stability while swimming, walking over bottom and primary propulsion in some species. *Taxonomic value*
22-23	Defines where second dorsal fin finishes and its relative position (see scheme before)	*Ecological meaning*: related to stability while swimming and life strategies. *Taxonomic value*
25-26	Defines where first dorsal fin starts and its relative position (see scheme before)	*Ecological meaning*: related to stability while swimming, primary propulsion in some species, large fins as strucutres for the detection food or atrracting preys or transformed in a suction cup type structure maintaining position. *Taxonomic value*
17-21	Defines shape of peduncle and caudal fin (from Bugas et al., 2009)	*Ecological meaning*: 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, $MR = \sum_{\mathrm{j}} \mathrm{CC}$, where CC is the cluster coefficient and j is the species, and the morpho-geometric diversity index, $EMI = \frac{\sum_{\mathrm{j}} \mathrm{CC}}{(\mathrm{N}-1)}$, 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

The comparison of diversity indices was performed using Spearman's correlation index and they were clustered in a dendrogram produced using the hierarchical method (Lyashevska and Farnsworth, 2012). It was carried out based on Euclidean distances, using Ward's aggregation algorithm. Previously, data were scaled using Z-score normalization because it is specially needed for distance metrics, such as Euclidean distance, which are sensitive to differences in the magnitude or scales of the attributes (Visalakshi and Thangavel, 2009).

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 (*MR*2= 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).

Table 4. Ecological, taxonomic, morphological and functional indices obtained for the localities considered. *d*, Margalef's richness index; *H*', Shannon’s diversity index; *S*, specific richness; *S*', Simpson index; *J*', Pielou’s evenness index; Δ, taxonomic diversity; Δ*, taxonomic distinctness; Δ+, average taxonomic distinctness; Λ+, variation in taxonomic distinctness; *EMI* and *EMI2*, morpho-geometric diversity; *MD* and *MD*2, morphological disparity; *MR* and *MR*2, morphological richness; *FD*, functional diversity.

Locality	Fish assemblages	Ecological					Taxonomic				Morphological						Functional
		S	*d*	*J'*	*H'*	*S'*	Δ	Δ^*	Δ^+	Λ^+	*EMI*	*MD*	*MR*	*EMI2*	*MD2*	*MR2*	*FD*
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	2.907	0.152	0.028	3.19	52.10
	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	2.755	0.206	0.037	3.09	41.50
	Sandy 10 m*	26	6.33	0.90	2.92	0.94	86.52	91.93	88.23	317.25	0.193	0.054	4.635	0.190	0.050	4.75	67.60
	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	3.84	0.204	0.044	4.08	53.00
	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	4.213	0.173	0.037	4.15	64.40
	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	4.22	0.206	0.041	4.33	61.50
	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	3.13	0.193	0.033	3.28	47.90
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	5.162	0.160	0.032	4.64	73.90
	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	4.68	0.169	0.031	6.60	96.40
	Sandy 20 m	27	6.79	0.92	3.02	0.95	79.93	83.90	85.26	339.96	0.209	0.045	5.832	0.182	0.043	6.59	68.90
	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	5.434	0.166	0.032	6.98	101.80
	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	4.4149	0.171	0.107	5.99	84.20
	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	4.7369	0.158	0.168	7.11	105.30

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

The mosphospace was determined by the peripheral morphology of fishes of each assemblage (Fig. 3). In the sandy sample, the morphology of these species was composed for flattened (Pleuronectiforms as *Bothus podas*, *Psetta maxima*, *Solea solea* and *Scophtalmus rhombus*) and elongated shapes (Ophidiiforms as *Ophidion rochei*; Perciforms as *Trachinus draco*; and Syngnathiforms as *Syngnathus acus*), who bury in the sand or live on the sea bottom. Conversely, the more extreme shapes in the rocky-seagrasses corresponded with species living closer to surface (Clupeiforms as *Sardinella aurita*; and Beloniforms as *Belone belone*), typical of rocky-bottoms (Perciforms as *Diplodus annularis*, *Symphodus rostratus* and *Scorpaena scrofa*), and in 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 (Δ) and taxonomic distinctness (Δ^*). Similarly to richness index, the Shannon diversity index was linked to morphological richness and functional diversity indices. Conversely, Pielou's evenness index (*J'*) was weekly associated to that morpho-geometric diversity index (*EMI*) (r_s= 0.561) and morphological disparity (*MD*) (r_s= 0.575) obtained from abundance data. The taxonomical indices were correlated among them and with ecological and morphological disparity indices (*MD* and *MD*2), except for the variation in taxonomic distinctness (Λ^+). Morpho-geometric diversity indices were correlated between them and with the two unrelated indices; *EMI* with Pielou's evenness and *EMI2* with the functional diversity. Finally, the functional diversity (*FD*) showed significant relation to some ecological and morphological richness indices, especially with specific richness (0.991) and morphological richness (*MR*2, 0.962) (Table 5).

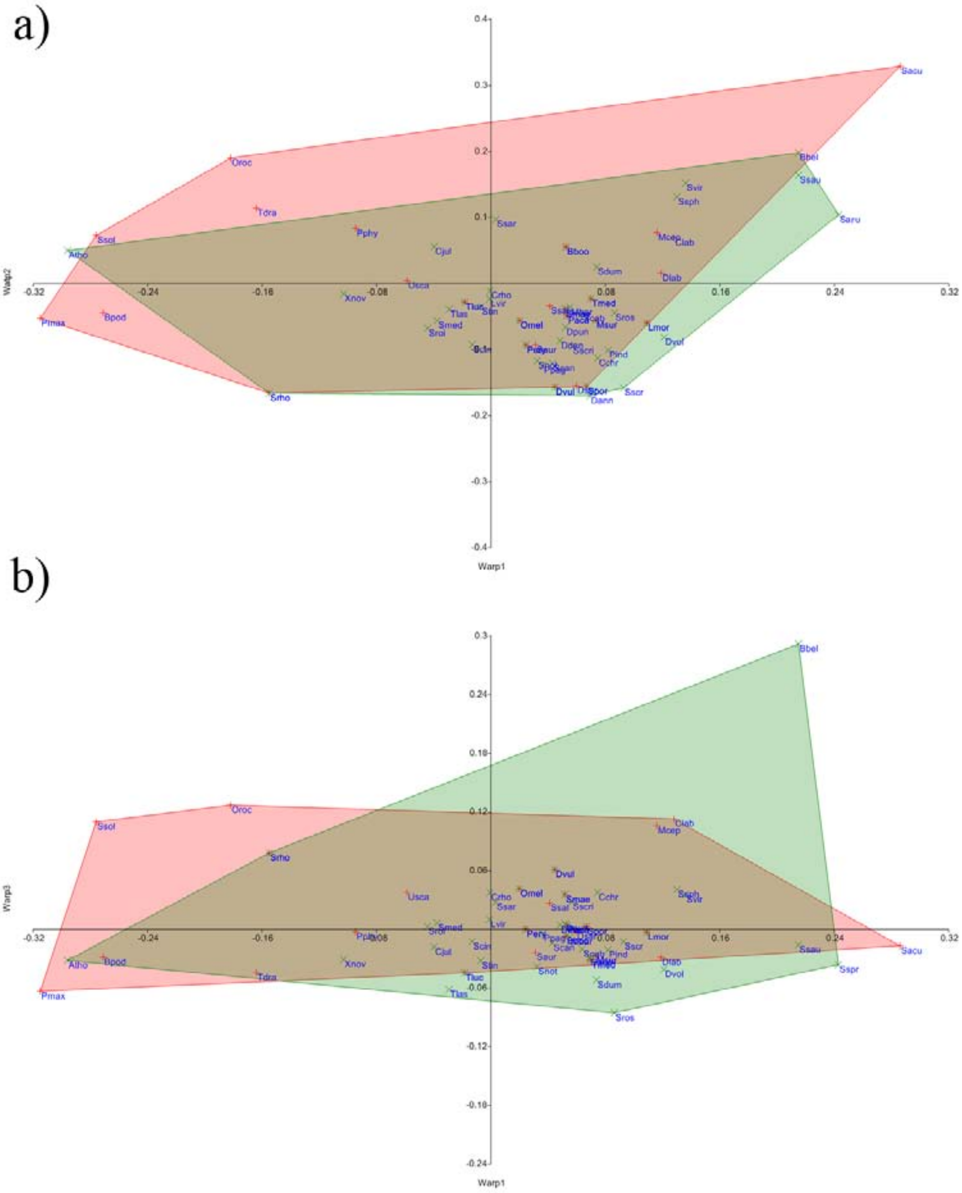


Figure 3. Morphospaces of two fish assemblages selected, sand < 10 m (red) and rocky-seagrasses (green), using relative warps1-2 (a) and 1-3 (b). In blue the acronyms of fishes.

Table 5. Spearman's correlation among ecological, taxonomic, morphological and functional indices. *d*, Margalef's richness index; *H*', Shannon's diversity index; *S*, specific richness; *S*', Simpson index; *J*', Pielou's evenness index; Δ, taxonomic diversity; Δ^*, taxonomic distinctness; Δ+, average taxonomic distinctness; Λ+, variation in taxonomic distinctness; *EMI* and *EMI*2, morpho-geometric diversity; *MD* and *MD*2, morphological disparity; *MR* and *MR*2, morphological richness; *FD*, functional diversity. In bold and grey-shaded the variables significantly correlated.

Indices		Ecological					Taxonomic				Morphological						Functional
		S	*d*	*J*'	*H*'	*S*'	Δ	Δ^*	Δ^+	Λ^+	*EMI*	*MD*	*MR*	*EMI2*	*MD2*	*MR2*	*FD*
Ecological	*S*	1															
	d	**0.821**	1														
	J'	0.063	0.292	1													
	H'	**0.601**	**0.726**	**0.815**	1												
	S'	0.448	**0.618**	**0.905**	**0.974**	1											
Taxonomic	Δ	0.385	0.456	**0.831**	**0.842**	**0.894**	1										
	Δ^*	0.393	0.363	0.525	**0.572**	**0.632**	**0.879**	1									
	Δ^+	0.237	0.231	0.473	0.443	0.458	**0.665**	**0.637**	1								
	Λ^+	-0.311	-0.258	-0.182	-0.316	-0.302	-0.423	-0.357	-0.324	1							
Morphological	*EMI*	-0.505	-0.275	**0.561**	0.074	0.254	0.264	0.126	0.379	0.038	1						
	MD	0.061	0.055	**0.575**	0.435	0.505	**0.632**	**0.571**	**0.797**	-0.099	0.522	1					
	MR	**0.825**	**0.907**	0.327	**0.669**	**0.604**	0.473	0.407	0.192	-0.297	-0.088	0.154	1				
	EMI2	**-0.693**	-0.468	0.344	-0.132	0.030	0.083	-0.058	0.297	-0.077	**0.839**	0.308	-0.410	1			
	MD2	0.124	0.052	0.425	0.353	0.409	**0.573**	**0.567**	**0.802**	-0.168	0.441	**0.953**	0.135	0.299	1		
	MR2	**0.941**	**0.934**	0.259	**0.724**	**0.615**	0.533	0.478	0.385	-0.481	-0.280	0.214	**0.885**	0.454	0.278	1	
Functional	*FD*	**0.991**	**0.901**	0.113	**0.630**	0.498	0.423	0.401	0.308	-0.346	-0.451	0.115	**0.846**	**-0.605**	0.193	**0.962**	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*, *DELT*, *DSTR*), where the morphological disparity depended on taxonomical groups.

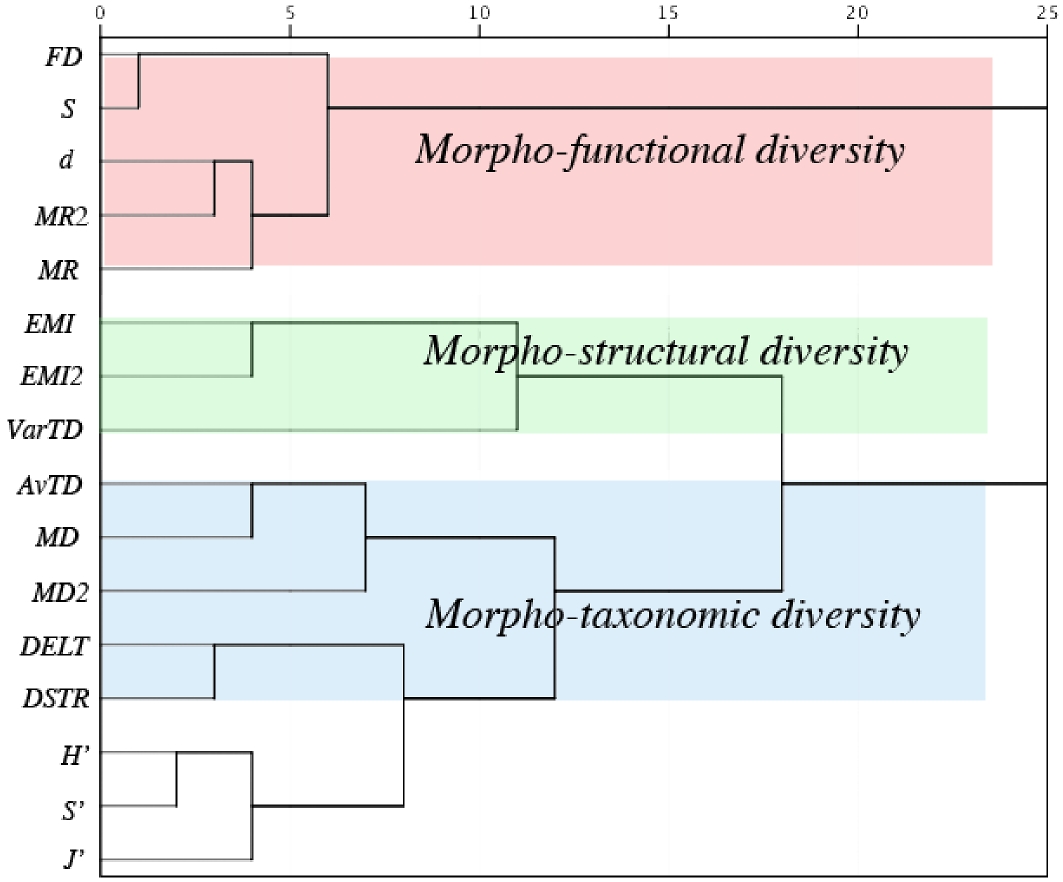


Figure 4. Hierarchical clustering of biodiversity indices using Ward distance indicating several clusters: 1, morpho-functional diversity (red); 2, morpho-structural diversity (green); 3, morpho-taxonomical diversity (blue).

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 (Lyashevska and Franswoth, 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 (Lyashevska and Franswoth, 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 taxonomical 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 (Δ) 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 that 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.

Acknowledgements

Data of this study were financed by project “ESCAL 1” (Ref. PCC30004/99), “ESCAL 2” (Ref. 02P30015) of the DG Fisheries of the Government of Catalonia, “CONFLICT” (Ref. CGL2008-00047) of the Spanish National Research Plans and “EMPAFISH” (E.U. DG MARE project Ref. 006539). Marc Farré Foix acknowledges a pre-doctoral grant from the Government of Andorra, ATC010-AND, academic year: 2012-2013. Dr. Víctor Tuset is worker of CSIC within the modality «JAE-Postdoc» of Programme «Junta para la Ampliación de Estudios» co-funded by the European Social Foundation (FSE).

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)

Víctor M. Tuset [1], Marc Farré [1], Antoni Lombarte [1], Fernando Bordes [2],
Rupert Wienerroither [3], Pilar Olivar [1]

[1] Institut de Ciències del Mar (ICM-CSIC), Passeig Marítim 37-49, 08003, Barcelona, Catalonia, Spain.
[2] Departamento de Recursos Pesqueros, Instituto Canario de Ciencias Marinas (ICCM ACIISI), Apartado de correos 56, 35200, Telde (Las Palmas), Islas Canarias, Spain.
[3] Institute of Marine Research, P.O. Box 1870 Nordnes, 5817 Bergen, Norway.

Published in *Ichthyological Research 61, 152-158* (2014)

DOI: 10.1007/s10228-014-0390-2

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 mes 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 (Tyszka, 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

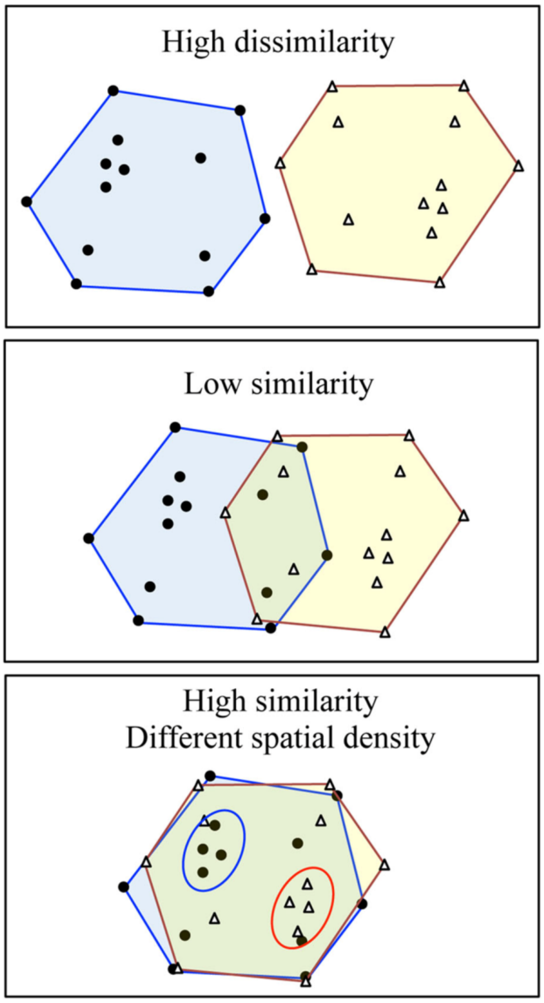


Figure 1. Similarity between theoretical spaces showing spatial distribution variation in the set data (*coloured circles*).

describe this patterning (Shen et al., 2008; Goatley et al., 2010; Rickflefs, 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 (Wienerrrither 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).

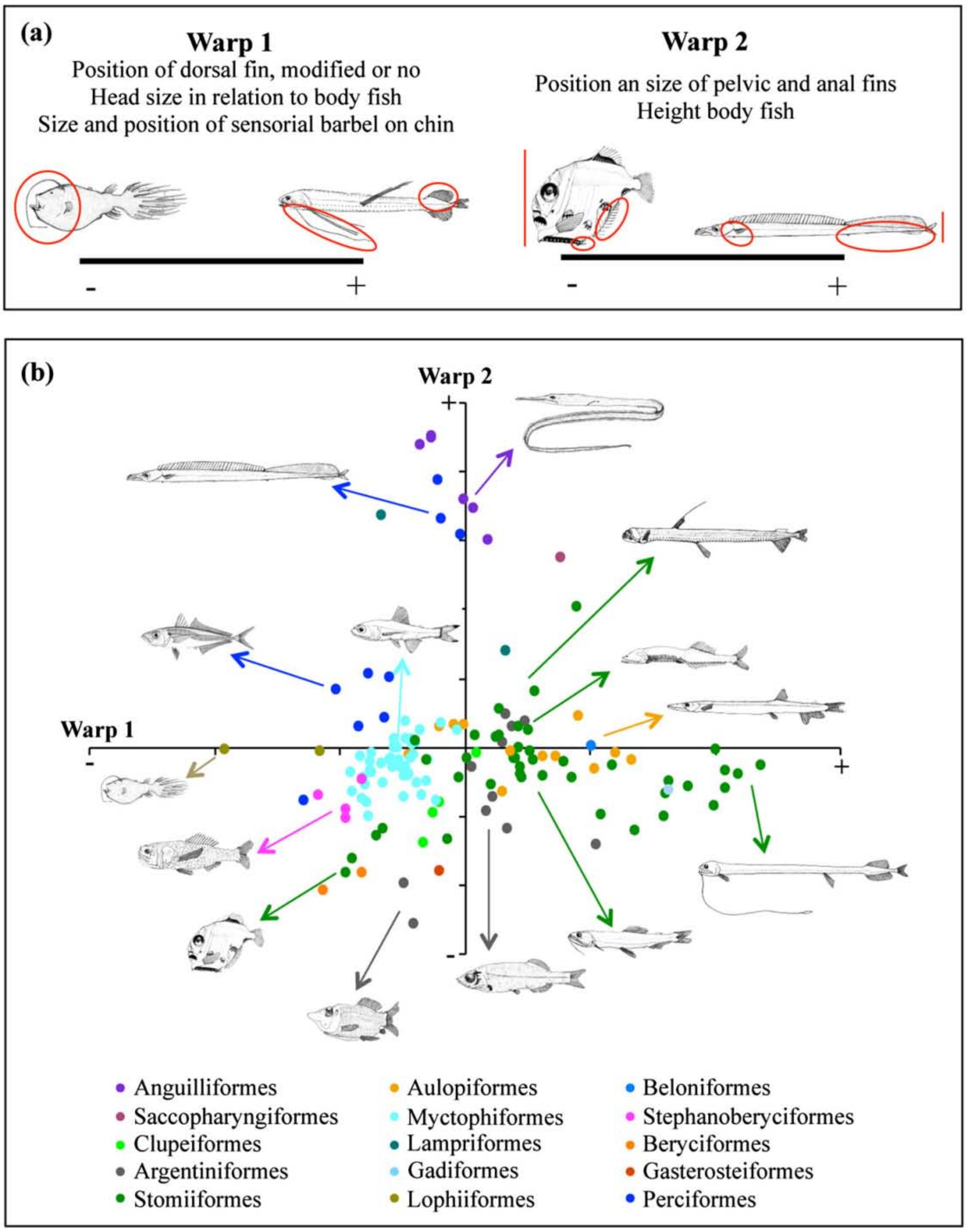


Figure 2. Morphological meaning of warps 1 and 2 (a), and plot representing all species in the morphospace helping to its comprehension (b).

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 sensorial barbels (Stomiidae, Stomiiformes), high body and big head (Sternoptychidae, Stomiiformes), big head and narrow caudal peduncle (Stephanoberyciformes), and high body and first spine of dorsal fin transformed into an illicium (Lophiiformes) (Figs. 2, 3).

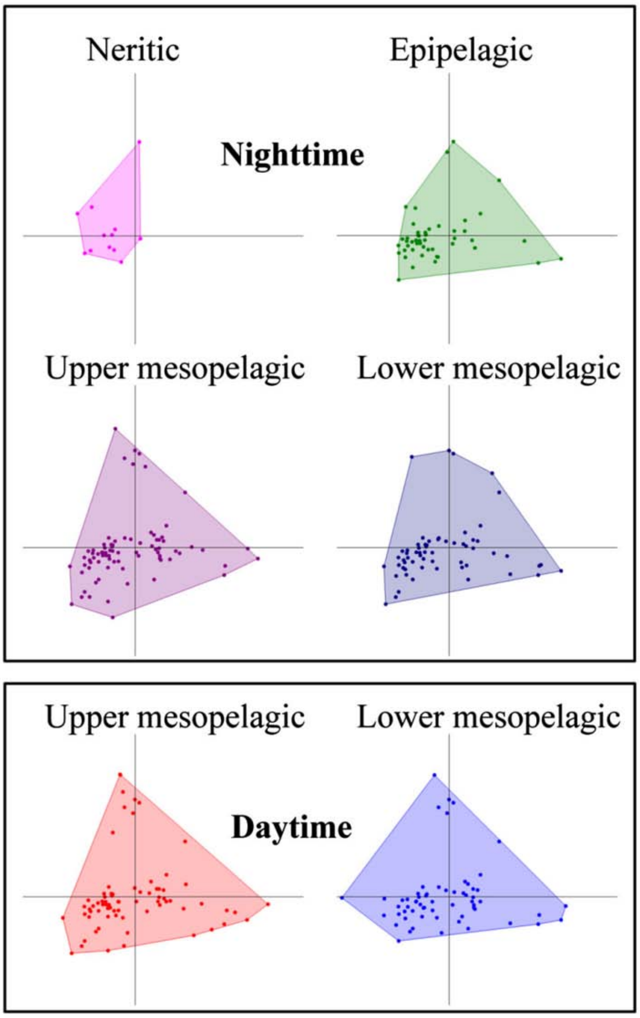


Figure 3. Warp plot with convex hull delineating the morphospace realised by mesopelagic fish assemblages.

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 *EN* assemblage was mainly composed of migratory species of the family Myctophidae and some species of Stomidae, 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).

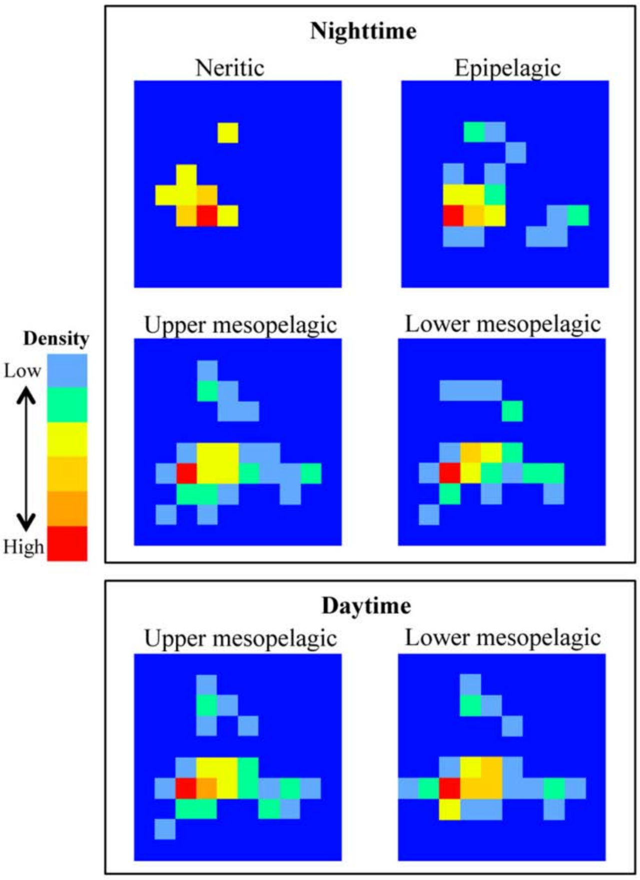


Figure 4. Warp plot with patterning of morphospace realized by mesopelagic fish assemblages. *Colours scale* indicates the density of species in each cell.

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.

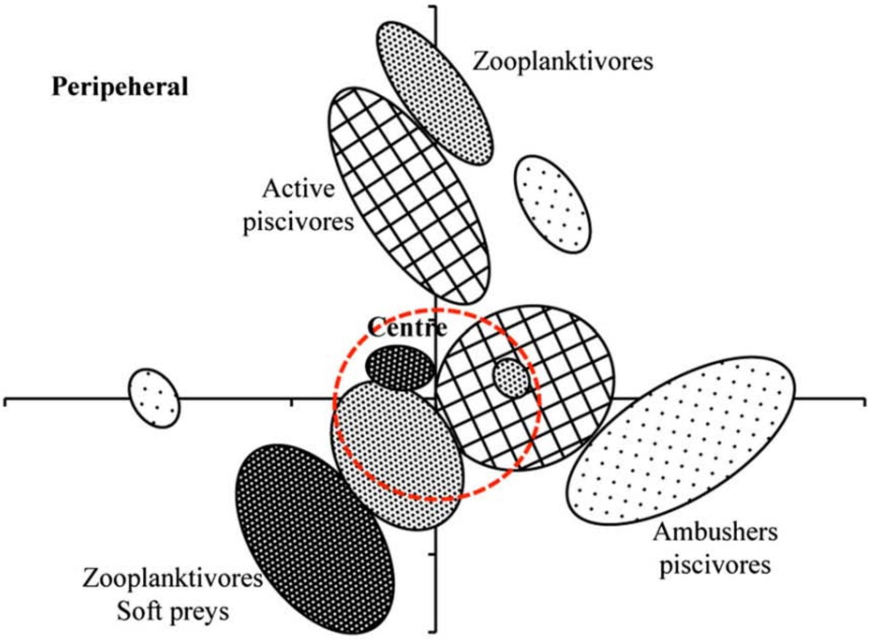


Figure 5. Warp plot with feeding groups of mesopelagic fishes.

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 Argentiniforrmes 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.

Acknowledgments

The surveys were carried out in projects supported by the Viceconsejería de Pesca del Gobierno de Canarias. We especially thank Mrs. Isabel Bordes Cabrera for the fish drawings in this paper by allowing its reproduction of the book “Catálogo de especies meso y batipelágicas. Peces, moluscos y crustáceos. Colectadas con arrastre en las Islas Canarias durante las campañas realizadas a bordo del B/E “La Bocaina”. ICCM-Gobierno de Canarias”. This research has been partially sponsored by the Spanish projects CTM2008-04489-C03-03 and CTM2012-39587-C04-03. Marc Farré Foix acknowledges a pre-doctoral grant from the Government of Andorra, ATC010-AND, academic year: 2012-2013.

7

Habitat influence in the morphological diversity of coastal fish assemblages

Habitat influence in the morphological diversity of coastal fish assemblages

Marc Farré [1], Antoni Lombarte [1], Laura Recasens [1], Francesc Maynou [1],
Víctor M. Tuset [1]

[1] Institut de Ciències del Mar (ICM-CSIC). Passeig Marítim de la Barceloneta 37-49,
08003 Barcelona, Catalonia, Spain

Published in *Journal of Sea Research 99: 107-117* (2015)

DOI: http://dx.doi.org/10.1016/j.seares.2015.03.002

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; Gordoa, 2009; Macpherson et al., 2000, 2002).

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).

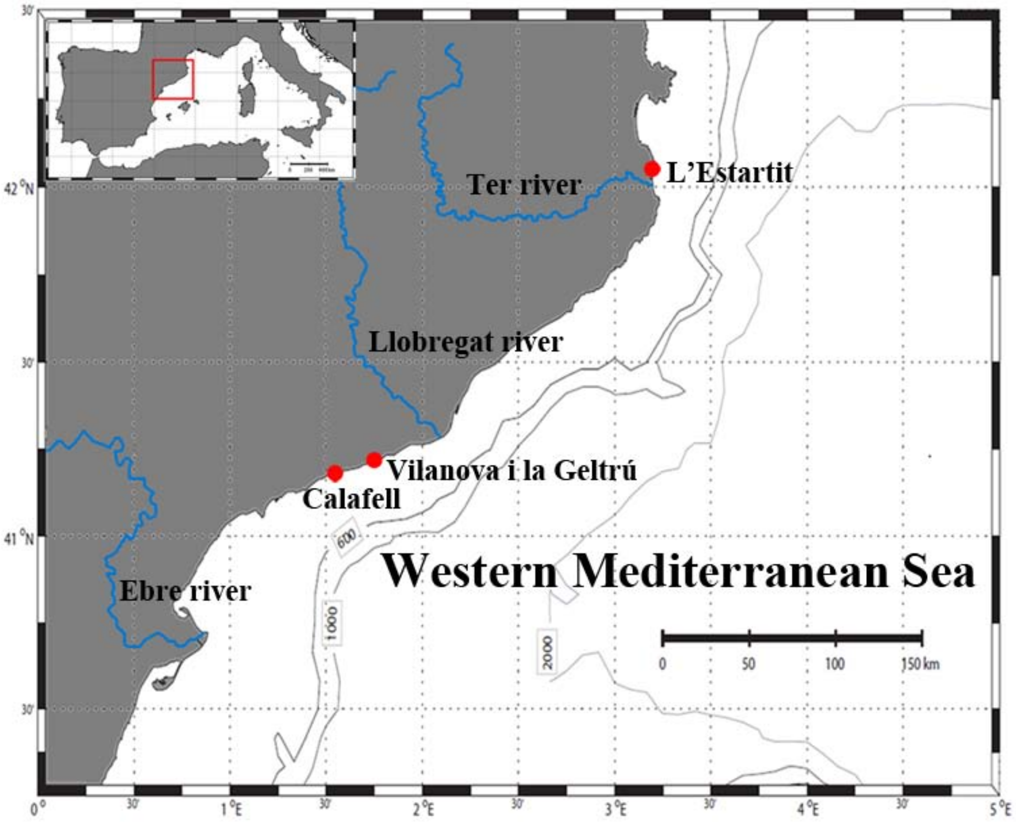


Figure 1. Geographical localization of study areas: Vilanova i la Geltrú-Calafell or Central zone and L'Estartit or Northern zone.

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

(*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).

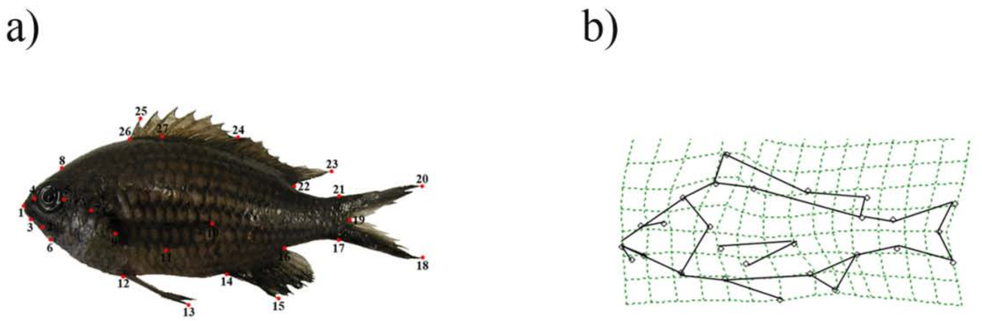
7.2.3 Ecological structure of assemblages

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

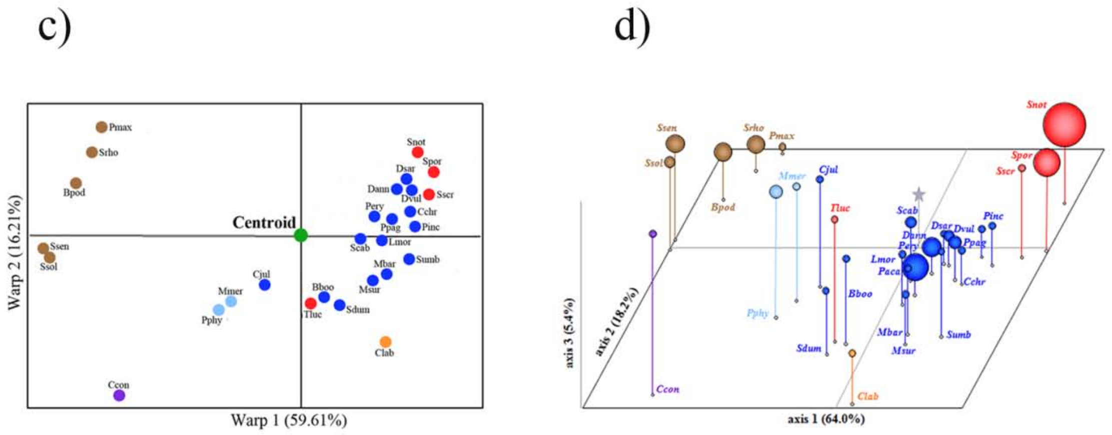
The configuration of the morphospaces of the fish assemblages was determined using the geometric morphological method. All steps realized during the morphological analysis process are schematically shown in Figure 2. The analysis of species morphology was realized using morphometric data obtained by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



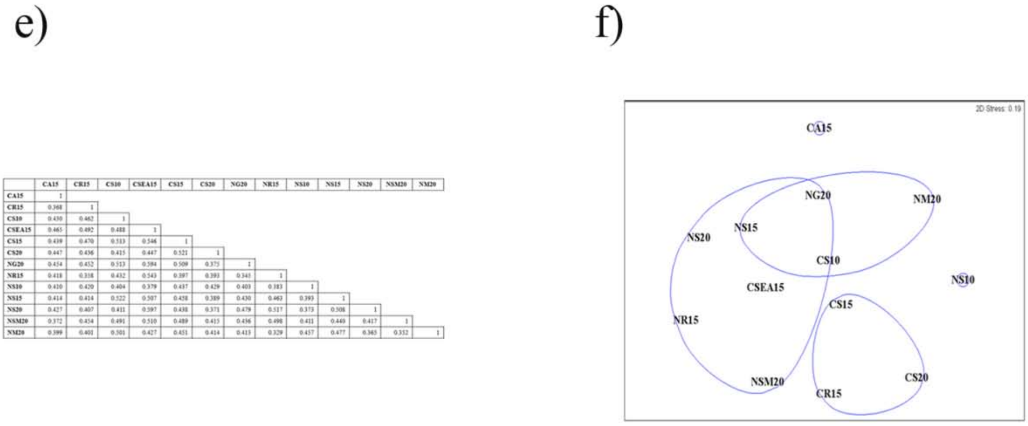
Selection of 27 landmarks
TPS Dig v. 2.16 (Rohlf 2010a)

Deformation grid
for each species



GLS procedure and thin-plate spline approach
Obtention consensus configuration and relative warps
TPS Relw v. 1.49 (Rohlf 2010b)

Construction of morphospaces using three first axes
Relative abundance data for each species (point sizes)



	CA15	CR15	CS10	CSEA15	CS15	CS20	NG20	NR15	NS10	NS15	NS20	NSM20	NM20
CA15	1												
CR15	0.368	1											
CS10	0.430	0.462	1										
CSEA15	0.465	0.492	0.488	1									
CS15	0.439	0.470	0.513	0.546	1								
CS20	0.447	0.436	0.415	0.447	0.521	1							
NG20	0.454	0.452	0.513	0.584	0.509	0.375	1						
NR15	0.418	0.358	0.432	0.543	0.397	0.393	0.341	1					
NS10	0.410	0.420	0.404	0.379	0.437	0.429	0.403	0.383	1				
NS15	0.414	0.414	0.522	0.507	0.458	0.389	0.430	0.463	0.393	1			
NS20	0.427	0.407	0.411	0.597	0.438	0.371	0.479	0.517	0.373	0.308	1		
NSM20	0.372	0.454	0.491	0.510	0.489	0.415	0.436	0.498	0.411	0.449	0.417	1	
NM20	0.399	0.401	0.501	0.427	0.451	0.414	0.413	0.329	0.457	0.477	0.365	0.332	1

Comparison between morphospaces
Correlation matrix
TPS Pls v. 1.18 (Rohlf 2006)

nMDS of morphospaces

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).

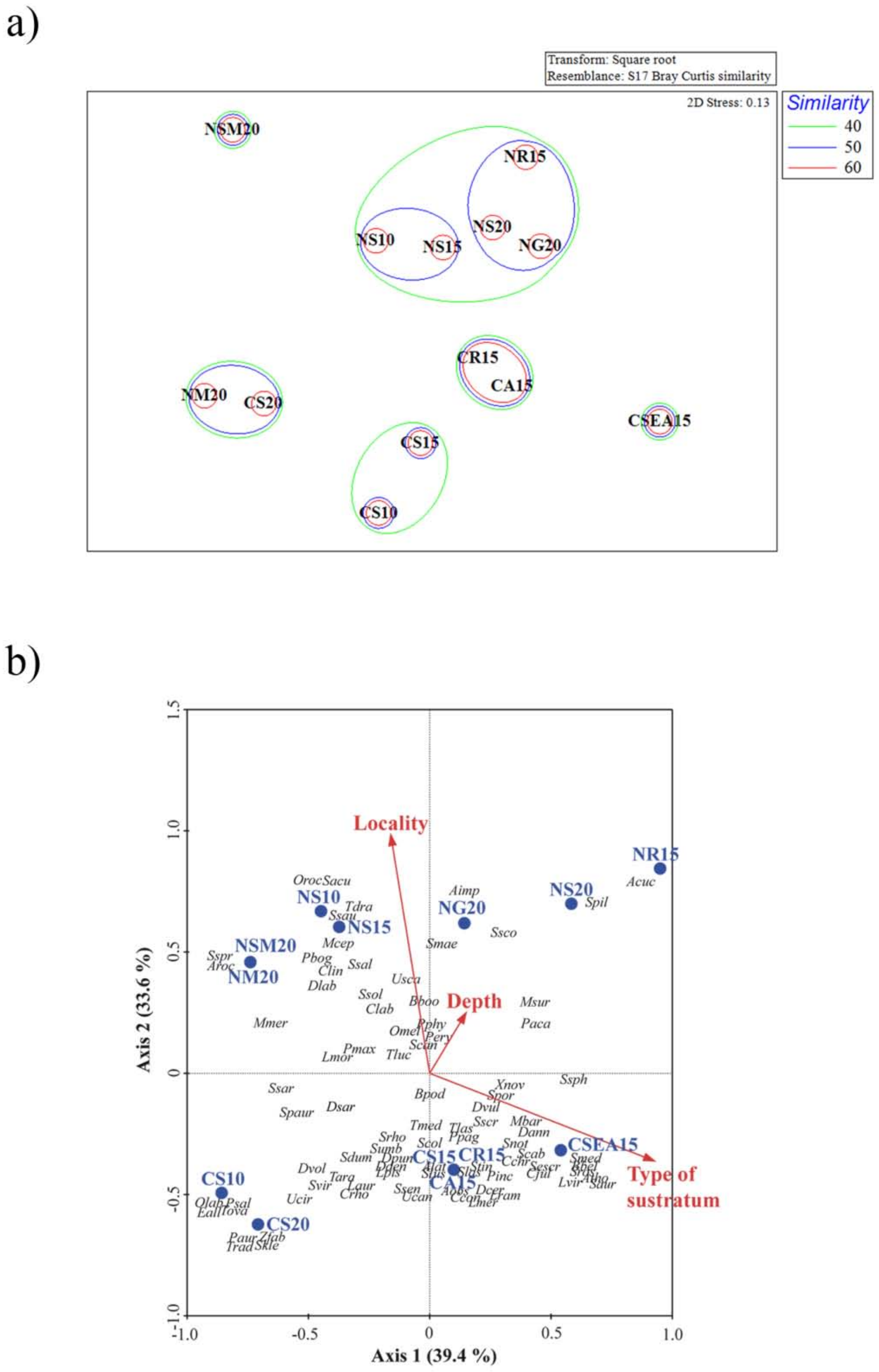


Figure 3. Non-metric multidimensional scaling ordination (nMDS) from abundance data of the assemblages using the Bray-Curtis similarity (a) and correspondence canonical analysis (CCA) based on specific abundances, with the communities represented by points and environmental variables by vectors (b).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

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.

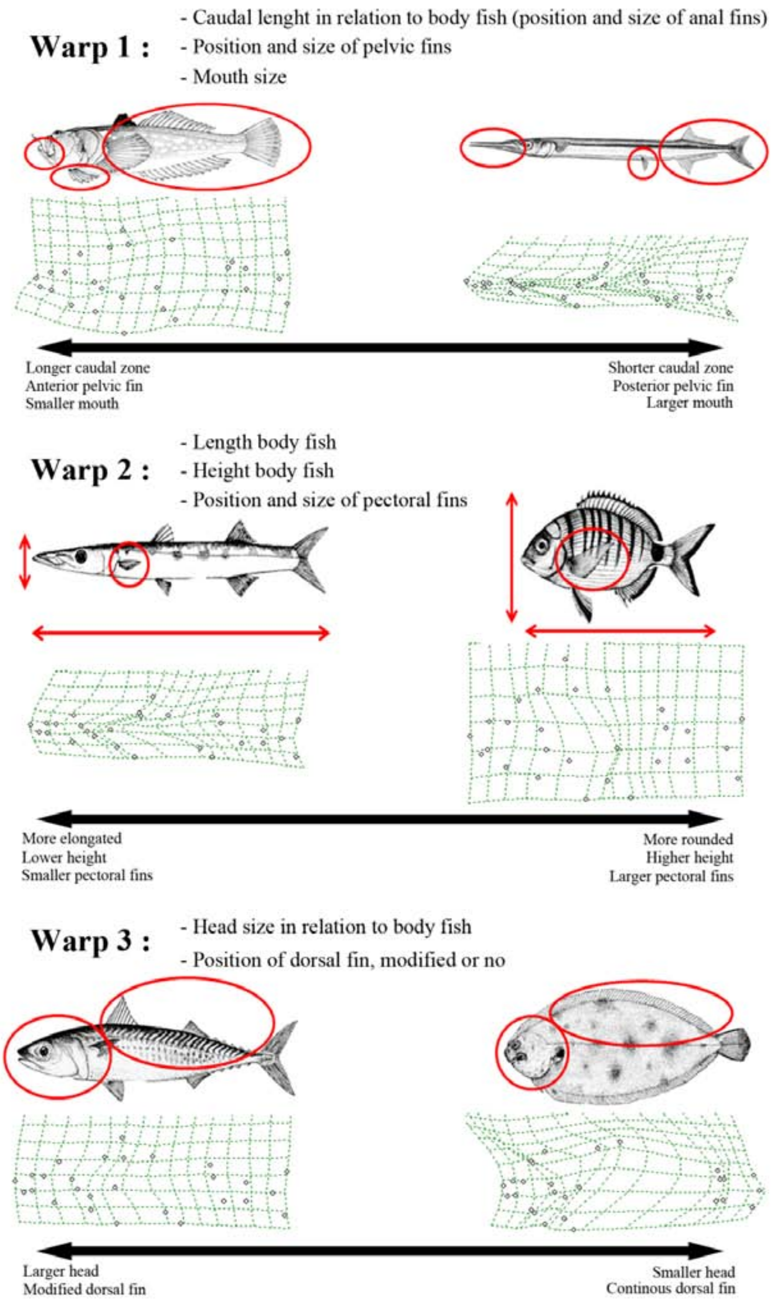


Figure 4. Scheme representing the main morphological characteristics defined by the three axis of the morphospace, coinciding with the first three relative warps.

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.

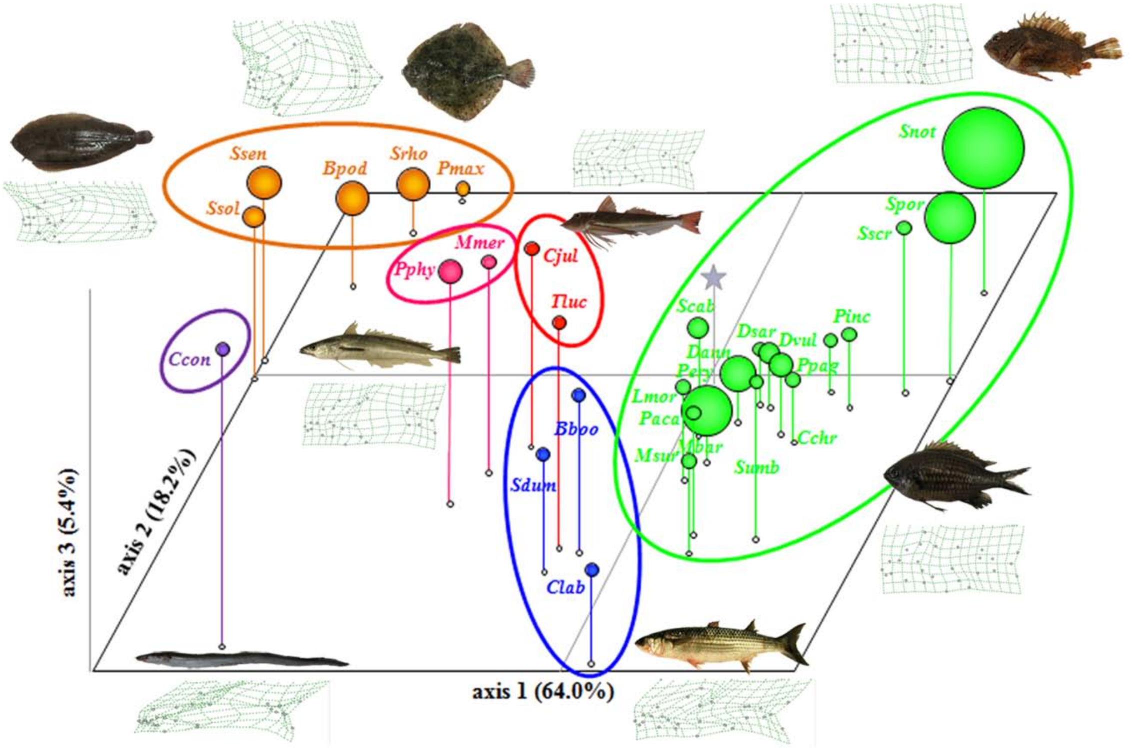


Figure 5. Example of the main morphological groups differentiated within the morphospaces, each of them represented by different colours. Deformation grids indicating shapes found within each group are provided, as well as images of the represented species.

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.

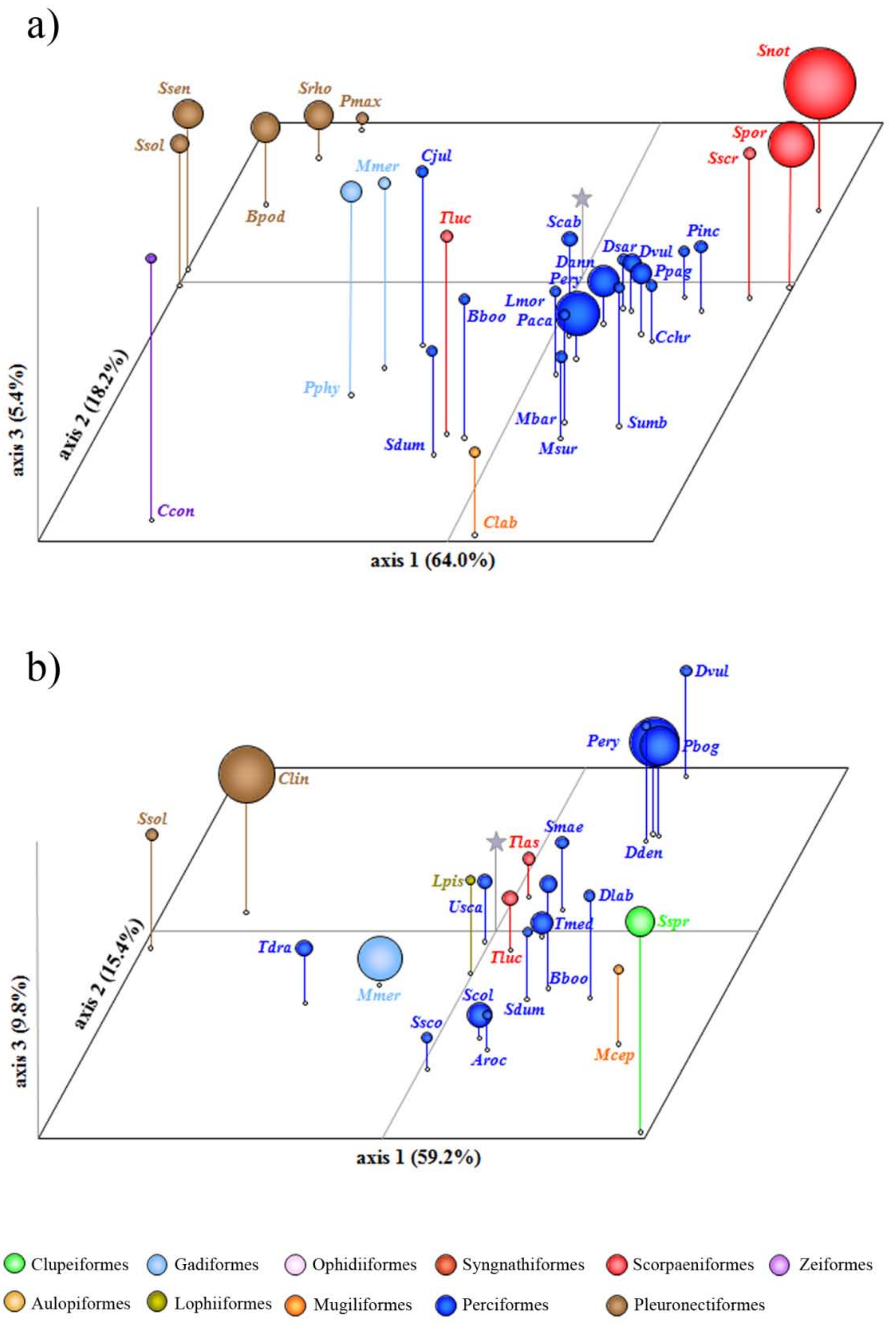

a)
Snot
Ssen
Srho
Pmax
Ssol
Spor
Sscr
Bpod
Mmer
Cjul
Tluc
Scab
Pinc
Dsar
Dvul
Dann
Ppag
Pery
Lmor
Bboo
Paca
Cchr
Pphy
Mbar
Sumb
Sdum
Msur
Ccon
Clab
axis 3 (5.4%)
axis 2 (18.2%)
axis 1 (64.0%)
b)
Dvul
Pery
Pbog
Clin
Ssol
Smae
Tlas
Dden
Lpis
Usca
Dlab
Tmed
Sspr
Tdra
Tluc
Mmer
Bboo
Scol
Sdum
Ssco
Aroc
Mcep
axis 3 (9.8%)
axis 2 (15.4%)
axis 1 (59.2%)
Clupeiformes
Gadiformes
Ophidiiformes
Syngnathiformes
Scorpaeniformes
Zeiformes
Aulopiformes
Lophiiformes
Mugiliformes
Perciformes
Pleuronectiformes

Table 1. Average correlation values among assemblages based on the PLS analysis (tps Pls v. 1.18; Rohlf, 2006). Bold values indicate correlations > 0.45.

		Central zone						Northern zone						
Locality	Assemblages	CA15	CR15	CS10	CSEA15	CS15	CS20	NG20	NR15	NS10	NS15	NS20	NSM20	NM20
Central zone	CA15	1												
	CR15	0.368	1											
	CS10	0.430	**0.462**	1										
	CSEA15	**0.465**	**0.492**	**0.488**	1									
	CS15	0.439	**0.470**	**0.513**	**0.546**	1								
	CS20	0.447	0.436	0.415	0.447	**0.521**	1							
Northern zone	NG20	**0.454**	**0.452**	**0.513**	**0.594**	**0.509**	0.375	1						
	NR15	0.418	0.358	0.432	**0.543**	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	**0.522**	**0.507**	**0.458**	0.389	0.430	**0.463**	0.393	1			
	NS20	0.427	0.407	0.411	**0.597**	0.438	0.371	**0.479**	**0.517**	0.373	**0.508**	1		
	NSM20	0.372	**0.454**	**0.491**	**0.510**	**0.489**	0.415	0.436	**0.498**	0.411	0.440	0.417	1	
	NM20	0.399	0.401	**0.501**	0.427	**0.451**	0.414	0.413	0.329	**0.457**	**0.477**	0.365	0.352	1

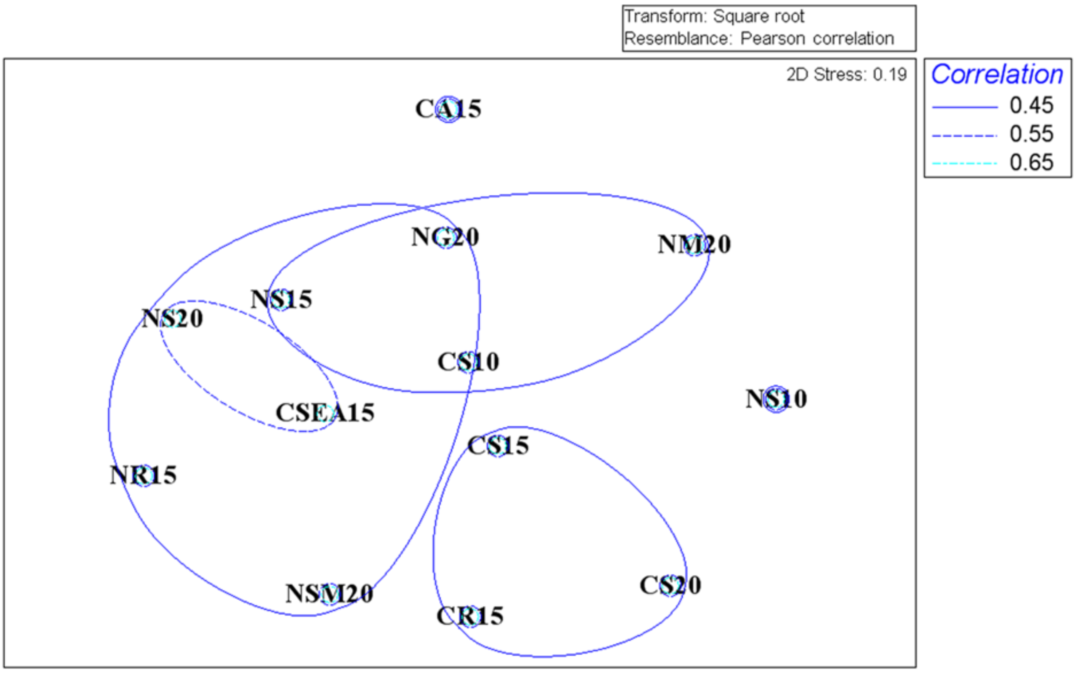


Figure 7. Non-metric multidimensional scaling ordination (nMDS) from the average correlation matrix between morphospaces using Pearson correlation.

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 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).

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.

Acknowledgements

Data of this study were financed by project “ESCAL 1” (Ref. PCC30004/99), “ESCAL 2” (Ref. 02P30015) of the DG Fisheries of the Government of Catalonia, “CONFLICT” (Ref. CGL2008-00047) of the Spanish National Research Plans and “EMPAFISH” (E.U. DG MARE project Ref. 006539). Marc Farré Foix acknowledges a pre-doctoral grant from the Government of Andorra, ATC010-AND, academic years: 2012-2013 and 2013-2014. Dr. Víctor Tuset was worker of CSIC (2010-2013) within the modality «JAE-Postdoc» of Programme «Junta para la Ampliación de Estudios» co-funded by the European Social Foundation (FSE).

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

Marc Farré [1], Víctor M. Tuset [1], Joan E. Cartes [1], Enric Massutí [2], Antoni Lombarte [1]

[1] Institut de Ciències del Mar (ICM-CSIC). Passeig Marítim de la Barceloneta, 27-49, 08003, Barcelona, Catalonia, Spain

[2] Centre Oceanogràfic de les Balears, Instituto Español de Oceanografía (IEO), Moll de Ponent, s/n, 07015, Palma de Mallorca, Illes Balears, Spain

Submitted and under revision in *Progress in Oceanography*

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 anàlisis 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 decréixer dràsticament. Aquests 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 on the slope of the Balearic Basin and in the continental shelf and insular slope around the Balearic Islands (vicinity of Mallorca and Menorca Islands) in the western Mediterranean Sea (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 13º (winter) and 27ºC (summer) and creating intense gradients between 50 and 100 m (Fernández de Puelles 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 (12.8-13º) and salinity (38-38.6‰) (Hopkins, 1985). These particular environmental conditions contribute to the more rapid degradation of the organic matter falling down to deeper levels given the high temperatures of the zone in comparison with other areas, causing a decrease in food availability with depth and, consequently, a decrease in the biomass of deep-living organisms (Cartes et al., 2015). For this reason, the deep Mediterranean Sea has been considered as an oligotrophic environment with respect to adjacent areas, such as the Atlantic Ocean (Pérès, 1985)

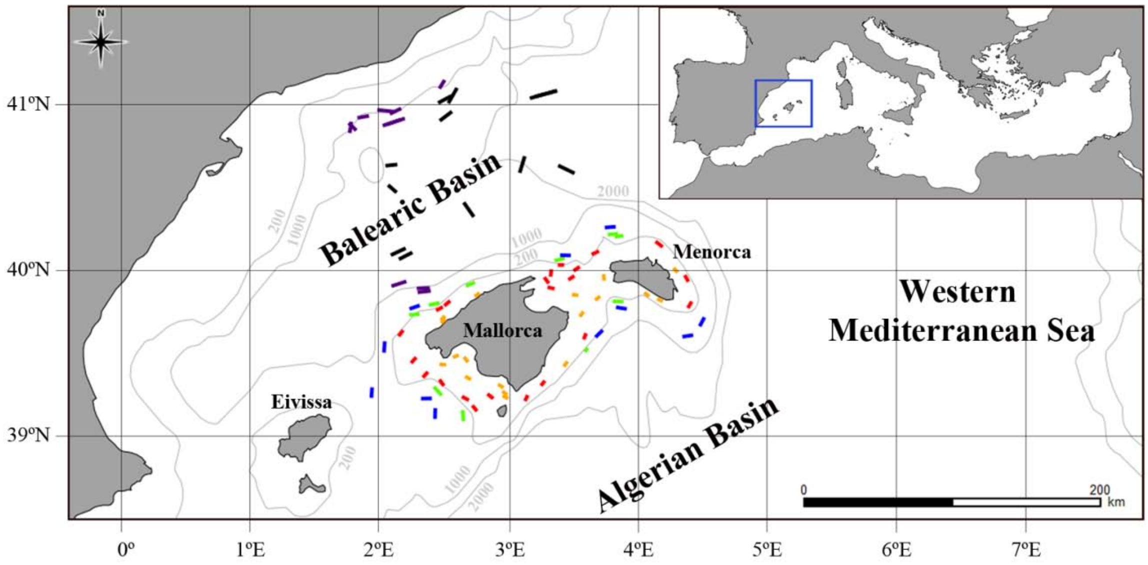


Figure 1. Map of the geographical location of the study area: Mallorca and Menorca Islands (Balearic Islands, western Mediterranean) and Balearic Basin, showing the position of the trawl hauls performed during the BALAR survey (in orange hauls performed between 40-80 m, in red 80-250 m, in green 250-500 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 along the Balearic Basin, between the Catalan coast and the western slope of the Balearic Islands, as well as in several zones of the north-west of Mallorca (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 are given 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 (for morphological purposes). 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; Moranta et al., 1998; 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 (uncentred 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.

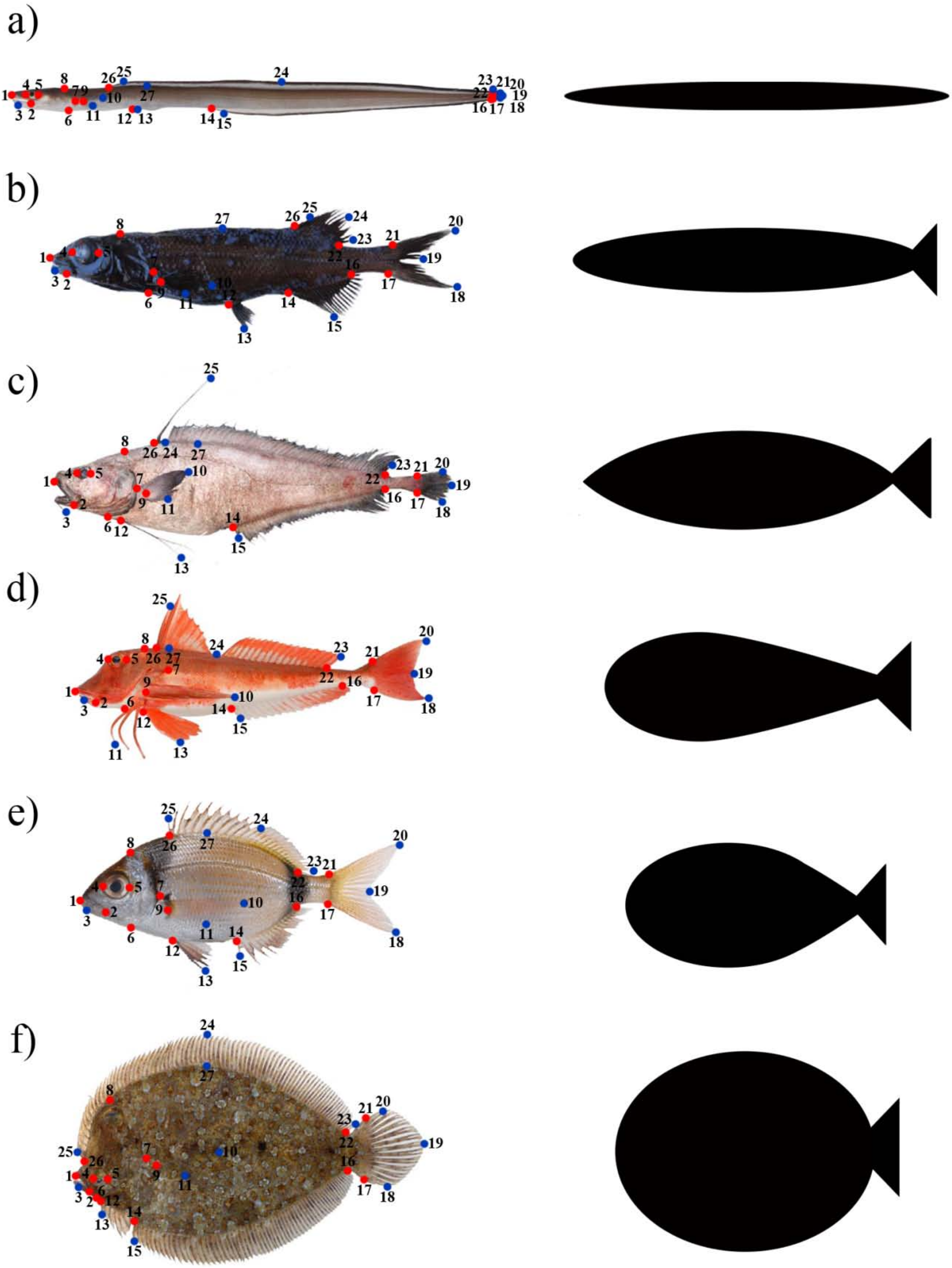


Figure 2. Location of the 27 landmarks (red points) and semilandmarks (blue points) used to characterize the body shape of fishes using geometric morphometry analyses, as well as geometric figures of the different body shapes considered in this study: *Conger conger*, anguilliform shape (a), *Alepocephalus 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 Supplementay 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 (*Feve*) (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). *Feve* is independent of specific richness and convex hull, and its value range between 0 and 1; b) functional divergence diversity (*Fdiv*) (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 (*Fdis*) (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 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
Body shape	Ang	Anguilliform	**Size**	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			
	Asy	Asymmetrical flatfish			
			Vertical distribution	EPIP	Epipelagic
Swimming type	Ang	Anguilliform		MESP	Mesopelagic
	Sub	Subcarangiform		BENTP	Benthopelagic
	Car	Carangiform		EPIB	Epibenthic
	Dio	Diodontiform		ENDB	Endobenthic
	Ami	Amiiform		BATHYP	Bathypelagic
	Bal	Balistiform			
	Lab	Labriform	**Diet (feeding guild)**	nmM	Non-migrator macroplankton
	Bat	Bathypteroiform		mM	Migrator macroplankton
				NS	Nectobenthos-suprabenthos
Motility	S	Sedentary or territorial		EPIB	Epibenthos
	R	Roving		INF	Infauna (endobenthos)
	H	High mobile or migratory		EPIP	Macroplankton epipelagic

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*, *Synganthus 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*).

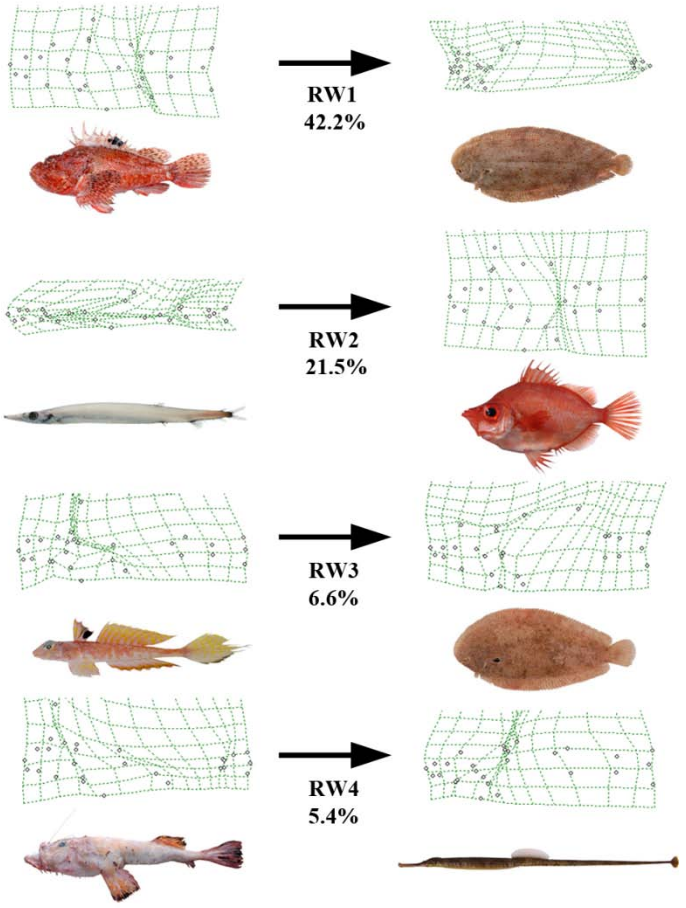


Figure 3. Explanatory scheme of the morphological variation observed along each of the first four axes (coinciding with the first four relative warps) from negative (left images) to positive extreme (right images), including images of representative species, the deformation grids and the percentage of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

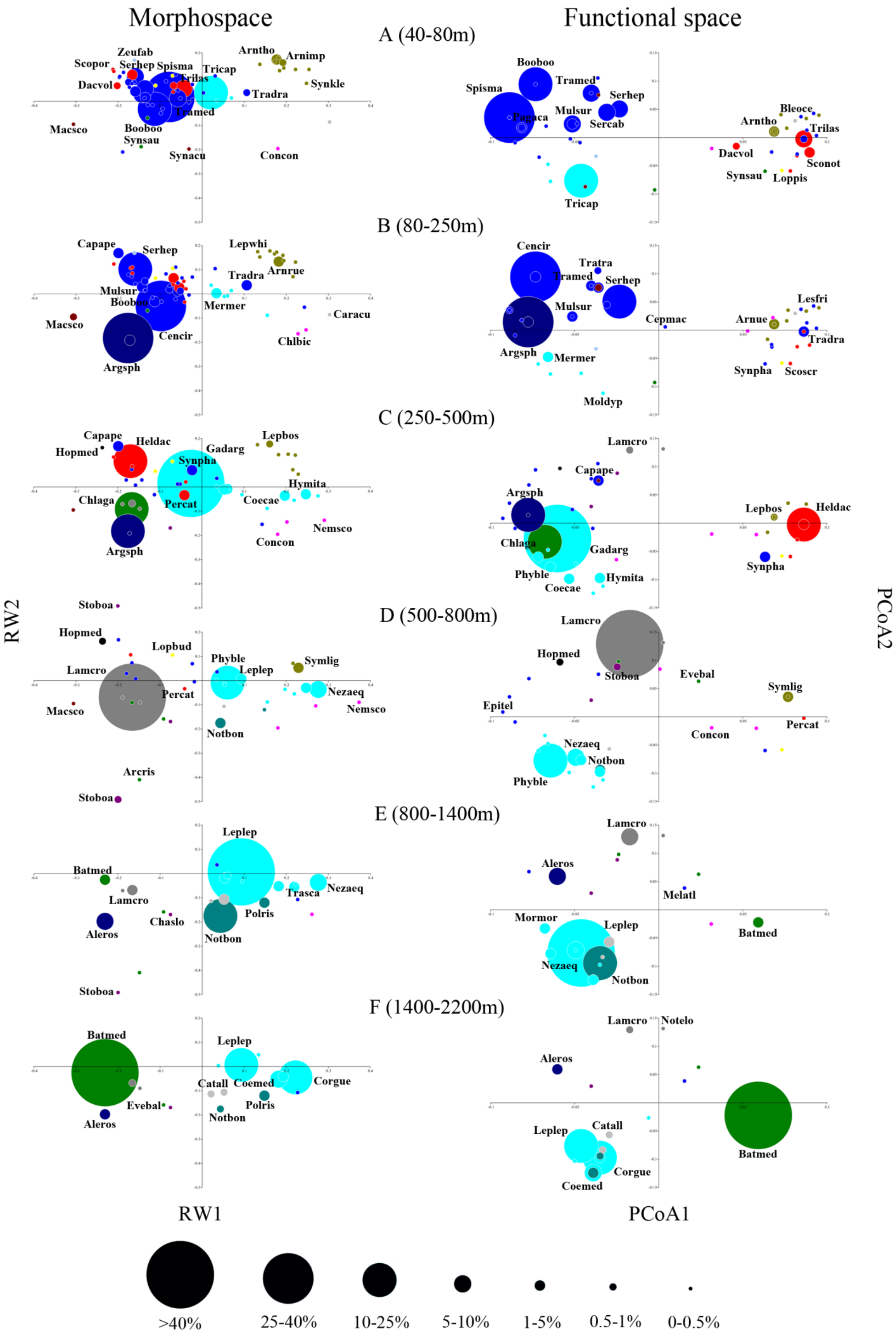
A strong variation in shape was noticed along the bathymetric range between the morphospaces of the different assemblages (RW1-RW2 representations in Fig. 4, RW3-RW4 in Fig. S1 of Supplementary Material). In the *A* assemblage (40-80 m), the most abundant species were modern Actinopterygian fishes (Perciformes)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


Morphospace
Functional space
A (40-80m)
Zeufab
Scopor
Serhep
Spisma
Arntho
Arnimp
Tricap
Trilas
Synkle
Dacvol
Tradra
Tramed
Macsco
Booboo
Synsau
Synacu
Concon
Booboo
Tramed
Spisma
Serhep
Pagaca
Mulsur
Sercab
Bleoce
Arntho
Trilas
Dacvol
Sconot
Synsau
Loppis
Tricap
B (80-250m)
Capape
Serhep
Lepwhi
Tradra
Arnrue
Mulsur
Booboo
Mermer
Caracu
Macsco
Cencir
Chlbic
Argsph
Cencir
Tratra
Tramed
Serhep
Mulsur
Cepmac
Lesfri
Arnue
Tradra
Argsph
Mermer
Synpha
Scoscr
Moldyp
C (250-500m)
Capape
Hopmed
Heldac
Lepbos
Gadarg
Synpha
Hymita
Chlaga
Percat
Coecae
Nemsco
Concon
Argsph
Lamcro
Capape
Argsph
Lepbos
Heldac
Chlaga
Gadarg
Phyble
Hymita
Coecae
Synpha
Stoboa
D (500-800m)
Hopmed
Lopbud
Lamcro
Phyble
Symlig
Leplep
Percat
Nezaeq
Macsco
Nemsco
Notbon
Arcris
Stoboa
Lamcro
Hopmed
Stoboa
Eveval
Symlig
Epitel
Concon
Percat
Nezaeq
Notbon
Phyble
E (800-1400m)
Leplep
Batmed
Lamcro
Trasca
Nezaeq
Chaslo
Polris
Aleros
Notbon
Stoboa
Lamcro
Aleros
Melatl
Mormor
Leplep
Batmed
Nezaeq
Notbon
F (1400-2200m)
Batmed
Leplep
Catall
Coemed
Corgue
Polris
Eveval
Notbon
Aleros
Lamcro
Notelo
Aleros
Leplep
Catall
Corgue
Coemed
Batmed
RW2
RW1
PCoA2
PCoA1
>40%
25-40%
10-25%
5-10%
1-5%
0.5-1%
0-0.5%

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 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.

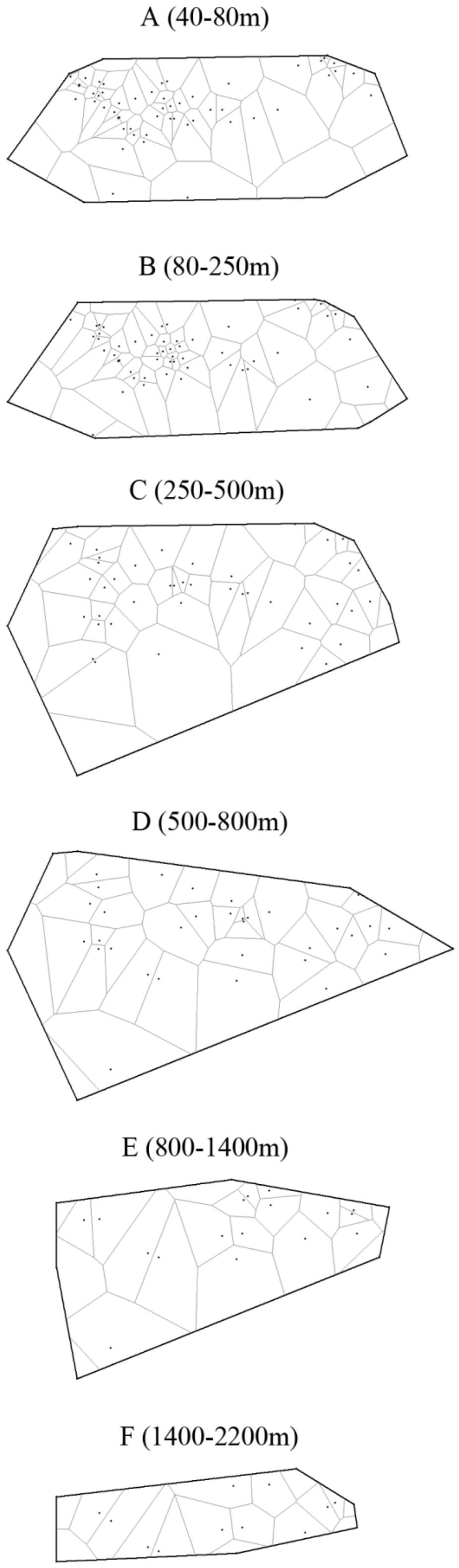


Figure 5. Representation of the Voronoi polygons from the morphospace RW1-RW2 for each assemblage along the bathymetric gradient. Each species are represented by a point.

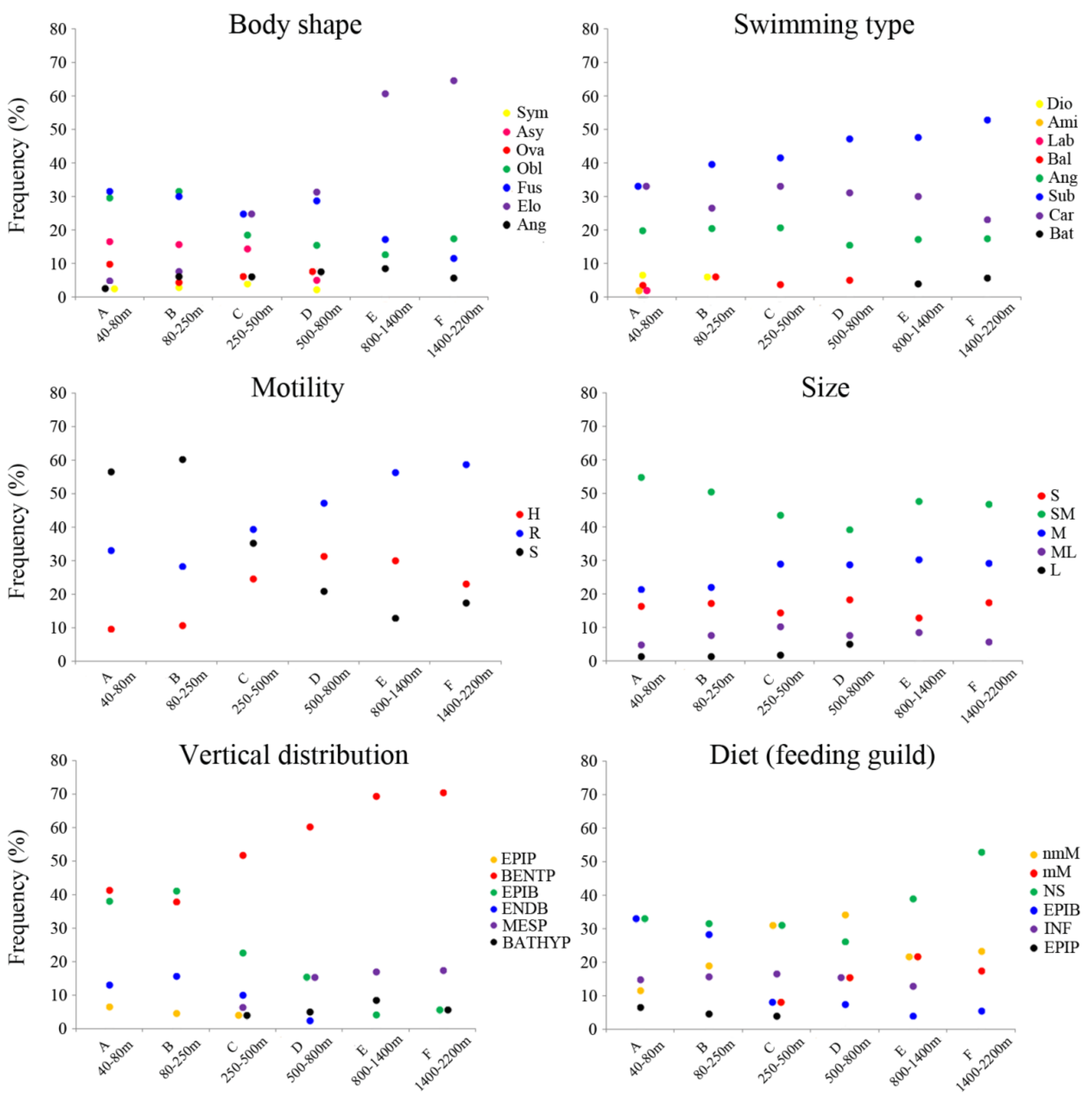


Figure 6. Changes of the occurrence frequency of the functional traits along the bathymetric range. Points of colours represent the different categories within each functional trait; *X* axis represents the assemblages with depth and *Y* axis the occurrence frequency (% of species) of each functional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

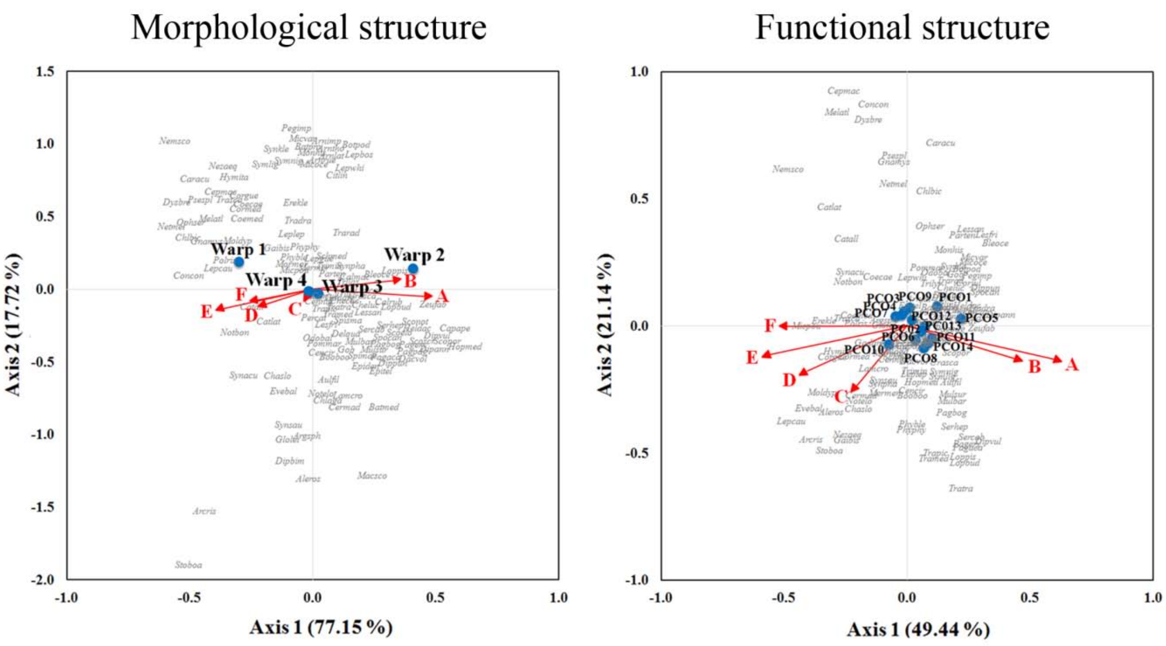


Figure 7. Redundancy analysis (RDA) applied to the morphological and to the functional structure based on presence/absence data of species. The percentage of explained variance by the first two axes is provided. The vectors in red represent each assemblage, and the blue point represents the position 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 intermediate depths 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 both the continental shelf and upper slope, 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.

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.

	Morphological			Functional			
Assemblages	*MD*	*EMI*	*MR*	*Feve*	*Fdiv*	*Fdis*	*FR*
A (40-80 m)	0.050	0.124	7.301	0.336	0.799	0.181	1.463
B (80-250 m)	0.045	0.115	7.138	0.301	0.858	0.172	1.575
C (250-500 m)	0.060	0.147	6.916	0.207	0.873	0.178	1.263
D (500-800 m)	0.067	0.174	6.420	0.389	0.916	0.172	1.226
E (800-1400 m)	0.078	0.185	4.059	0.374	0.948	0.191	1.150
F (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-Wienner diversity index.

	GOC73				OTSB-14			
	S		*H'*		S		*H'*	
Assemblages	Mean	SD	Mean	SD	Mean	SD	Mean	SD
A (40-80 m)	19.4	4.90	2.528	0.23	-	-	-	-
B (80-250 m)	24.1	4.93	2.582	0.34	20.3	2.31	1.529	0.14
C (250-500 m)	23.1	4.38	2.551	0.21	16.2	2.37	1.684	0.26
D (500-800 m)	13.6	3.20	2.173	0.39	17.2	3.16	2.062	0.42
E (800-1400 m)	-	-	-	-	14.1	2.83	1.827	0.29
F (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 indices considering species abundance (*H'*) agree with this trend (especially over the slope), 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 faunistic zonation with depth in the northwestern Mediterranean, which identified a bathymetric zonation of fish assemblages associated with the different levels of the slope (Stefanescu et al., 1992, 1993): the assemblage of the middle slope (1000-1400 m) and the less diversified assemblage of the lower slope (1400-2200 m), separated by a critical boundary of reduction of food availability (1200-1400 m) because it 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 determined 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, abundance 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 optimal 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 zooplankcton/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. In parallel, the diversity indices agreed with these trends: *MD* and *EMI* significantly increased with depth, confirming the expansion of the morphospace and the lower morphological redundancy in the deeper assemblages, 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 (*Feve* and *Fdis*), which remained relatively constants along the bathymetry. In contrast, functional divergence (*Fdiv*) 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 despite the reduction of prey hunting and the increasing consumption of suprabenthos. 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 in terms of variability of different functions.

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, and as corroborated by the present study, this tendency seemed to be linked to the almost exclusive use of 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 dypterigia*, 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 somehow agree with the visual-interactions hypothesis (Childress et al., 1995; Seibel and Drazen 2007), though we are discussing such trends in benthopelagic fish. For midwater fauna, this hypothesis links the reduction of metabolic rates of deep-living organisms to the light availability. The progressive loss of light with depth and the clear diet shift from macroplankton to suprabenthos prey (below *ca.* 1200 m in our case) would favor the selection towards less energetic locomotion strategies and lower metabolic rates, since downwards, in darker environments, the search of less mobile prey (suprabenthos) instead to mobile zooplankton would contribute to the reduction of the locomotor activity of predators. 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).

Given the low energetic turnover and food availability in deep-sea ecosystems, feeding habits represent a key aspect of the species adaptation as depth increases (Maynou and Cartes, 1998). The 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; Cartes and Carrassón, 2004; Papiol et al., 2012). To survive this food scarcity and coexist, deep-sea fishes have developed efficient resource partitioning strategies based on the bathymetric substitution and segregation of predators and the size and swimming capacity of the available prey near the bottom (Cartes, 1998; Carrassón and Cartes, 2002; Cartes et al., 2002, 2009b; Papiol et al., 2013). According to the literature, we found a predominance of suprabenthic and, to a lesser extent, macroplanktonic wandering feeders inhabiting benthopelagic habits in the deepest assemblages (below 800-1000 m) (Carrassón and Cartes, 2002). In addition, the 250 m layer represented a transitional boundary, the shelf-slope break, regarding the feeding habits of species. For instance, 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, 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 this depth until the deepest assemblage, where they decreased due to the reduction of mesopelagic (*A. risso*, *Ceratoscopelus maderensis*) and bathypelagic (*S. boa*) species. There, we found that nectobenthos-suprabenthos feeders (*B. mediterraneus*, *Coryphaenoides* spp., *Lepidion* spp., *Cataetyx* spp.) increased as the most dominant guild, supporting the hypothesis that lower slope species are trophically adapted to essentially prey on a unique compartment (the suprabenthos) because zooplankton and benthos clearly decrease at these levels (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, progressively decrease 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.

Acknowledgements

Data of this study was obtained and financed within the framework of the projects MEDER, financed by the Spanish Institute of Oceanography (IEO), and ANTROMARE (Ref. CTM2009-12214-C02-01-MAR). The authors thank all people enrolled in these projects and that helped to collect all the data. Marc Farré Foix acknowledges a pre-doctoral grant and a tuition fee to third cycle grant from the Government of Andorra, ATC010-AND and AMTC010-AND/2014, academic years: 2013-2014 and 2014-2015.

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 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 (Zeldtich 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 landamarks 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 (Zeldtich 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*, Zeldtich 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; Lyashevska 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 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 was 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 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.

11

References

Adams, D.C., 1999. Methods for shape analysis of landmark data from articulated structures. Evol. Ecol. Res. 1, 959-970.

Adams, D.C., Rohlf, F.J., Slice D.E., 2004. Geometric morphometrics: ten years of progress following the ‘revolution’. It. J. Zool. 71, 5-16.

Adams, D.C., Rohlf, F.J., Slice D.E., 2013. A field comes of age: geometric morphometrics in the 21st century. Hystrix It. J. Mamm. 24, 7-14.

Akin, S., Buhan, E., Winemiller, K.O., Yilmaz, H., 2005. Fish assemblage structure of Koycegiz Lagoon-Estuary, Turkey: spatial and temporal distribution patterns in relation to environmental variation. Estuar. Coast. Shelf Sci. 64, 671-684.

Albertson, R.C., Kocher, T.D., 2005. Genetic architecture sets limits on transgressive segregation in hybrid cichlid fishes. Evolution 59(3), 686-690.

Albouy, C., Guilhaumon, F., Villéger, S., Mouchet, M., Mercier, L., Culioli, J.M., Tomasini, J.A., Le Loc’h, F., Mouillot, D., 2011. Predicting trophic guild and diet overlap from functional traits: statistics, opportunities, and limitations for marine ecology. Mar. Ecol. Prog. Ser. 436, 17-28.

Allen, J.A., 1907. The Influence of Physical Conditions in the Genesis of Species. Sci. Am. 63, 26247-26248.

Almany, G.R., 2004. Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? Oikos 106, 275-284.

Amaral, A.R., Coelho, M.M., Marugán-Lobón, J., Rohlf F.J., 2009. Cranial shape differentiation in three closely related delphinid cetacean species: Insights into evolutionary history. Zoology 112, 38-47.

Ambrosio, P.P., Costa, C., Sánchez, P., Flos, R., 2008. Stocking density and its influence on shape of Senegalese sole adults. Aquacult Int. 16, 333-343.

Anderson, R.M., Gordon, D.M., Crawley, M.J., Hassell, M.P., 1982. Variability in the abundance of animal and plant species. Nature 296, 245-248.

Angeles, A.D.J., Gorospe, J.G., Torres, M.A.J., Demayo, C.G., 2014. Length-weight relationship, body shape variation and asymmetry in body morphology of *Siganus guttatus* from selected areas in five Mindanao bays. Int. J. Aqu. Sci. 5, 40-57.

Antonucci, F., Costa, C., Aguzzi, J., Cautadella, S., 2009. Ecomorphology of morpho-functional relationships in the family of Sparidae: A quantitative statistic approach. J. Morphol. 270, 843-855.

Azzurro, E., Tuset, V.M., Lombarte, A., Maynou, F., Simberloff, D., Rodríguez-Pérez, A., Solé, R.V., 2014. External morphology explains the success of biological invasions. Ecol. Lett. 17, 1455-1463.

Barros, F., Underwood, A.J., Lindegarth, M., 2001. The influence of rocky reefs on structure of benthic macrofauna in nearby soft-sediments. Estuar. Coast. Shelf Sci. 52, 191-199.

Bastir, M., Rosas, A., 2004. Comparative ontogeny in humans and chimpanzees: Similarities, differences and paradoxes in postnatal growth and development of the skull. Ann. Anat. 186, 503-509.

Bellwood, D.R., Wainwright, P.C., Fulton, C.J., Hoey, A.S., 2006. Functional versatility supports coral reef biodiversity. Proc. R. Soc. B 273, 101-107.

Bertrand, J.A., Gil de Sola, L., Papaconstantinou, C., Relini, G., Souplet, A., 2002. The general specifications of the MEDITS surveys*. Sci. Mar. 66(2), 9-17.

Bianchi, G., 1992. Study of the demersal assemblages of the continental shelf and upper slope off Congo and Gabon, based on the trawl surveys of the RV "Dr Fridtjof Nansen’. Mar. Ecol. Prog. Ser. 85, 9-23.

Blake, R.W., 2004. Fish functional design and swimming performance. J. Fish Biol. 65, 1193-1222.

Bock, W.J., 1990. From biologische anatomie to ecomorphology. Neth. J. Zool. 40(1-2), 254-277.

Bock, W.J., von Wahlert, G., 1965. Adaptation and the form-function complex. Evolution 19, 269-299.

Böker, H., 1935. Vergleichende biologische Anatomie der Wirbeltiere. Jena, G. Fischer Verlag.

Bookstein, F.L., 1991. Morphometric Tools for Landmark Data. Geometry and Biology. Cambridge University Press, New York.

Bookstein F.L., 1997. Landmark methods for forms without landmarks: localizing group differences in outline shape. Med. Image Anal. 1, 225-243.

Bookstein, F.L., 1998. A hundred years of morphometrics. Acta Zool. Acad. Sci. Hung. 44, 7-59.

Bookstein, F.L., Schäfer, K., Prossinger, H., Seidler, H., Fieder, M., Stringer, C., Weber, G.W., Arsuaga, J.L., Slice, D.E., Rohlf, F.J., Recheis, W., Mariam, A.J., Marcus, L.F., 1999. Comparing frontal cranial profiles in archaic and modern *Homo* by morphometric analysis. Anat. Rec. 257, 217-224.

Borazjani, I., Sotiropoulos, F., 2009. Numerical investigation of the hydrodynamics of anguilliform swimming in the transitional and inertial flow regimes. J. Exp. Biol. 212, 576-592.

Bordes, F., Wienerroither, R., Uiblein, F., Moreno, T., Bordes, I., Hernàndez, V., Caballero, C., 2009. Catálogo con las especies meso y batipelágicas. Peces, moluscos y crustáceos. Colectadas con arrastre en las islas Canarias durante las campañas a bordo del B/E “La Bocaina”. ICCM-ASCII-Gobierno de Canarias. Las Palmas, Spain.

Brusatte, M.L., Sakamoto, M., Montanari, S., Harcourt Smith W.E.H., 2012. The evolution of cranial form and function in theropod dinosaurs: insights from geometric morphometrics. J. Evol. Biol. 25, 365-377.

Bugas Jr., P.E., Copeland, J.R., Murphy, B., 2009. Virginia Master Naturist Training Manual. Virginia.

Cadotte, M.W., Davies, T.J., Regetz, J., Kembel, S.W., Cleland, E., Oakley, T.H., 2010. Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. Ecol. Lett. 13, 96-105.

Cadrin, S.X., 2000. Advances in morphometric identification of fishery stocks. Rev. Fish Biol. Fisher. 10, 91-112.

Cadrin, S.X., Friedland, K.D., 1999. The utility of image processing techniques for morphometric analysis and stock identification. Fish. Res. 43, 129-139.

Campbell, N., Neat, F., Burns, F., Kunzlik, P., 2011. Species richness, taxonomic diversity, and taxonomic distinctness of the deep-water demersal fish community on the Northeast Atlantic continental slope (ICES Subdivision VIa). ICES J. Mar. Sci. 68, 365-376.

Cardini, A., O'Higgins, P., 2004. Patterns of morphological evolution in *Marmota* (Rodentia, Sciuridae): geometric morphometrics of the cranium in the context of marmot phylogeny, ecology and conservation. Biol. J. Linn. Soc. 82, 385-407.

Carrassón, M., Cartes, J.E., 2002. Trophic relationships in a Mediterranean deep-sea fish community: Partition of food resources, dietary overlap and connections within the benthic boundary layer. Mar. Ecol. Prog. Ser. 241, 41-55.

Carrassón, M., Matallanas, J., 2001. Feeding ecology of the Mediterranean spiderfish, *Bathypterois mediterraneus* (Pisces: Chlorophthalmidae), on the western Mediterranean slope. Fish. Bull. 99(2), 266-274.

Cartes, J.E., 1998. Dynamics of the bathyal Benthic Boundary Layer in the northwestern Mediterranean: depth and temporal variations in macrofaunal-megafaunal communities and their possible connections within deep-sea trophic webs. Prog. Oceanogr. 41, 111-139.

Cartes, J.E., Abelló, P., Lloris, D., Carbonell, A., Torres, P., Maynou, F., Gil de Sola, L., 2002. Feeding guilds of western Mediterranean demersal fish and crustaceans: an analysis based on a spring survey*. Sci. Mar. 66, 209-220.

Cartes, J.E., Carrassón, M., 2004. Influence of trophic variables on the depth-range distributions and zonation rates of deep-sea megafauna: the case of the Western Mediterranean assemblages. Deep Sea Res. I 51, 263-279.

Cartes, J.E., Fanelli, E., López-Pérez, C., Lebrato, M., 2013. Deep-sea macroplankton distribution (at 400 to 2300 m) in the northwestern Mediterranean in relation to environmental factors. J. Marine Syst. 113-114, 75-87.

Cartes, J.E., Hidalgo, M., Papiol, V., Massutí, E., Moranta, J., 2009a. Changes in the diet and feeding of the hake *Merluccius merluccius* at the shelf-break of the Balearic Islands: influence of the mesopelagic-boundary community. Deep Sea Res. I 56, 344-365.

Cartes, J.E., Mamouridis, V., Fanelli, E., 2011. Deep-sea suprabenthos assemblages (Crustacea) off the Balearic Islands (western Mediterranean): Mesoscale variability in diversity and production. J. Sea Res. 65, 340-354.

Cartes, J.E., Maynou, F., Fanelli, E., López-Pérez, C., Papiol, V., 2015. Changes in deep-sea fish and crustacean communities at 1000–2200 m in the Western Mediterranean after 25 years: Relation to hydro-climatic conditions. J. Marine Syst. 143, 138-153.

Cartes, J.E., Maynou, F., Fanelli, E., Romano, C., Mamouridis, V., Papiol, V., 2009b. The distribution of megabenthic, invertebrate epifauna in the Balearic Basin (western Mediterranean) between 400 and 2300 m: Environmental gradients influencing assemblages composition and biomass trends. J. Sea Res. 61, 244-257.

Cartes, J.E., Maynou, F., Lloris, D., Gil de Sola, L., Garcia, M., 2009c. Influence of trawl type on the composition and diversity of deep benthopelagic fish and decapod assemblages off the Catalan coasts (western Mediterranean). Sci. Mar. 73(4), 725-737.

Cartes, J.E., Maynou, F., Moranta, J., Massutí, E., Lloris, D., Morales-Nin, B., 2004. Patterns of bathymetric distribution among deep-sea fauna at local spatial scale: comparison of mainland vs. insular areas. Prog. Oceanogr. 60, 29-45.

Cartes, J.E., Papiol, V., Guijarro, B., 2008. The feeding and diet of the deep-sea shrimp *Aristeus antennatus* off the Balearic Islands (Western Mediterranean): Influence of environmental factors and relationship with the biological cycle. Prog. Oceanogr. 79, 37-54.

Cartes, J.E., Sardà, F., 1993. Zonation of deep-sea decapod fauna in the Catalan Sea (Western Mediterranean). Mar. Ecol. Prog. Ser. 94, 27-34.

Carvajal-Rodríguez, A., Conde-Padín, P., Rolán-Álvarez, E., 2005. Decomposing shell form into size and shape by geometric morphometric methods in two sympatric ecotypes of *Littorina saxatilis*. J. Mollus. Stud.71, 313-318.

Casanoves, F., Di Renzo, J.A., Pla, L., 2008. User Manual FDiversity: Statistical software for the analysis of functional diversity, 1rst Edition, Argentina.

Caumul, R., Polly, P.D., 2005. Phylogenetic and Environmental components of morphological variation: skull, mandible, and molar shape in marmots (*Marmota*, Rodentia). Evolution 59(11), 2460-2472.

Cavalcanti, M.J., Monteiro, L.R., Lopes, P.R.D., 1999. Landmark-based morphometric analysis in selected species of serranid fishes (Perciformes: Teleostei). Zool. Stud. 38, 287-294.

Chakrabarty, P., 2005. Testing conjectures about morphological diversity in cichlids of lakes Malawi and Tanganyika. Copeia 2005(2), 359-373.

Charbonnel, E., Serre, C., Ruitton, S., Harmelin, J.G., Jensen, A., 2002. Effects of increased habitat complexity on fish assemblages associated with large artificial reef units (French Mediterranean coast). ICES J. Mar. Sci. 59, 208-213.

Childress, J.J., 1995. Are there physiological and biochemical adaptations of metabolism in deep-sea animals? Trends Ecol. Evol. 10, 30-36.

Childress, J.J., Seibel, B.A., 1998. Life At Stable Low Oxygen Levels: Adaptations of Animals To Oceanic Oxygen Minimum Layers. J. Exp. Biol. 201, 1223-1232.

Ciampaglio, C.N., Kemp, M., McShea, D.W., 2001. Detecting changes in morphospace occupation patterns in the fossil record: characterization and analysis of measures of disparity. Paleobiology 27, 695-715.

Clabaut, C., Bunje, P.M.E., Salzburger, W., Meyer, A., 2007. Geometric morphometric analyses provide evidence for the adaptative caracter of the Tanganyikan cichlid fish radiations. Evolution 61, 560-578.

Clark, P.J., Evans, F.C., 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35(4), 445-453.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v. 6: User Manual/Tutorial. PRIMER-E, Plymouth, 192 pp.

Clarke, K.R., Warwick, R.M., 1998. A taxonomic distinctness index and its statistical properties. J. Appl. Ecol. 35, 523-531.

Clarke, K.R., Warwick, R.M., 2001. A further biodiversity index applicable to species lists, variation in taxonomic distinctness. Mar. Ecol. Prog. Ser. 216, 265-278.

Claude, J., Paradis, E., Tong, H., Auffray, J.C., 2003. A geometric morphometric assessment of the effects of environment and cladogenesis on the evolution of the turtle shell. Biol. J. Linn. Soc. 79, 485-501.

Claudet, J., García-Charton, J.A., Lenfant, P., 2011. Combined effects of levels of protection and environmental variables at different spatial resolutions on fish assemblages in a marine protected area. Conserv. Biol. 25(1), 105-114.

Claudet, J., Pelletier, D., Jouvenel, J.Y., Bachet, F., Galzin, R., 2006. Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: Identifying community-based indicators. Biol. Conserv. 130, 349-369.

Claverie, T., Wainwright, P.C., 2014. A Morphospace for Reef Fishes: Elongation Is the Dominant Axis of Body Shape Evolution. PLoS One 9, e112732.

Cody, M.L., Mooney, H.A., 1978. Convergence versus nonconvergence in mediterranean-climate ecosystems. Ann. Rev. Ecol. Syst. 9, 265-321.

Colgate, J.E., Lynch, K.M., 2004. Mechanics and control of swimming: a review. IEEE J. Oceanic Eng. 29 (3), 660-673.

Collin, S.P., Partridge, J.C., 2006. Retinal specializations in the eyes of deep-sea teleost. J. Fish Biol. 49, 157-174.

Colloca, F., Cardinale, M., Belluscio, A., Ardizzone, G., 2003. Pattern of distribution and diversity of demersal assemblages in the central Mediterranean sea. Estuar. Coast. Shelf Sci. 56, 469-480.

Consoli, P., Romeo, T., Ferraro, M., Sarà, G., Andaloro, F., 2013. Factors affecting fish assemblages associated with gas platforms in the Mediterranean Sea. J. Sea Res. 77, 45-52.

Cooper, W.J., Parsons, K., McIntyre, A., Kern, B., McGee-Moore, A., Albertson, R.C., 2010. Bentho-Pelagic Divergence of Cichlid Feeding Architecture Was Prodigious and Consistent during Multiple Adaptive Radiations within African Rift-Lakes. PLoS One 5(3): e9551.

Cooper, W.J., Westneat, M.W., 2009. Form and function of damselfish skulls: rapid and repeated evolution into a limited number of trophic niches. BMC Evol. Biol. 9, 24.

Cornwell, W.K., Schwilk, D.W., Ackerly, D., 2006. A trait-based test for habitat filtering: convex hull volume. Ecology 87 (6), 1465-1471.

Corti, M., 1993. Geometric morphometrics: An extension of the revolution. Trends Ecol. Evol. 8, 302.303.

Costa, C., Cataudella, S., 2007. Relationship between shape and trophic ecology of selected species of Sparids of the Caprolace coastal lagoon (Central Tyrrhenian sea). Environ. Biol. Fish. 78, 115-123.

Crespi-Abril, A.C., Morsan, E.M., Barón, P.J., 2010. Analysis of the ontogenetic variation in body and beak shape of the Illex argentinus inner shelf spawning groups by geometric morphometrics. J. Mar. Biol. Ass. UK 90(3), 547-553.

D'Onghia, G., Politou, C.Y., Bozzano, A., Lloris, D., Rotllant, G., Sion, L., Mastrototaro, F., 2004. Deep-water fish assemblages in the Mediterranean Sea*. Sci. Mar. 68, 87-99.

Dale, M.R.T., Fortin, M.J., 2010. From graphs to spatial graphs. Annu. Rev. Ecol. Evol. Syst. 41, 21-38.

Danovaro, R., Gambi, C., Dell'Anno, A., Corinaldesi, C., Fraschetti, S., Vanreusel, A., Vincx, M., Gooday, A.J., 2008. Exponential Decline of Deep-Sea Ecosystem Functioning Linked to Benthic Biodiversity Loss. Curr. Biol. 18, 1-8.

Darwin, C., 1859. On the origin of species by means of natural selection, or the preservation of favored races in the struggle for life. Murray, London.

Davenport, J., 1994. How and why do flying fish fly? Rev. Fish Biol. Fisher. 40, 184-214.

Davis, J.C., 1986. Statistics and data analysis in geology. John Wiley & Sons, New York.

Davis, M.P., Chakrabarty, P., 2011. Tripodfish (Aulopiformes: *Bathypterois*) locomotion and landing behaviour from video observation at bathypelagic depths in the Campos Basin of Brazil. Mar. Biol. Res. 7, 297-303.

De Busserolles, F., Fitzpatrick, J.L., Paxton, J.R., Marshall, N.J., Collin, S.P., 2013. Eye-Size Variability in Deep-Sea Lanternfishes (Myctophidae): An Ecological and Phylogenetic Study. PLoS One 8, e58519.

De Juan, S., Demestre, M., Thrush, S.F., 2009. Defining ecological indicators of trawling disturbance when everywhere that can be fished is fished: A Mediterranean case study. Mar. Policy 33, 472-478.

De Juan, S., Lo Iacono, C., Demestre, M., 2013. Benthic habitat characterisation of soft-bottom continental shelves: Integration of acoustic surveys, benthic samples and trawling disturbance intensity. Estuar. Coast. Shelf Sci. 117, 199-209.

De Juan, S., Thrush, S.F., Demestre, M., 2007. Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea)**.** Mar. Ecol. Prog. Ser. 334, 117-129.

De Schepper, N., De Kegel, B., Adriaens, D., 2007. Morphological specializations in Heterocongrinae (Anguilliformes: Congridae) related to burrowing and feeding. J. Morphol. 268, 343-356.

De Witt, F.A., Cailliet, G.M., 1972. Feeding habits of two bristlemouth fishes, *Cyclothone acclidens* and *C. signata* (Gonostomatidae). Copeia 3, 868-871.

Degrange, F.J., Picasso, M.B.J., 2010. Geometric morphometrics of the skull of Tinamidae (Aves, Palaeognathae). Zoology 113, 334-338.

Demestre, M., Sánchez, P., Abelló, P., 2000a. Demersal fish assemblages and habitat characteristics on the continental shelf and upper slope on the north-western Mediterranean. J. Mar. Biol. Ass. UK 80, 981-988.

Demestre, M., Sánchez, P., Kaiser, M., 2000b. The behavioural response of benthic scavengers to otter-trawling disturbance in the Mediterranean. In: Kaiser, M.J., de Groot, S.J. (Eds.) Effects of fishing on non-target species and habitats. Blackwell Science, Oxford, pp 121-129.

Demestre, M. Sbrana, M., Alvarez, F., Sánchez, P., 1997. Analysis of the interaction of fishing gear in *Mullus barbatus* fisheries of the Western Mediterranean. J. Appl. Ichtyol. 13. 49-56.

Di Renzo, J.A., Casanoves, F., Pla, L., 2008. FDiversity, version 2008.

Dixon, P.M., 2002. Ripley's K function. In: El-Shaarawi A.H., Piergorsch W.W. (Eds.), Encyclopedia of Environmetrics, vol. 3, John Wiley & Sons, New York, USA, pp. 1796-1803.

Dobzhansky, T., 1937. Genetics and the Origin of Species. Columbia University Press.

Dornburg, A., Sidlauskas, B., Santini, F., Sorenson, L., Near, T.J., Alfaro, M.E., 2011. The influence of an innovative locomotor strategy on the phenotypic diversification of triggerfish (Family: Balistidae). Evolution 65(7), 1912-1926.

Douglas, M.E., Matthews, W.J., 1992. Does morphology predict ecology? Hypothesis testing within a freshwater stream fish assemblage. Oikos 65, 213-224.

Drazen, J.C., 2007. Depth related trends in proximate composition of demersal fishes in the eastern North Pacific. Deep Sea Res. I 54, 203-219.

Drazen, J.C., Haedrich, R.L., 2012. A continuum of life histories in deep-sea demersal fishes. Deep Sea Res. I 61, 34-42.

Drazen, J.C., Seibel, B.A., 2007. Depth-related trends in metabolism of benthic and benthopelagic deep-sea fishes. Limnol. Oceanogr. 52, 2306-2316.

Drew, J.A., Buxman, C.L., Holmes, D.D., Mandecki, J.L., Mungkaje, A.J., Richardson, A.C., Westneat, M.W., 2012. Biodiversity inventories and conservation of the marine fishes of Bootless Bay, Papua New Guinea. BMC Ecol. 12, 15.

Dryden, I.L., Mardia, K.V., 1998. Statistical shape analysis. John Wiley & Sons, New York, 376 p.

Dumay, O., Tari, P.S., Tomasini, J.A., Mouillot, D., 2004. Functional groups of lagoon fish species in Languedoc Roussillon, southern France. J. Fish Biol. 64, 970-983.

Eklöv, P., Svanbäck, R., 2006. Predation risk influences adaptive morphological variation in fish populations. Am. Nat. 167(3), 440-452.

Ernst, R., Linsenmair, K.E., Rodel, M.O., 2006. Diversity erosion beyond the species level: dramatic loss of functional diversity after selective logging in two tropical amphibian communities. Biol. Conserv. 133, 143-155.

Evin, A., Baylac, M., Ruedi, M., Mucedda, M., Pons, J.M., 2008. Taxonomy, skull diversity and evolution in a species complex of Myotis (Chiroptera: Vespertilionidae): a geometric morphometric appraisal. Biol. J. Linn. Soc. 95, 529-538.

Farré, M., Lombarte, A., Recasens, L., Maynou, F., Tuset, V.M., 2015. Habitat influence in the morphological diversity of coastal fish assemblages. J. Sea Res. 99, 107-117.

Farré, M., Tuset, V.M., Maynou, F., Recasens, L., Lombarte, A., 2013. Geometric morphology as an alternative for measuring the diversity of fish assemblages. Ecol. Ind. 29, 159-166.

Félix-Hackradt, F.C., Hackradt, C.W., Treviño-Otón, J., Pérez-Ruzafa, A., García-Charton, J.A., 2013. Habitat use and ontogenetic shifts of fish life stages at rocky reefs in South-western Mediterranean Sea. J. Sea Res. 88, 67-77.

Fernandez-Arcaya, U., Rotllant, G., Ramirez-Llodra, E., Recasens, L., Aguzzi, J., Flexas, M.M., Sanchez-Vidal, A., López-Fernández, P., García, J.A., Company, J.B., 2013. Reproductive biology and recruitment of the deep-sea fish community from the NW Mediterranean continental margin. Prog. Oceanogr. 118, 222-234.

Fernández de Puelles, M.L., Valencia, J., Vicente, L., 2004. Zooplankton variability and climatic anomalies from 1994 to 2001 in the Balearic Sea (Western Mediterranean). ICES J. Mar. Sci. 61, 492-500.

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M., DeClerck, F., 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecol. Lett. 12, 22-33.

Foote, M., 1993. Discordance and concordance between morphological and taxonomic diversity. Paleobiology 19, 185-204.

Foote, M., 1997. The evolution of morphological diversity. Annu. Rev. Ecol. Evol. Syst. 28, 129-152.

Fortin, M.J., Keitt, T.H., Maurer, B.A., Taper, M.L., Kaufman, D.M., Blackburn, B.M., 2005. Species' geographic ranges and distributional limits: pattern analysis and statistical issues. Oikos 108, 7-17.

Franco, A., Franzoi, P., Malavasi, S., Riccato, F., Torricelli, P., Mainardi, D., 2006. Use of shallow water habitats by fish assemblages in a Mediterranean coastal lagoon. Estuar. Coast. Shelf Sci. 66, 67-83.

Franklin, D., Oxnard, C.E., O'Higgins, P., Dadour, I., 2007. Sexual dimorphism in the subadult mandible: quantification using geometric morphometrics. J. Forensic Sci 52(1), 6-10.

Fraschetti, S., Terlizzi, A., Bussotti, S., Guarnieri, G., D'Ambrosio, P., Boero, F., 2005. Conservation of Mediterranean seascapes: analyses of existing protection schemes. Mar. Environ. Res. 59, 309-332.

Frederich, B., Adriaens, D., Vandewalle, P., 2008. Ontogenetic shape changes in Pomacentridae (Teleostei, Perciformes) and their relationships with feeding strategies: a geometric morphometric approach. Biol. J. Linn. Soc. 95, 92-105.

Friedman, M., 2010. Explosive morphological diversification of spiny-finned teleost fishes in the aftermath of the end-Cretaceous extinction. Proc. R. Soc. B 277, 1675-1683.

Froese, R., Pauly, D., (Eds.), 2011. FishBase. World Wide Web electronic publication. www.fishbase.org.

Frost, S.R., Marcus, L.F., Bookstein, F.L., Reddy, D.P., Delson, E., 2003. Cranial Allometry, Phylogeography, and Systematics of Large-Bodied Papionins (Primates:Cercopithecinae) Inferred From Geometric Morphometric Analysis of Landmark Data. Anat. Record A 275A, 1048-1072.

Fujita, T., Inada, T., Ishito, Y., 1995. Depth-gradient structure of the demersal fish community on the continental shelf and upper slope off Sendai Bay, Japan. Mar. Ecol. Prog. Ser. 118, 13-23.

Fulton, C.J., Bellwood, D.R., Wainwright, P.C., 2001. The relationship between swimming ability and habitat use in wrasses (Labridae). Mar. Biol. 139, 25-33.

Gabriel, K.R., Sokal, R.R., 1969. A new statistical approach to geographic variation analysis. Syst. Biol. 18, 259-278.

Gaertner, J.C., Bertrand, J.A., Gil de Sola, L., Durbec, J.P., Ferrandis, E., Souplet, A., 2005. Large spatial scale variation of demersal fish assemblage structure on the continental shelf of the NW Mediterranean Sea. Mar. Ecol. Prog. Ser. 297, 245-257.

Gaertner, J.C., Maiorano, P., Mérigot, B., Colloca, F., Politou, C.Y., Gil de Sola, L., Bertrand, J.A., Murenu, M., Durbec, J.P., Kallianiotis, A., Mannini, A., 2013. Large-

Scale Diversity of Slope Fishes: Pattern Inconsistency between Multiple Diversity Indices. PLoS One 8, e66753.

Gaertner, J.C., Mazouni, N., Sabatier, R., Millet, B., 1999. Spatial structure and habitat associations of demersal assemblages in the Gulf of Lions: a multicompartmental approach. Mar. Biol. 135, 199-208.

Gage, J.D., Tyler, P.A., 1991. Deep-sea biology: a natural history of organisms at the deep-sea floor. Cambridge University Press, Cambridge.

García-Charton, J.A., Pérez-Ruzafa, A., 2001. Spatial pattern and the habitat structure of a Mediterranean rocky reef fish local assemblage. Mar. Biol. 138, 917-934.

García-Charton, J.A., Pérez-Ruzafa, A., Marcos, C., Claudet, J., Badalamenti, F., Benedetti-Cecchi, L., Falcón, J.M., Milazzo, M., Schembri, P.J., Stobart, B., Vandeperre, F., Brito, A., Chemello, R., Dimech, M., Domenici, P., Guala, I., Le Diréac'h, L., Maggi, E., Planes, S., 2008. Effectiveness of European Atlanto-Mediterranean MPAs: Do they accomplish the expected effects on populations, communities and ecosystems? J. Nat. Conserv. 16, 193-221.

García-Rubies, A., 1999. Effects of fishing on community structure and on selected populations of Mediterranean coastal reef fish. Nat. Sicil. 23 (supplement), 59-81.

García-Rubies, A., Zabala, M., 1990. Effects of total fishing prohibition on the rocky fish assamblages of Medes Islands marine reserve (NW Mediterranean). Sci. Mar. 54, 317-328.

Gartner, J.V., Crabtree, R.E., Sulak, K.J., 1997. Feeding at depth. In: Randal, D.J., Farrel, A.P., (Eds.), Deep-sea fishes. Academic Press, New York, pp. 115–93.

Gaston, K.J., 1996. What is biodiversity? In: Gaston, K.J., (Ed.) Biodiversity: A Biology of Numbers and Difference, pp. 1-9. Blackwell Science, Oxford.

Gatz Jr., A.J., 1979. Community organization in fishes as indicated by morphological features. Ecology 60, 711-718.

Gayzik, F.S., Yu, M.M., Danelson, K.A., Slice, D.E., Stitzel, J.D., 2008. Quantification of age-related shape change of the human rib cage through geometric morphometrics. J. Biomech. 41, 1545-1554.

Gerber, S., Eble, G.J., Neige, P., 2008. Allometric space and allometric disparity: a developmental perspective in the macroevolutionary analysis of morphological disparity. Evolution 62, 1450-1457.

Gili, J.M., Ros, J., 1985. Study and cartography of the benthic communities of Medes Islands (NE Spain). PSZN I: Mar. Ecol. 6, 219-238.

Goatley, C.H.R., Bellwood, D.R., Bellwood, O., 2010. Fishes on coral reefs: changing roles over the past 240 million years. Paleobiology 36, 415-427.

Gómez, J.M., Bosch, J., Perfectti, F., Fernández, J.D., Abdelaziz, M., Camacho, J.P.M., 2008. Spatial variation in selection on corolla shape in a generalist plant is promoted by the preference patterns of its local pollinators. Proc. R. Soc. B 275, 2241-2249.

Gordoa, A., 2009. Characterization of the infralittoral system along the north-east Spanish coast based on sport shore-based fishing tournament catches. Estuar. Coast. Shelf Sci. 82, 41-49.

Gosline, W.A., 1994. Function and structure in the paired fins of scorpaenifom fishes. Environ. Biol. Fish. 40, 219-226.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4, 379-391.

Gratwicke, B., Speight, M.R., 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. J. Fish Biol. 66, 650-667.

Gray, J.S., 2000. The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. J. Exp. Mar. Biol. Ecol. 250, 23-49.

Guidetti, P., 2000. Differences among fish assemblages associated with nearshore *Posidonia oceanica* seagrass beds, rocky–algal reefs and unvegetated sand habitats in the Adriatic Sea. Estuar. Coast. Shelf Sci. 50, 515-529.

Guillemot, N., Kulbicki, M., Chabanet, P., Vigliola, L., 2011. Functional Redundancy Patterns Reveal Non-Random Assembly Rules in a Species-Rich Marine Assemblage. PLoS One 6, e26735.

Haddock, S.H.D., Moline, M.A., Case, J.F., 2010. Bioluminescence in the Sea. Annu. Rev. Mar. Sci. 2, 443-493.

Haedrich, R.L., Rowe, G.T., 1977. Megafaunal biomass in the deep sea. Nature 269, 141-142.

Haedrich, R.L., Rowe, G.T., Polloni, P.T., 1975. Zonation and faunal composition of epibenthic populations on the continental slope south of New England. J. Mar. Res. 33, 191-212.

Haedrich, R.L., Rowe, G.T., Polloni, P.T., 1980. The megabenthic fauna in the deep sea south of New England, USA. Mar. Biol. 57, 165-179.

Halpern, B.S., Floeter, S.R., 2008. Functional diversity responses to changing species richness in reef fish communities. Mar. Ecol. Prog. Ser. 364, 147-156.

Hammer, Ø., Harper, D.A.T., 2006. Paleontological data analysis. Blackwell Publishing, Oxford.

Harmelin-Vivien, M., Le Diréac'h, L., Bayle-Sempere, J., Charbonnel, E., García-Charton, J.A., Ody, D., Pérez-Ruzafa, A., Reñones, O., Sánchez-Jerez, P., Valle, C., 2008. Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: Evidence of fish spillover? Biol. Conserv. 141, 1829-1839.

Head, J.J., Polly, P.D., 2015. Evolution of the snake body formreveals homoplasy in amniote *Hox* gene function. Nature 520, 86-89.

Heino, J., Soininen, J., Lappalainen, J., Virtanen, R., 2005. The relationship between species richness and taxonomic distinctness in firewater organisms. Limnol. Oceanogr. 50 (3), 978-986.

Helfman, G.S., Collette, B.B., Facey, D.E., 1997. The diversity of fishes. Blackwell Science, Oxford.

Herring, P., 2002. The biology of the deep ocean. Oxford University Press, Oxford.

Hopkins, T.S., 1985. Physics of the Sea. In: Margalef, R., (Eds.), Key Environments: Western Mediterranean. Pergamon Press, New York, pp. 100-125.

Hopkins, T.L., Sutton, T.T., Lancarft, T.M., 1996. The trophic structure and predation impact of a low latitude midwater fish assemblage. Prog. Oceanogr. 38, 205-239.

Humphries, A.T., La Peyre, M.K., Kimball, M.E., Rozas, L.P., 2011. Testing the effect of habitat structure and complexity on nekton assemblages using experimental oyster reefs. J. Exp. Mar. Biol. Ecol. 409, 172-179.

Hutchings, K., Griffiths, M.H., 2005. Identity and distribution of southern African sciaenid fish species of the genus *Umbrina*. Afr. J. Mar. Sci. 27, 1-21.

Hutchinson, G.E., 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? Am. Nat. 93, 145-159.

Ibañez, A.L., Cowx. I.G., O'Higgins, P., 2007a. Geometric morphometric analysis of fish scales for identifying genera, species, and local populations within the Mugilidae. Can. J. Fish. Aquat. Sci. 64, 1091-1100.

Ibañez, C., Tedesco, P.A., Bigorne, R., Hugueny, B., Pouilly, M., Zepita, C., Zubieta, J., Oberdorff, T., 2007b. Dietary-morphological relationships in fish assemblages of small forested streams in the Bolivian Amazon. Aquat. Living Resour. 20, 131-142.

Iglésias, S.P., 2013. Actinopterygians from the North-eastern Atlantic and the Mediterranean (A natural classification based on collection specimens, with DNA barcodes and standardized photograps), Volume I (plates), Version 09, 01 april 2013. 273 pp. External link http://www.mnhn.fr/iccanam.

Ingram, T., 2011. Speciation along a depth gradient in a marine adaptive radiation. Proc. R. Soc. B 278, 613-618.

Ingram, T., 2015. Diversification of body shape in *Sebastes* rockfishes of the north-east Pacific. Biol. J. Linn. Soc. 116, 805-818.

Inoue, J.G., Miya, M., Miller, M.J., Sado, T., Hanel, R., Hatooka, K., Aoyama, J., Minegishi, Y., Nishida, M., Tsukamoto, K., 2010. Deep-ocean origin of the freshwater eels. Biol. Lett. 6, 363-366.

Jamon, M., Renous, S., Gasc, J.P., Bels, V., Davenport, J., 2007. Evidence of force exchanges during the six-legged walking of the bottom-dwelling fish, *Chelidonichthys lucerna*. J. Exp. Zool. 307A, 542-547.

Jenkins, R.E., Burkhead, N.M., 1993. Freshwater Fishes of Virginia. American Fisheries Society, Bethesda, Maryland.

Johansson, F., Söderquist, M., Bokma, F., 2009. Insect wing shape evolution: independent effects of migratory and mate guarding flight on dragonfly wings. Biol. J. Linn. Soc. 97, 362-372.

Kaliontzopoulou, A., 2011. Geometric morphometrics in herpetology: modern tools for enhancing the study of morphological variation in amphibians and reptiles. Basic Appl. Herpetol. 25, 5-32.

Kallianiotis, A., Sophronidis, K., Vidoris, P., Tselepides, A., 2000. Demersal fish and megafaunal assemblages on the Cretan continental shelf and slope (NE Mediterranean): Seasonal variation in species density, biomass and diversity. Prog. Oceanogr. 46, 429-455.

Karr, J.R., James, F.C., 1975. Eco-morphological configurations and convergent evolution of species and communities. In: Cody, M.L., Diamond, J.M. (Eds.), Ecology and Evolution of Communities. Harvard University Press, Cambridge, pp. 258-291.

Kassam, D.D., Adams, D.C., Ambali, A.J.D., Yamaoka, K., 2003. Body shape variation in relation to resource partitioning within cichlid trophic guilds coexisting along the rocky shore of Lake Malawi. Anim. Biol. 53, 59-70.

Kassam, D.D., Sato, T., Yamaoka, K. 2002. Landmark-based morphometric analysis of the body shape of two sympatric species, *Ctenopharynx pictus* and *Otopharynx* sp. “heterodon nankhumba” (Teleostei: Cichlidae), from Lake Malawi. Ichthyol. Res. 49, 340-345.

Kasumyan, A.O., 2011. Tactile reception and behavior of fish. J. Ichthyol. 51, 1035-1103.

Keast, A., Webb, D., 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinion, Ontario. J. Fish. Bd. Canada 23, 1845-1874.

Kendall, D.G., 1984. Shape-manifolds, Procrustean metrics and complex projective spaces. Bull. London Math. Soc. 16, 81-121.

Kendall, D.G., 1985. Exact distributions for shapes of random triangles in convex sets. Adv. Appl. Prob. 17, 308-329.

Killen, S.S., Atkinson, D., Glazier, D.S., 2010. The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. Ecol. Lett. 13, 184-193.

Kimmerle, E.H., Ross, A., Slice, D., 2008. Sexual dimorphism in America: geometric morphometric analysis of the craniofacial region. J. Forensic Sci. 53(1), 54-57.

Klingenberg, C.P., 2010. Evolution and development of shape: integrating quantitative approaches. Nat. Rev. Genet. 11, 623-635.

Klingenberg, C.P, Badyaev, A.V., Sowry, S.M., Beckwith, N.J., 2001. Inferring Developmental Modularity from Morphological Integration: Analysis of Individual Variation and Asymmetry in Bumblebee Wings. Am. Nat. 157, 11-23.

Klingenberg, C.P., Ekau, W., 1996. A combined morphometric and phylogenetic analysis of an ecomorphological trend: pelagization in Antarctic fishes (Perciformes: Nototheniidae). Biol. J. Linn. Soc. 59, 143-177.

Klingenberg, C.P., Magurán-Lobón, J., 2013. Evolutionary Covariation in Geometric Morphometric Data: Analyzing Integration, Modularity, and Allometry in a Phylogenetic Context. Syst. Biol. 62(4), 591-610.

Klingenberg, C.P., McIntyre, G.S., 1998. Geometric morphometrics of developmental instability: analyzing patterns of fluctuating asymmetry with Procrustes methods. Evolution 52, 1363-1375.

Kneitel, J.M., Chase, J.M., 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. Ecol. Lett. 7, 69-80.

Korn, D., Hopkins, M.J., Walton, S.A., 2013. Extinction space – A method for the quantification and classification of changes in morphospace across extinction boundaries. Evolution 67, 2795-2810.

Kovalenko, K.E., Thomaz, S.M., Warfe, D.M., 2012. Habitat complexity: approaches and future directions. Hydrobiologia 685, 1-17.

La Mesa, G., Molinari, A., Gambaccini, S., Tunesi, L., 2010. Spatial pattern of coastal fish assemblages in different habitats in North-western Mediterranean. Mar. Ecol. 32, 104-114.

Labropoulou, M., Eleftheriou, A., 1997. The foraging ecology of two pairs of congeneric demersal fish species: importance of morphological characteristics in prey selection. J. Fish Biol. 50, 324-340.

Labropoulou, M., Papaconstantinou, C., 2000. Community structure of deep-sea demersal fish in the North Aegean Sea (northeastern Mediterranean). Hydrobiologia 440, 281-296.

Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91(1), 299-305.

Langerhans, R.B., Chapman, L.J., DeWitt, T.J., 2007. Complex phenotype–environment associations revealed in an East African cyprinid. J. Evol. Biol. 20(3), 1171-1181.

Langerhans, R.B., Layman, C.A., Langerhans, A.K., Dewitt, T.J., 2003. Habitat-associated morphological divergence in two Neotropical fish species. Biol. J. Linnean Soc. 80, 689-698.

Langerhans, R.B., Layman, C.A., Shokrollahi, A.M., DeWitt, T.J., 2004. Predator-driven phenotypic diversification in *Gambusia affinis*. Evolution 58, 2305-2318.

Langerhans, R.B., Reznick, D.N., 2010. Ecology and Evolution of Swimming Performance in Fishes: Predicting Evolution with Biomechanics. In: Domenici, P., Kapoor, B.G., (Eds.), Fish Locomotion: an eco-ethological perspective, pp. 200-248.

Laurenson, C.H., Hudson, I.R., Jones, D.O.B., Priede, I.G. 2004. Deep water observations of *Lophius piscatorius* in the north-eastern Atlantic Ocean by means of a remotely operated vehicle. J. Fish Biol. 65, 947-960.

Lavin, P.A., Mcphail, J.D., 1985. The evolution of freshwater diversity in threespine stickleback (*Gasterosteus aculeatus*): site-specific differentiation of trophic morphology. Can. J. Zool. 63, 2632-2638.

Layman, C.A., Langerhans, R.B., Winemiller, K.O., 2005. Body size, not other morphological traits, characterizes cascading effects in fish assemblage composition following commercial netting. Can. J. Fish. Aquat. Sci. 62, 2802-2810.

Legendre, P., Legendre, L., 1998. Numerical Ecology, 2nd Edition. Ed. Elsevier Science.

Leisler, B., Winkler, H., 1985. Ecomorphology. Curr. Ornithol. 2, 155-186.

Letourneur, Y., Darnaude, A., Salen-Picard, C., Harmelin-Vivien, M., 2001. Spatial and temporal variations of fish assemblages in a shallow Mediterranean soft bottom area (Gulf of Fos, France). Oceanol. Acta 24, 273-285.

Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., Pawson, D., 2001. Environmental influences on regional deep-sea species diversity. Annu. Rev. Ecol. Syst. 32, 51-93.

Liao, J.C., 2002. Swimming in needlefish (Belonidae): anguilliform locomotion with fins. J. Exp. Biol. 205, 2875-2884.

Lleonart, J., Salat, J., Torres, G.J., 2000. Removing allometric effects of body size in morphological analysis. J. Theor. Biol. 205, 85-93.

Loiseau, N., Gaertner, J.C., 2015. Indices for assessing coral reef fish biodiversity: the need for a change in habits. Ecol. Evol. 5(18), 4018-4027.

Lombarte, A., Aguirre, H., 1997. Quantitative differences in the chemoreceptor systems in the barbels of two species of Mullidae (*Mullus surmuletus* and *M. barbatus*) with different bottom habitats. Mar. Biol. Prog. Ser. 150, 57-64.

Lombarte, A., Cruz, A., 2007. Otolith size trends in marine fish communities from different depth strata. J. Fish Biol. 71, 53-76.

Lombarte, A., Gordoa, A., Whitfield, A.K., James, N.C., Tuset, V.M., 2012. Ecomorphological analysis as a complementary tool to detect changes in fish communities following major perturbations in two South African estuarine systems. Environ. Biol. Fish. 94, 601-614.

Lombarte, A., Olaso, I., Bozzano, A., 2003. Ecomorphological trends in Artedidraconidae (Pisces: Perciformes: Notothenioidei) of the Weddell Sea. Antarct. Sci. 15, 211-218.

Lombarte, A., Palmer, M., Matallanas, J., Gómez-Zurita, J., Morales-Nin, B., 2010. Ecomorphological trends and phylogenetic inertia of otolith sagittae in Nototheniidae. Environ. Biol. Fish. 89, 607-618.

Lombarte, A., Rufino, M.M., Sánchez, P., 2006. Statolith identification of Mediterranean Octopodidae, Sepiidae, Loliginidae, Ommastrephidae and Enoploteuthidae based on warp analyses. J. Mar. Biol. Ass. UK 86, 767-771.

Loreau, M., 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos 91, 3-17.

Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412, 72-76.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804-808.

Losos, J.B., 1990. The evolution of form and function: Morphology and locomotor performance in West Indian *Anolis* lizards. Evolution 44, 1189-1203.

Loy, A., Bertelletti, M., Costa, C., Ferlin, L., Cataudella, S., 2001. Shape changes and growth trajectories in the early stages of three species of the genus *Diplodus* (Perciformes, Sparidae). J. Morphol. 250, 24-33.

Loy, A., Boglione, C., Cataudella, S., 1999. Geometric morphometrics and morpho-anatomy: a combined tool in the study of seabream (*Sparus aurata*, sparidae) shape. J. Appl. Ichthyol. 15, 104-110.

Loy, A., Mariani, L., Bertelletti, M., Tunesi, L., 1998. Visualizing Allometry: Geometric Morphometrics in the Study of Shape Changes in the Early Stages of the Two-Banded Sea Bream, *Diplodus vulgaris* (Perciformes, Sparidae). J. Morphol. 237, 137-146.

Lyashevska, O., Farnsworth, K.D., 2012. How many dimensions of diversity do we need? Ecol. Indic. 18, 485-492.

MacArthur, R.H., 1968. The theory of the niche. In: Lewontin, R.C., (Ed.), Population Biology and Evolution. Syracuse University Press.

Maci, S., Basset A., 2009. Composition, structural characteristics and temporal patterns of fish assemblages in non-tidal Mediterranean lagoons: A case study. Estuar. Coast. Shelf Sci. 83, 602-612.

Macpherson, E., 1994. Substrate utilisation in a Mediterranean littoral fish community. Mar. Ecol. Prog. Ser. 114, 211-218.

Macpherson, E., Duarte, C.M., 1991. Bathymetric trends in demersal fish size: is there a general relationship? Mar. Ecol. Prog. Ser. 71(2), 103-112.

Macpherson, E., García-Rubies, A., Gordoa, A., 2000. Direct estimation of natural mortality rates for littoral marine fishes using populational data from a marine reserve. Mar. Biol. 137, 1067-1076.

Macpherson, E., Gordoa, A., García-Rubies, A., 2002. Biomass size spectra in littoral fishes in protected and unprotected areas in the NW Mediterranean. Estuar. Coast. Shelf Sci. 55, 777-788.

Magnussen, E., 2002. Demersal fish assemblages of Faroe Bank: species composition, distribution, biomass spectrum and diversity. Mar. Ecol. Prog. Ser. 238, 211-225.

Magrini, S., Scoppola, A., 2010. Geometric morphometrics as a tool to resolve taxonomic problems: the case of *Ophioglossum* species (ferns). In Nimis, P.L, Lebbe, R.V., (Eds.), Tools for Identifying Biodiversity: Progress and Problems. Proceedings of the International Congress, Paris, September 2010, EUT Edizioni Università di Trieste, pp. 251-256.

Magurán-Lobón, J., Buscalioni, A.D., 2006. Avian skull morphological evolution: exploring exo- and endocranial covariation with two-block partial least squares. Zoology 109, 217-230.

Magurran, A.E., 1988. Ecological diversity and its measurement. Princeton University Press, New Jersey.

Magurran, A.E. 2013. Measuring biological diversity. John Wiley & Sons, Hoboken.

Mantel, N., 1967. The Detection of Disease Clustering and a Generalized Regression Approach. Cancer Res. 27(1), 209-220.

Marcus, L.F., 1990. Traditional morphometrics. In: Rohlf, F.J., Bookstein, F.L., (Eds.), Proceedings of the Michigan morphometrics workshop. University of Michigan Museum of Zoology, Ann Arbor, pp. 77-122.

Marcus, L.F., Hingst-Zaher, E., Zaher, H., 2000. Application of landmark morphometrics to skulls representing the orders of living mammals. Hystrix 1, 27-47.

Margalef, R., 1958. Information theory in ecology. Gen. Syst. 3, 36-71.

Martín, P., Maynou, F., Stelzenmüller, V., Sacanell, M., 2012. A small scale fishery near a rocky littoral marine reserve in the northwestern Mediterranean (Medes Islands) after two decades of fishing prohibition. Sci. Mar. 76(3), 607-618.

Martins, G.M., Faria, J., Rubal, M., Neto, A.I., 2013. Linkages between rocky reefs and soft-bottom habitats: Effects of predation and granulometry on sandy macrofaunal assemblages. J. Sea Res. 81, 1-9.

Mason, N.W.H., Lanoiselee, C., Mouillot, D., Irz, P., Argillier, C., 2007. Functional characters combined with null models reveal inconsistency in mechanisms of species turnover in lacustrine fish communities. Oecologia 153, 441-452.

Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional and functional evenness divergence: the primary of functional components diversity. Oikos 111, 112-118.

Massutí, E., Gordon, J.D.M., Moranta, J., Swan, S.C., Stefanescu, C., Merrett, N.R., 2004. Mediterranean and Atlantic deep-sea fish assemblages: differences in biomass composition and size-related structure*. Sci. Mar. 68(3), 101-115.

Massutí, E., Olivar, M.P., Monserrat, S., Rueda, L., Oliver, P. 2014. Towards understanding the influence of environmental conditions on demersal resources and ecosystems in the western Mediterranean: Motivations, aims and methods of the IDEADOS project. J. Marine Syst. 138, 3-19.

Massutí, E., Reñones, O., 2005. Demersal resource assemblages in the trawl fishing grounds off the Balearic Islands (western Mediterranean). Sci. Mar. 69(1), 167-181.

Mauchile, J., Gordon, J.D.M., 1986. Foraging strategies of deep-sea fish. Mar. Ecol. Prog. Ser. 27, 227-238.

Maynou, F., Cartes, J.E., 1998. Daily ration estimates and comparative study of food consumption in nine species of deep-water decapod crustaceans of the NW Mediterranean. Mar. Ecol. Prog. Ser. 171, 221-231.

Maynou, F., Recasens, L., Lombarte, A., 2011. Fishing tactics dynamics of a Mediterranean small-scale coastal fishery. Aquat. Living Resour. 24, 149-159.

Mayr, E., 1942. Systematics and the origin of species, from the viewpoint of a zoologist. Harvard University Press.

McClain, C.R., Johnson, N.A., Rex, M.A., 2004. Morphological disparity as a biodiversity metric in lower bathyal and abyssal gastropod assemblages. Evolution 58(2), 338-348.

McClatchie, S., Millar, R.B., Webster, F., Lester, P.J., Hurst, R., Bagley, N., 1997. Demersal fish community diversity off New Zealand: Is it related to depth, latitude and regional surface phytoplankton? Deep Sea Res. I 44, 647-667.

McCormick, M.I., 1994. Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. Mar. Ecol. Prog. Ser. 112, 87-96.

Menezes, G.M., Sigler, M.F., Silva, H.M., Pinho, M.R., 2006. Structure and zonation of demersal fish assemblages off the Azores Archipelago (mid-Atlantic). Mar. Ecol. Prog. Ser. 324, 241-260.

Mercader, L., Lloris, D., Rucabado, J.A., 2001. Tots els peixos del mar Català: Diagnosis i claus d'identificació. Institut d'Estudis Catalans, Barcelona.

Mérigot, B., Bertrand, J.A., Gaertner, J.C., Durbec, J.P., Mazouni, N., Manté, C., 2007a. The multi-component structuration of the species diversity of groundfish assemblages of the east coast of Corsica (Mediterranean Sea): Variation according to the bathymetric strata. Fish. Res. 88, 120-132.

Mérigot, B., Bertrand, J.A., Mazouni, N., Manté, C., Durbec, J.P., Gaertner, J.C., 2007b. A multi-component analysis of species diversity of groundfish assemblages on the continental shelf of the Gulf of Lions (north-western Mediterranean Sea). Estuar. Coast. Shelf Sci. 73, 123-136.

Merrett, N.R., Haedrich, R.L., 1997. Deep-sea Demersal Fish and Fisheries. Chapman & Hall, London.

Micheli, F., Halpern, B.S., 2005. Low functional redundancy in coastal marine assemblages. Ecol. Lett. 8, 391-400.

Miles, D.B., Ricklefs, R.E., Travis, J., 1987. Concordance of eco-morphological relationships in three assemblages of passerine birds. Am. Nat. 129, 347-364.

Mindel, B.L., Webb, T.J., Neat, F.C., Blanchard, J.L., 2015. A trait-based metric sheds new light on the nature of the body size–depth relationship in the deep sea. J. Anim. Ecol. 85(2), 427-436.

Miquel, J.C., Fowler, S.W., La Rosa, J., Buat-Menard, P., 1994. Dynamics of the downward flux of particles and carbon in the open northwestern Mediterranean Sea. Deep Sea Res. I 41(2), 243-261.

Mitteroecker, P., Gunz, P., 2009. Advances in Geometric Morphometrics. Evol.Biol. 36, 235-247.

Mitteroecker, P., Gunz, P., Windhage, S., Schaefer, K., 2013. A brief review of shape, form, and allometry in geometric morphometrics, with applications to human facial morphology. Hystrix It. J. Mamm. 24, 59-66.

Moermond, T.C., 1979. Habitat constraints on the behaviour, morphology, and communityt structure of *Anolis* lizards. Ecology 60, 152-164.

Montaña, C.G., Winemiller, K.O., 2010. Local-scale habitat influences morphological diversity of species assemblages of cichlid fishes in a tropical floodplain river. Ecol. Freshw. Fish 19, 216-227.

Montaña, C.G., Winemiller, K.O., Sutton, A., 2014. Intercontinental comparison of fish ecomorphology: null model tests of community assembly at the patch scale in rivers. Ecol. Monogr. 84(1), 91-107.

Monteiro, L.R., 2000. Geometric morphometrics and the development of complex structures: ontogenetic changes in scapular shape of dasypodid armadillos. Hystrix 11(1), 91-98.

Monteiro, L.R., Di Beneditto, A.P.M., Guillermo, L.H., Rivera, L.A., 2005. Allometric changes and shape differentiation of sagitta otoliths in sciaenid fishes. Fish. Res. 74, 288-299.

Morales-Nin, B., Maynou, F., Sardà, F., Cartes, J., Moranta, J., Massutí, E., Company, J., Rotllant, G., Bozzano, A., Stefanescu, C., 2003. Size influence in zonation patterns in fishes and crustaceans from deep- water communities of the Western Mediterranean. J. Northw. Atl. Fish. Sci. 31, 413-430.

Moranta, J., Massutí, E., Stefanescu, C., Palmer, M., Morales-Nin, B., 2008a. Short-term temporal variability in fish community structure at two western Mediterranean slope locations. Deep Sea Res. I 55, 866-880.

Moranta, J., Palmer, M., Massutí, E., Stefanescu, C., Morales-Nin, B., 2004. Body fish size tendencies within and among species in the deep-sea of the western Mediterranean*. Sci. Mar. 68, 141-152.

Moranta, J., Quetglas, A., Massutí, E., Guijarro, B., Hidalgo, M., Diaz, P., 2008b. Spatio-temporal variations in deep-sea demersal communities off the Balearic Islands (western Mediterranean). J. Marine Syst. 71, 346-366.

Moranta, J., Stefanescu, C., Massutí, E., Morales-Nin, B., Lloris, D., 1998. Fish community structure and depth-related trends on the continental slope of the Balearic Islands (Algerian basin, western Mediterranean). Mar. Ecol. Prog. Ser. 171, 247-259.

Morgan, C.C., 2009. Geometric morphometrics of the scapula of South American caviomorph rodents (Rodentia: Hystricognathi): Form, function and phylogeny. Mamm. Biol. 74, 497-506.

Motta, P.J., Clifton, K., Hernandez, P., Eggold, B.T., 1995a. Ecomorphological correlates in ten species of subtropical seagrass fishes: diet and microhabitat utilization. Environ. Biol. Fish. 44, 37-60.

Motta, P.J, Kotrschal, K.M., 1992. Correlative, experimental and comparative evolutionary approaches in ecomorphology. Neth. J. Zool. 42(2-3), 400-415.

Motta, P.J., Norton, S.F., Luczkovich, J.J., 1995b. Perspectives on the ecomorphology of bony fishes. Environ. Biol. Fish. 44, 11-20.

Mouillot, D., Gaillard, S., Aliaume, C., Verlaque, M., Belsher, T., Troussellier, M., Chi, T.D., 2005. Ability of taxonomic diversity indices to discriminate coastal lagoon environments based on macrophyte communities. Ecol. Indic. 5(1), 1-17.

Mouillot, D., Villéger, S., Paravaccini, V., Kulbicki, M., Arias-González, J.E., Bender, M., Chabanet, P., Floeter, S.R., Friedlander, A., Vigliola, L., Bellwood, D.R., 2014. Functional over-redundancy and high functional vulnerability in global fish faunas of tropical reefs. P. Natl. Acad. Sci. USA 111, 13757-13762.

Muntadas, A., De Juan, S., Demestre, M., 2015. Integrating the provision of ecosystem services and trawl fisheries for the management of the marine environment. Sci. Total Environ. 506-507, 594-603.

Muntadas, A., De Juan, S., Demestre, M., 2016. Assessing functional redundancy in chronically trawled benthic communities. Ecol. Ind. 61, 882-892.

Muss, B.J., Nielsen, J.G., 1999. Sea fish. Scandinavian Fishing Year Book. Hedehusene, Denmark.

Neat, F.C., Campbell, N., 2013. Proliferation of elongate fishes in the deep sea. J. Fish Biol. 83, 1576-1591.

Neige, P., 2003. Spatial patterns of disparity and diversity of the recent cuttlefishes (Cephalopoda) across the Old World. J. Biogeogr. 30, 1125-1137.

Neige, P., 2006. Morphometrics of hard structures in cuttlefish. Vie Milieu 56, 121-127.

Nelson, J.S., 2006. Fishes of the World, 4rth Edition. Ed. Wiley and Sons, New Jersey.

Norton, S.F., 1995. A functional approach to ecomorphological patterns of feeding in cottid fishes. Environ. Biol. Fish. 44, 61-78.

Norton, S.F, Luczkovich, J.J., Motta, P.J., 1995. The role of ecomorphological studies in the comparative biology of fishes. Environ. Biol. Fish. 44, 287-304.

O’Higgins, P., 2000. The study of morphological variation in the hominid fossil record: biology, landmarks and geometry. J. Anat. 197, 103-120.

Okabe, A., Boots, B., Sugihara, K., Chiu, S.N., 2009. Spatial tessellations: concepts and applications of Voronoi diagrams. John Wiley & Sons.

Olden, J.D., Poff, N.L., Bestgen, K.R., 2008. Trait synergisms and the rarity, extirpation, and extinction risk of desert fishes. Ecology 89, 847-856.

Olivar, M.P., Bernal, A., Molí, B., Peña, M., Balbín, R., Castellón, A., Miquel, J., Massutí, E., 2012. Vertical distribution, diversity and assemblages of mesopelagic fishes in the western Mediterranean. Deep Sea Res I 62, 53-69.

Ordines, F., Massutí, E., 2009. Relationships between macro-epibenthic communities and fish on the shelf grounds of the western Mediterranean. Aquat. Conserv. 19, 370-383.

Papiol, V., Cartes, J.E., Fanelli, E., Maynou, F., 2012. Influence of environmental variables on the spatio-temporal dynamics of bentho-pelagic assemblages in the middle slope of the Balearic Basin (NW Mediterranean). Deep Sea Res. I 61, 84-99.

Papiol, V., Cartes, J.E., Fanelli, E., Rumolo, P., 2013. Food web structure and seasonality of slope megafauna in the NW Mediterranean elucidated by stable isotopes: Relationship with available food sources. J. Sea Res. 77, 53-69.

Parisi-Baradad, V., Lombarte, A., Garcia-Ladona, E., Cabestany, J., Piera, J., Chic, O., 2005. Otolith shape contour analysis using affine transformation invariant wavelet transforms and curvature scale space representation. Mar. Freshw. Res. 56, 795-804.

Pavoine, S., Bonsall, M.B., 2011. Measuring biodiversity to explain community assembly: a unified approach. Biol. Rev. 86, 792-812.

Pavoine, S., Vallet, J., Dufour, A.B., Gachet, S., Daniel, H., 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. Oikos 118, 391-402.

Pease, A.A., González-Díaz, A.A., Rodiles-Hernández, R., Winemiller, K.O., 2012. Functional diversity and trait-environment relationships of stream fish assemblages in a large tropical catchment. Fresh. Biol. 57 (5), 1060-1075.

Pérès, J.M., 1985. History of the Mediterranean biota and colonisation of the depths. In: Margalef, R., (Ed.), Key Environments: Western Mediterranean. Pergamon Press, New York, pp. 198-232.

Peres-Neto, P.R., 2004. Patterns in the co-occurrence of fish species in streams: the role of site suitability, morphology and phylogeny versus species interactions. Oecologia 140, 352-360.

Perez, S.I., Bernal, V., Gonzalez, P.N., 2006. Differences between sliding semi-landmark methods in geometric morphometrics, with an application to human craniofacial and dental variation. J. Anat. 208, 769-784.

Perry, G.L.W., Miller, B.P., Enright, N.J., 2006. A comparison of methods for the statistical analysis of spatial point patterns in plant ecology. Plant. Ecol. 187, 59-82.

Pessanha Pais, M., Henriques, S., Murta, A.G., Azevedo, M., Costa, M.J., Cabral, H.N., 2010. Identifying functional homogeneity in a dynamic environment: Application to soft-substrate fish assemblages off the Portuguese coast. J. Sea Res. 89, 30-43.

Petchey, O.L., Gaston, K.J., 2002. Functional diversity (FD), species richness and community composition. Ecol. Lett. 5, 402-411.

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741-758.

Pie, M.R., Traniello, J.F.A., 2007. Morphological evolution in a hyperdiverse clade: the ant genus *Pheidole*. J. Zool. 271, 99-109.

Pielou, E.C., 1975. Ecological Diversity. Wiley, New York.

Pierce, S.E., Angielczyk, K.D., Rayfield, E.J., 2008. Patterns of Morphospace Occupation and Mechanical Performance in Extant Crocodilian Skulls: A Combined Geometric Morphometric and Finite Element Modeling Approach. J. Morphol. 269, 840-864.

Pierce, S.E., Angielczyk, K.D., Rayfield, E.J., 2009. Morphospace occupation in thalattosuchian crocodylomorphs: skull shape variation, species delineation and temporal patterns. Palaeontology 52, 1057-1097.

Pietsch, T.W., 2009. Oceanic anglerfishes: extraordinary diversity in the deep sea. University of California Press, Berkeley, California.

Pinault, M., Bissery, C., Gassiole, G., Magalon, H., Quod, J.P., Galzin, R., 2014. Fish community structure in relation to environmental variation in coastal volcanic habitats. J. Exp. Mar. Biol. Ecol. 460, 62-71.

Pitcher, T.J., 1986. Functions of shoaling behaviour in teleosts. In: Pitcher, T.J., (Ed.), The behaviour of teleost fishes, Springer US, pp. 294-337.

Ponce de León, M.S., Zollikofer, C.P.E., 2001. Neanderthal cranial ontogeny and its implications for late hominid diversity. Nature 412, 534-538.

Ponton, D., 2006. Is Geometric Morphometrics Efficient for Comparing Otolith Shape of Different Fish Species? J. Morphol. 267, 750-757.

Postl, L., Herler, J., Bauer, C., Maderbacher, M., Makasa, L., Sturmbauer, C., 2008. Geometric morphometrics applied to viscerocranial bones in three populations of the Lake Tanganyika cichlid fish Tropheus moorii. J. Zool. Syst. Evol. Res. 46, 240-248.

Powell, S.M., Haedrich, R.L., McEachran, J.D., 2003. The deep-sea demersal fish fauna of the northern Gulf of Mexico. J. Northw. Atl. Fish. Sci. 31, 19-33.

Price, S.A., Holzman, R., Near, T.J., Wainwright, P.C., 2011. Coral reefs promote the evolution of morphological diversity and ecological novelty in labrid fishes. Ecol. Lett. 14, 462-469.

Puig, P., Palanques, A., Guillén, J., García-Ladona, E., 2000. Deep slope currents and suspended particle fluxes in and around the Foix submarine canyon (NW Mediterranean). Deep Sea Res. I 47, 343-366.

Pulcini, D., Costa, C., Aguzzi, J., Cataudella, S., 2008. Light and Shape: A Contribution to Demonstrate Morphological Differences in Diurnal and Nocturnal Teleosts. J. Morphol. 269, 375-385.

Purvis, A., Hector, A., 2000. Getting the measure of biodiversity. Nature 405, 212-219.

Pusch, C., Beckmann, A., Porteiro, F.M., von Westernhagen, H., 2004. The influence of seamounts on mesopelagic fish communities. Arch. Fish. Mar. Res. 51, 165-186.

Recasens, L., Lombarte, A., Sánchez, P., 2006. Teleostean fish assemblages in an artificial reef and a natural rocky area in Catalonia (Northwestern Mediterranean): An ecomorphological approach. B. Mar. Sci. 78(1), 71-82.

Rex, M.A., 1977. Zonation in deep-sea gastropods: the importance of biological interactions to rates of zonation. In: Keenan, B.F., Ceidigh, P.O., Boaden, P.J.S. (Eds.), Biology of benthic organisms. 11th European Symposium on Marine Biology, Galway, pp. 521-530.

Rex, M.A., Etter, R.J., 1998. Bathymetric patterns of body size: implications for deep-sea biodiversity. Deep Sea Res. II 45, 103-127.

Rex, M.A., Etter, R.J., 2010. Deep-sea biodiversity: pattern and scale. Harvard University Press.

Richtsmeier, J.T., Burke Deleon, V., Lele, S.R., 2002. The Promise of Geometric Morphometrics. Yearbook Phys. Anthropol. 45, 63-91.

Ricklefs, R.E., 1990. Ecology. 3rd edition, W.H. Freeman, New York.

Ricklefs, R.E., 2010. Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. P. Natl. Acad. Sci. USA 107(4), 1265-1272.

Ricklefs, R.E., 2012. Species richness and morphological diversity of passerine birds. P. Natl. Acad. Sci. USA 109, 14482-14487.

Ricklefs, R.E., Miles, D.B., 1994. Ecological and evolutionary inferences from morphology: an ecological perspective. In: Wainwright, P.C., Reilly, S.M., (Eds.) Ecological morphology: integrative organismal biology. University of Chicago Press, pp.13-41.

Ricklefs, R.E., Travis, J., 1980. A morphological approach to the study of avian community organization. Auk 97, 321-338.

Ripley, B.D., 1979. Tests of ‘randomness’ for spatial point patterns. J. Roy. Stat. Soc. B 41, 368-374.

Rohlf, F.J., 1998. On Applications of Geometric Morphometrics to Studies of Ontogeny and Phylogeny. Syst. Biol. 47, 147-158.

Rohlf, F.J., 1999. Shape statistics: Procrustes superimpositions and tangent spaces. J. Classif. 16, 197-223.

Rohlf, F.J., 2006. TpsPls Version 1.18. Department of Ecology and Evolution, State University of New York at Stony Brook, New York.

Rohlf, F.J., 2010a. TpsDig Version 2.16. Department of Ecology and Evolution, State University of New York at Stony Brook, New York.

Rohlf, F.J., 2010b. TpsRelw Version 1.49. Department of Ecology and Evolution, State University of New York at Stony Brook, New York.

Rohlf, F.J., 2013. TpsSmall Version 1.28. Department of Ecology and Evolution, State University of New York at Stony Brook, New York.

Rohlf, F.J., Corti, M., 2000. Use of two-block partial least-squares to study covariation in shape. Syst. Biol. 49(4), 740-753.

Rohlf, F.J., Marcus, L.F. 1993. A Revolution in Morphometrics. Trends Ecol. Evol. 8, 129-132.

Rohlf, F.J., Slice, D.E., 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. Syst. Zool. 39, 40-59.

Ross, S.W., Quattrini, A.M., Roa-Varón, A.Y., McClain, J.P., 2010. Species composition and distributions of mesopelagic fishes over the slope of the north-central Gulf of Mexico. Deep Sea Res. II 57, 1926-1956.

Roxburgh, S.H., Shea, K., Wilson, J.B., 2004. The Intermediate Disturbance Hypothesis: Patch Dynamics and Mechanisms of Species Coexistence. Ecology 85(2), 359-371.

Roy, K., Balch, D.P., Helberg, M.E., 2001. Spatial patterns of morphological diversity across the Indo-Pacific: analyses using strombid gastropods. Proc. R. Soc. Lond. B 268, 2503-2508.

Roy, K., Foote, M., 1997. Morphological approaches to measuring biodiversity. Trends Ecol. Evol. 12, 277-281.

Rüber, L., Adams, D.C., 2001. Evolutionary convergence of body shape and trophic morphology in cichlids from Lake Tanganyika. J. Evolution. Biol. 14, 352-332.

Rucabado, J., Lloris, D., Stefanescu, C., 1991. OTSB-14: un arte de arrastre bentónico para la pesca profunda (por debajo de los mil metros). Informes Técnicos de Scientia Marina 165, 1-27.

Rufino, M.M., Gaspar, M.B., Pereira, A.M., Vasconcelos, P., 2006. Use of Shape to Distinguish *Chamelea gallina* and *Chamelea striatula* (Bivalvia: Veneridae): Linear and Geometric Morphometric Methods. J. Morphol. 267, 1433-1440.

Ruitton, S., Francour, P., Boudouresque, C.F., 2000. Relationships between algae, benthic herbivorous invertebrates and fishes in rocky sublittoral communities of a Temperate Sea (Mediterranean). Estuar. Coast. Shelf Sci. 50, 217-230.

Russell, E.S., 1916. Form and function: a contribution to the history of animal morphology. American edition. EP Dutton and Co., New York.

Sallan, L.C., Friedman, M., 2012. Heads or tails: staged diversification in vertebrate evolutionary radiations. Proc. R. Soc. B 279, 2025-2032.

Salvanes, A.G.V., Kristoffersen, J.B., 2001. Mesopelagic Fishes. In: Steel, J., Thorpe, S., Turekian, K., (Eds.), Encyclopedia of Ocean Sciences. Academic Press, San Diego, pp. 1711-1717.

Schoener, T.W., 1974. Resource partitioning in ecological communities. Science 185, 27-39.

Schoenfuss, H.L., Blob, R.W., 2003. Kinematics of waterfall climbing in Hawaiian freshwater fishes (Gobiidae): vertical propulsion at the aquatic–terrestrial interface. J. Zool. 261, 191-205.

Seibel, B.A., Drazen, J.C., 2007. The rate of metabolism in marine animals: environmental constraints, ecological demands and energetic opportunities. Philos. T. Roy. Soc. B 362, 2061-2078.

Selleslagh, J., Amara, R., 2008. Environmental factors structuring fish composition and assemblages in a small macrotidal estuary (eastern English Channel). Estuar. Coast. Shelf Sci. 79, 507-517.

Serb, J.M., Alejandrino, A., Otárola-Castillo, E., Adams, D.C., 2011. Morphological convergence of shell shape in distantly related scallop species (Mollusca: Pectinidae). Zool. J. Linn. Soc. 163, 571-584.

Sfakiotakis, M., Lane, D.M., Davies, J.B.C., 1999. Review of fish swimming modes for aquatic locomotion. IEEE J. Oceanic Eng. 24(2), 237-252.

Shannon, C.E., Weaver, W., 1949. The Mathematical Theory of Communication. University of Illinois Press, Illinois.

Shen, B., Dong, L., Xiao, S., Kowalewski, M., 2008. The Avalon explosion: evolution of Ediacara morphospace. Science 319, 81-84.

Shimazaki, M., Nakaya, K., 2004. Functional anatomy of the luring apparatus of the deep-sea ceratioid anglerfish *Cryptopsaras couesii* (Lophiiformes: Ceratiidae). Ichthyol. Res. 51, 33-37.

Silverman, B.W., 1986. Density estimation for statistics and data analysis. Monographs on Statistics and Applied Probability, Chapman and Hall, London.

Simberloff, D., Dayan, T., 1991. The Guild Concept and the Structure of Ecological Communities. Annu. Rev. Ecol. Syst. 22, 115-143.

Simpson, E.H., 1949. Measurement of species diversity. Nature 163, 688.

Slice, D.E., 2007. Geometric Morphometrics. Annu. Rev. Anthropol. 36, 261-81.

Smith, U.E., Hendricks, J.R., 2013. Geometric morphometric character suites as phylogenetic data: extracting phylogenetic signal from gastropod shells. Syst. Biol. 62, 366-385.

Smouse, P.E., Long, J.C., Sokal, R.R., 1986. Multiple Regression and Correlation Extensions of the Mantel Test of Matrix Correspondence. Syst. Zool. 35(4), 627-632.

Somerfield, P.J., Clarke, K.R., Warwick, R.M., Dulvy, N.K., 2008. Average functional distinctness as a measure of the composition of assemblages. ICES J. Mar. Sci. 65, 1462-1468.

Somerfield, P.J., Olsgard, F., Carr, M.R., 1997. A further examination of two new taxonomic distinctness measures. Mar. Ecol. Prog. Ser. 154, 303-306.

Stayton, C.T., 2005. Morphological Evolution of the Lizard Skull: A Geometric Morphometrics Survey. J. Morphol. 263, 47-59.

Stayton, C.T., Ruta, M., 2006. Geometric morphometrics of the skull roof of Stereospondyls (Amphibia:Temnospondyli). Palaeontology 49(2), 307-337.

Stefanescu, C., Lloris, D., Rucabado, J., 1993. Deep-sea fish assemblages in the Catalan Sea (Western Mediterranean) below a depth of 1000 m. Deep Sea Res. I 40(4), 695-707.

Stefanescu, C., Morales-Nin, B., Massutí, E., 1994. Fish assemblages on the slope in the Catalan Sea (western Mediterranean): influence of a submarine canyon. J. Mar. Biol. Assoc. UK 74(3), 499-512.

Stefanescu, C., Rucabado, J., Lloris, D., 1992. Depth-size trends in western Mediterranean demersal deep-sea fishes . Mar. Ecol. Prog. Ser. 81, 205-213.

Stelzenmüller, V., Maynou, F., Martín, P., 2007. Spatial assessment of benefits of a coastal Mediterranean Marine Protected Area. Biol. Conserv. 136, 571-583.

Stelzenmüller, V., Maynou, F., Martín, P., 2009. Patterns of species and functional diversity around a coastal marine reserve: a fisheries perspective. Aquat. Conserv. 19, 554-565.

Stergiou, K.I., Karpouzi, V.S., 2002. Feeding habits and trophic levels of Mediterranean fish. Rev. Fish Biol. Fisher. 11, 217-254.

Strauss, R.E., Bookstein, F.L., 1982. The truss: body form reconstructions in morphometrics. Syst. Biol. 31, 113-135.

Strogatz, S.H., 2001. Exploring complex networks. Nature 410, 268-276.

Sutton, T.T., 2005. Trophic ecology of the deep-sea fish *Malacosteus niger* (Pisces: Stomiidae): An enigmatic feeding ecology to facilitate a unique visual system? Deep Sea Res. I 52, 2065-2076.

Sutton, T.T., Hopkins, T.L., 1996. The species composition, abundance and vertical distribution of the stomiid (Pisces: Stomiiformes) fish assemblage of the Gulf of Mexico. B. Mar. Sci. 59, 530-542.

Svanbäck, R., Eklöv, P., 2002. Effects of habitat and food resources on morphology and ontogenetic growth trajectories in perch. Oecologia 131, 61-70.

ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 65(7), 1167-1179.

ter Braak, C.J.F., Šmilauer, P., 2002. CANOCO Reference Manual and CANODRAW for Windows User's Guide: Software for Canonical Community Ordination, Version 4.5, Microcomputer Power, Ithaca, New York.

Thompson, D.W., 1915. Morphology and mathematics. T. Roy. Soc. Edin. 50, 857-895.

Thompson, D.W., 1917. On Growth and Form. Cambridge, London.

Thurber, A.R., Sweetman, A.K., Narayanaswamy, B.E., Jones, D.O.B., Ingels, J., Hansman, R.L., 2014. Ecosystem function and services provided by the deep sea. Biogeosciences 11, 3941-3963.

Tunesi, L., Molinari, A., Salvati, E., 2006. Fish assemblage of the marine protected area of Cinque Terre (NW Mediterranean Sea): First characterization and assessment by visual census. Chem. Ecol. 22(1), 245-253.

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). Ichthyol. Res. 61, 152-158.

Tuset, V.M., Farré, M., Otero-Ferrer, J.L., Vilar, A., Morales-Nin, B., Lombarte, A., 2016. Testing otolith morphology for measuring marine fish biodiversity. Mar. Freshw. Res.

Tuset, V.M., Imondi, R., Aguado, G., Otero-Ferrer, J.L., Santschi, L., Lombarte, A., Love, M., 2015. Otolith patterns of rockfishes from the Northeastern Pacific. J. Morphol. 276, 458-469.

Tuya, F., Boyra, A., Sanchez-Jerez, P., Haroun, R.J., 2005. Multivariate analysis of the bentho-demersal ichthyofauna along soft bottoms of the Eastern Atlantic: comparison between unvegetated substrates, seagrass meadows and sandy bottoms beneath sea-cage fish farms. Mar. Biol. 147, 1229-1237.

Tyszka, J., 2006. Morphospace of foraminiferal shells: results from the moving reference model. Lethaia 39, 1-12.

Tytell, E.D., Borazjani, I., Sotiropoulos, F., Baker, T.V., Anderson, E.J., Lauder, G.V., 2010. Disentangling the functional roles of morphology and motion in the swimming of fish. Integr. Comp. Biol. 50(6), 1140-1154.

Tytell, E.D., Lauder, G.V., 2004. The hydrodynamics of eel swimming I. Wake structure. J. Exp. Biol. 207, 1825-1841.

Uiblein, F., Bordes, F., 1999. Complex trophic interactions around ocean islands. Ocean Chall. 9, 15-16.

Valentin, A., Sévigny, J.M., Chanut, J.P., 2002. Geometric morphometrics reveals body shape differences between sympatric redfish *Sebastes mentella, Sebastes fasciatus* and their hybrids in the Gulf of St Lawrence. J. Fish Biol. 60, 857-875.

Van Bocxlaer, B., Schultheiß, R., 2010. Comparison of morphometric techniques for shapes with few homologous landmarks based on machine-learning approaches to biological discrimination. Paleobiology 36, 497-515.

van der Niet, T., Zollikofer, C.P.E, Ponce de León, M.S., Johnson, S.D., Linder, H.P., 2010. Three-dimensional geometric morphometrics for studying floral shape variation. Trends Plant Sci. 15(8), 423-426.

Vergara-Solana, F.J., García-Rodriguez, F.J., Tavera, J.J., De Luna, E., De la Cruz-Agüero, J., 2014. Molecular and morphometric systematics of *Diapterus* (Perciformes, Gerreidae). Zool. Scripta 43, 338-350.

Verhaegen, Y., Adriaens, D., De Wolf, T., Dhert, P., Sorgeloos, P., 2007. Deformities in larval gilthead sea bream (Sparus aurata): A qualitative and quantitative analysis using geometric morphometrics. Aquaculture 268, 156-168.

Vieira, K.S., Arzabe, C., Hernández, M.I.M., Vieira, W.L.S., 2008. An Examination of Morphometric Variations in a Neotropical Toad Population (Proceratophrys cristiceps, Amphibia, Anura, Cycloramphidae). PLoS One 3(12), e3934.

Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology. Ecology 89(8), 2290-2301.

Villéger, S., Miranda, J.R., Hernandez, D.F., Mouillot, D., 2012. Low functional *β*-diversity despite high taxonomic *β*-diversity among tropical estuarine fish communities. PLoS One 7, e40679.

Villéger, S., Novack-Gottshall, P.M., Mouillot, D., 2011. The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. Ecol. Lett. 14, 561-568.

Villéger, S., Ramos Miranda, J., Flores Hernandez, D., Mouillot, D., 2010. Contrasting changes in taxonomic and functional diversity of tropical fish communities after habitat degradation. Ecol. Appl. 20(6), 1512-1522.

Villemant, C., Simbolotti, G., Kenis, M., 2007. Discrimination of *Eubazus* (Hymenoptera, Braconidae) sibling species using geometric morphometrics analysis of wing venation. Syst. Entomol. 32, 625-634.

Visalakshi, N.K., Thangavel, K., 2009. Impact of normalization in distributed K-means clustering. Inter. J. Soft Comput. 4, 168-172.

Viscosi, V., 2015. Geometric morphometrics and leaf phenotypic plasticity: assessing fluctuating asymmetry and allometry in European white oaks (*Quercus*). Biol. J. Linn. Soc. 179, 335-348.

Viscosi, V., Cardini, A., 2011. Leaf Morphology, Taxonomy and Geometric Morphometrics: A Simplified Protocol for Beginners. PLoS One 6, e25630.

Vorus, W.S., Taravella, B.M., 2011. Anguilliform fish propulsion of highest hydrodynamic efficiency. J. Marine Sci. Appl. 10, 163-174.

Wagner, C.E., McIntyre, P.B., Buels, K.S., Gilbert, D.M., Michel, E., 2009. Diet predicts intestine length in Lake Tanganyika's cichlid fishes. Funct. Ecol. 23, 1122-1131.

Wainwright, P.C., 1988. Morphology and Ecology: Functional Basis of Feeding Constraints in Caribbean Labrid Fishes. Ecology 69(3), 635-645.

Wainwright, P.C., Belwood, D.R., Westneat, M.W. 2002. Ecomorphology of locomotion in labrid fishes. Environ. Biol. Fish. 65, 47-62.

Wainwright, P.C., Belwood, D.R., Westneat, M.W., Grubich, J.R., Hoey, A.S., 2004. A functional morphospace for the skull of labrid fishes: patterns of diversity in a complex biomechanical system. Biol. J. Linn. Soc. 82, 1-25.

Wainwright, P.C., Reilly, S.M., 1994. Ecological morphology: integrative organismal biology. University of Chicago Press.

Wainwright, P.C., Richard, B.A., 1995. Predicting patterns of prey use from morphology of fishes. Environ. Biol. Fish. 44, 97-113.

Walker, J.A., 2010. An integrative model of evolutionary covariance: A symposium on body shape in fishes. Integr. Comp. Biol. 50(6), 1051-1056.

Ward, A.B., Mehta, R.S., 2010. Axial elongation in fishes: Using morphological approaches to elucidate developmental mechanisms in studying body shape. Integr. Comp. Biol. 50(6), 1106-1119.

Warrant, E.J., Locket, N.A., 2004. Vision in the deep sea. Biol. Rev. 79, 671-712.

Warwick, R.M., Clarke, K.R., 1995. New ‘biodiversity’ measures reveal a decrease in taxonomic distinctness with increasing stress. Mar. Ecol. Prog. Ser. 129, 301-305.

Webb, P.W., 1984. Body form, locomotion and foraging in aquatic vertebrates. Am. Zool. 24(1), 107-120.

Wedding, L.M., Friedlander, A.M., McGranaghan, M., Yost, R.S., Monaco, M.E., 2008. Using bathymetric lidar to define nearshore benthic habitat complexity: Implications for management of reef fish assemblages in Hawaii. Remote Sens. Environ. 112, 4159-4165.

Weissburg, M.J., Browman, H.I., 2005. Sensory biology: linking the internal and external ecologies of marine organisms. Mar. Ecol. Prog. Ser. 287: 263-307.

Werdelin, L., Lewis, M.E., 2013. Temporal change in functional richness and evenness in the Eastern African Plio-Pleistocene carnivoran guild. PLoS One 8, e57944.

Wiegand, T., Moloney, K.A., 2004. Rings, circles, and null-models for point pattern analysis in ecology. Oikos 104, 209-229.

Wienerroither, R., Uiblein, F., Bordes, F., Moreno, T., 2009. Composition, distribution, and diversity of pelagic fishes around the Canary Islands, Eastern Central Atlantic. Mar. Biol. 5, 328-344.

Willis, S.C., Winemiller, K.O., Lopez-Fernandez, H., 2005. Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river. Oecologia 142, 284-295.

Wills, M.A., 2001. Morphological disparity: a primer. In: Adrain, J.M., Edgecombe, G.D., Lieberman, B.S., (Eds.), Fossils, phylogeny, and form: an analytical approach. Kluwer Academic/Plenum Publishers, New York.

Wilsey, B.J, Chalcraft, D.R, Bowles, C.M., Willig, M.R., 2005. Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. Ecology 86(5), 1178-1184.

Winemiller, K.O., 1991. Ecomorphological Diversification in Lowland Freshwater Fish Assemblages from Five Biotic Regions. Ecol. Monogr. 61(4), 343-365.

Winemiller, K.O., Kelso-Winemiller, L.C., Brenkert, B.L., 1995. Ecomorphological diversification and convergence in fluvial cichlid fishes. Environ. Biol. Fish. 44, 235-261.

Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70, 164-168.

Yamanoue, Y., Setiamarga, D.H.E., Matsuura, K., 2010. Pelvic fins in teleosts: structure, function and evolution. J. Fish Biol. 77, 1173-1208.

Young, M.T., Larvan, M.D., 2010. Macroevolutionary trends in the skull of sauropodomorph dinosaurs–the largest terrestrial animals to have ever lived. In: Morphometrics for Nonmorphometricians, pp. 259-269. Springer Berlin Heidelberg.

Young, K.A., Snoeks, J., Seehausen, O., 2009. Morphological diversity and the roles of contingency, chance and determinism in African cichlid radiations. PLoS ONE 4(3), e4740.

Zar, J.H., 1996. Biostatistical Analysis, 3rd Edition. Ed. Prentice Hall, Upper Saddle River, USA.

Zelditch, M.L., Sheets, H.D., Fink, W.L., 2000. Spatiotemporal reorganitzation of growth rates in the evolution of ontogeny. Evolution 54(4), 1363-1371.

Zelditch, M.L., Sheets, H.D., Fink, W.L., 2003. The ontogenetic dynamics of shape disparity. Paleobiology 29, 139-156.

Zelditch, M.L., Swidersky, D.L., Sheeds, H.D., Fink, W.L., 2004. Geometric morphometrics for biologists: a primer. Elsevier Academic Press, London.

Zelditch, M.L., Swidersky, D.L., Sheeds, H.D., 2012. Geometric morphometrics for biologists: a primer. 2nd Edition, Elsevier Academic Press, London.

Zuanon, J., Bockmann, F.A., Sazima, I., 2006. A remarkable sand-dwelling fish assemblage from central Amazonia, with comments on the evolution of psammophily in South American freshwater fishes. Neotrop. Ichthyol. 4, 107-118.

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 anàlisis 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 obtindre 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 obtindre 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 extés, 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 mes 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 (Lyashevska and Farnsworth, 2012). Actualment, els índexs de diversitat funcional son 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 tesis 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 mes específics son 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 morfoespai, i es va establir que el mètodes d'agregació de punts son 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 anàlisis 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 anàlisi 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 decréixer 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 mostrejos heterogenis.

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 mes 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 un 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 decréixer 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.

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

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

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

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

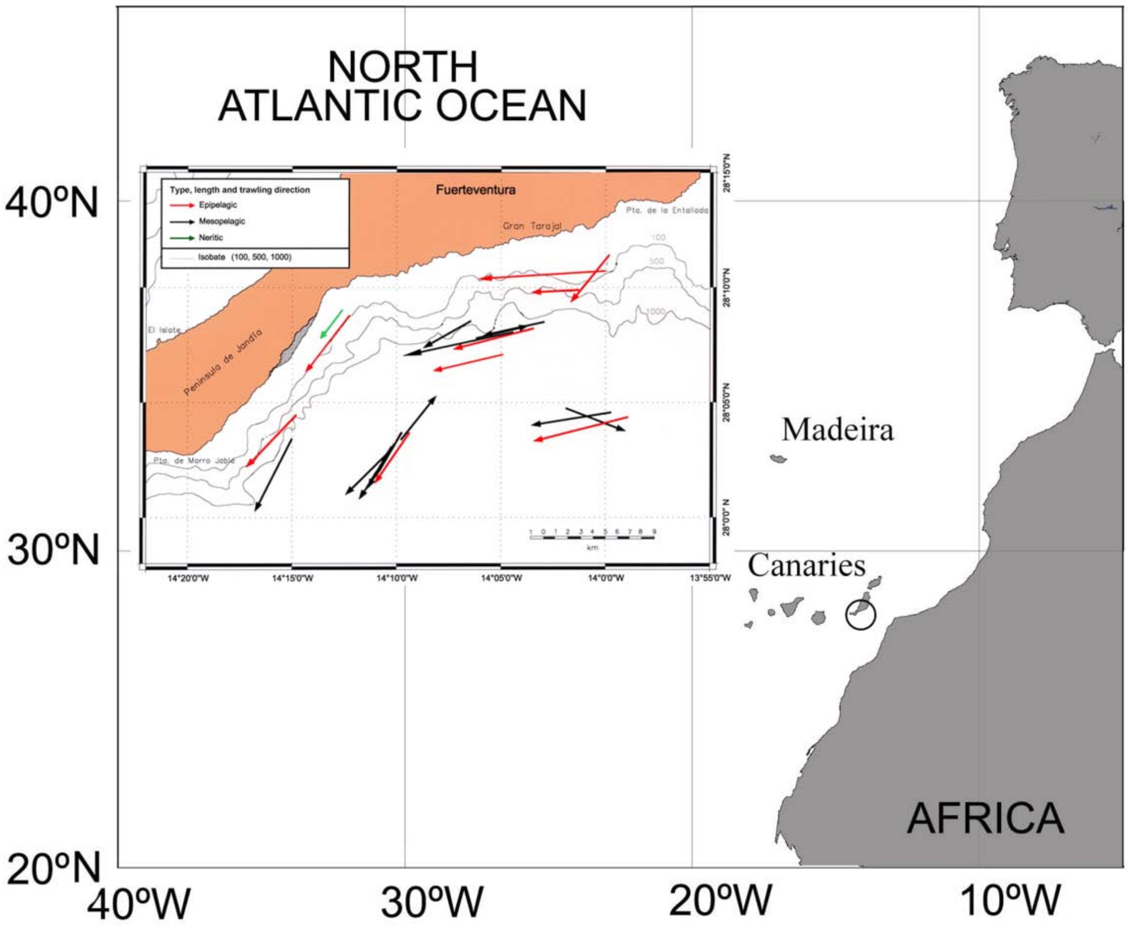


Figure S1. Localization of the study area and trawl tows.

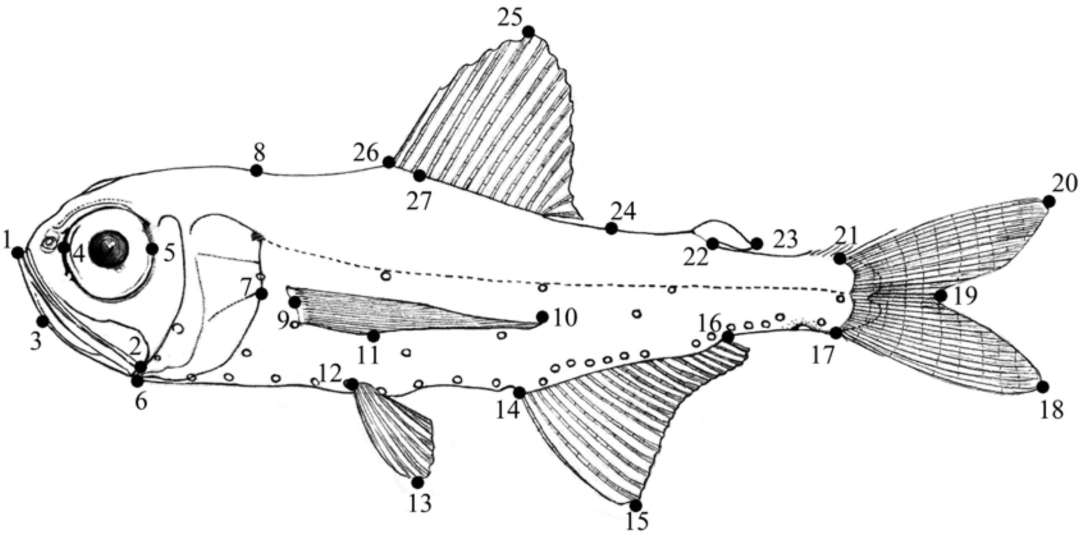


Figure S2. Scheme of a mesopelagic fish showing the landmarks used in the study. Drawn by Mrs. Isabel Bordes.

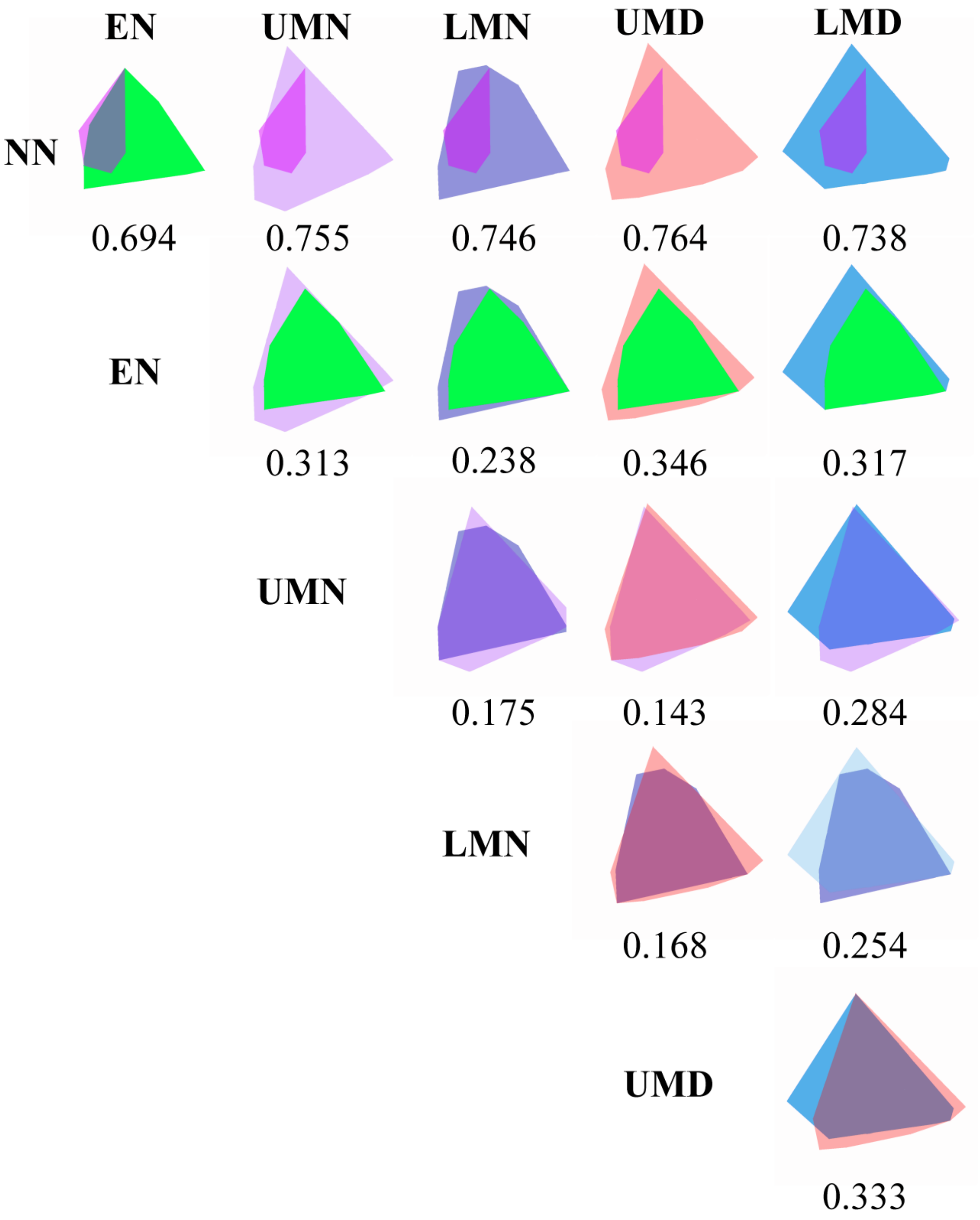
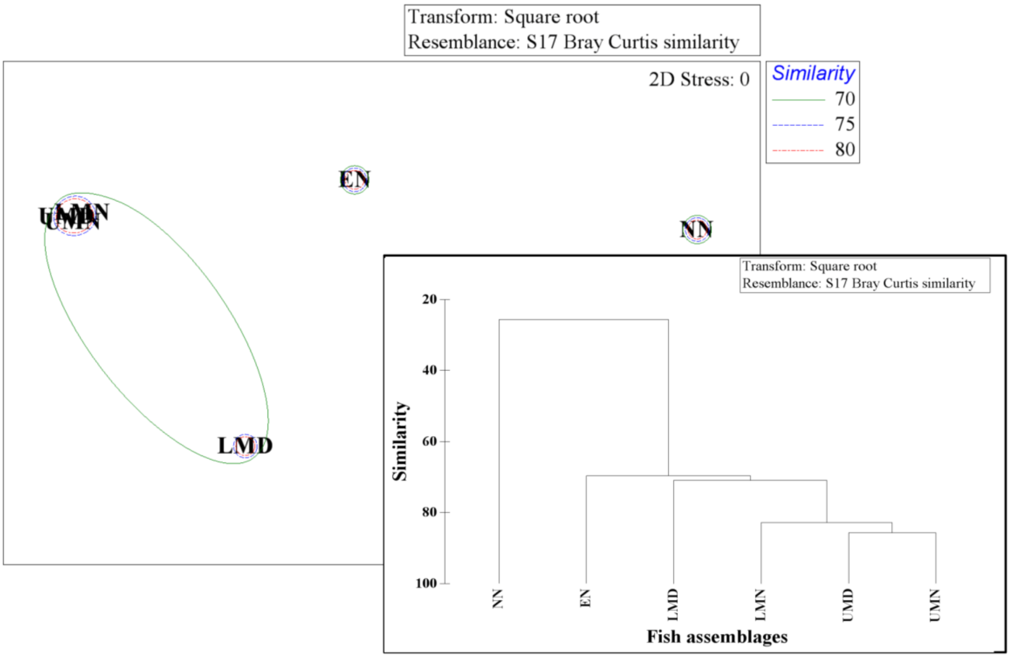


Figure S3. Graphical illustration showing the dissimilarity in the convex hull between the studied fish assemblages.

(a) Convex hull



(b) Patterning

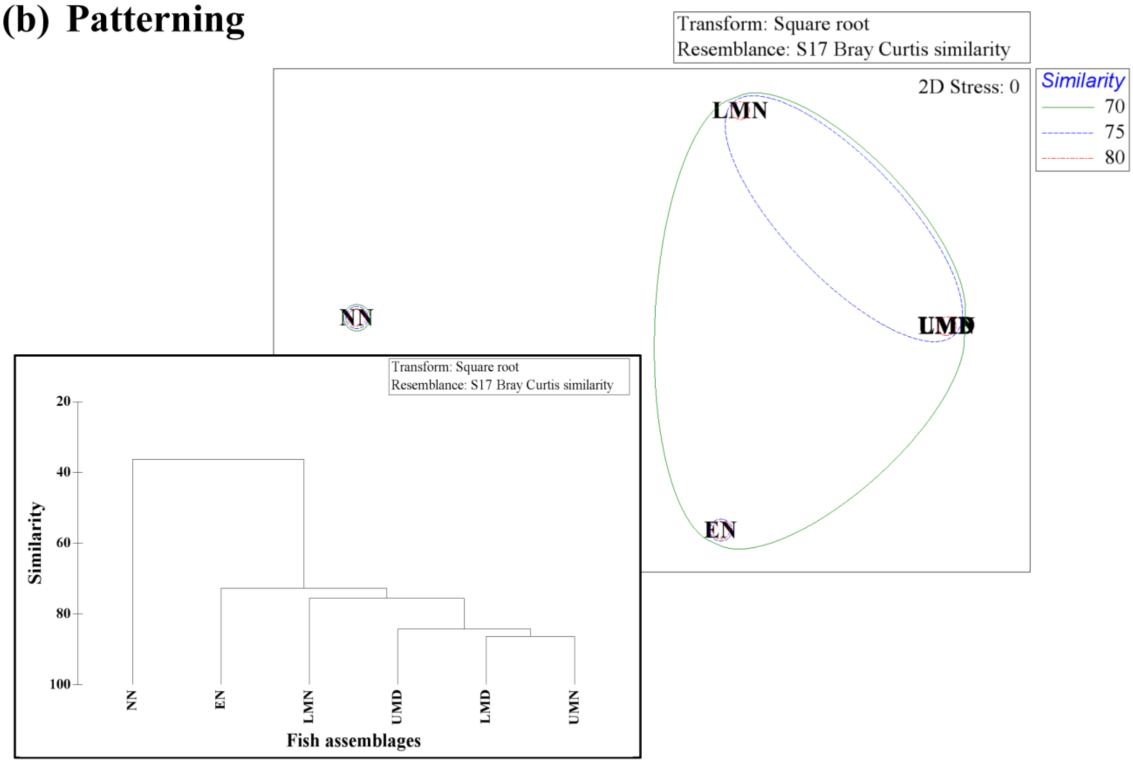


Figure S4. Cluster dendrogram and MDS plot representing the similarity among fish assemblages according to convex hull (a) and patterning (b) of morphospace. *NN* neritic assemblage at nighttime, *EN* epipelagic assemblage at nighttime, *UMN* upper mesopelagic assemblage at nighttime, *LMN* lower mesopelagic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

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

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

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

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

				Number of individuals												
				Central Zone						Northern zone						
Order	Family	Specie	Acronym	CS10	CSEA15	CS15	CS20	CA15	CR15	NG20	NR15	NS10	NS15	NS20	NSM20	NM20
		Individuals		343	2501	539	121	629	356	456	168	461	261	514	242	120
		Specific richness		30	43	40	27	48	37	22	16	26	21	25	22	18

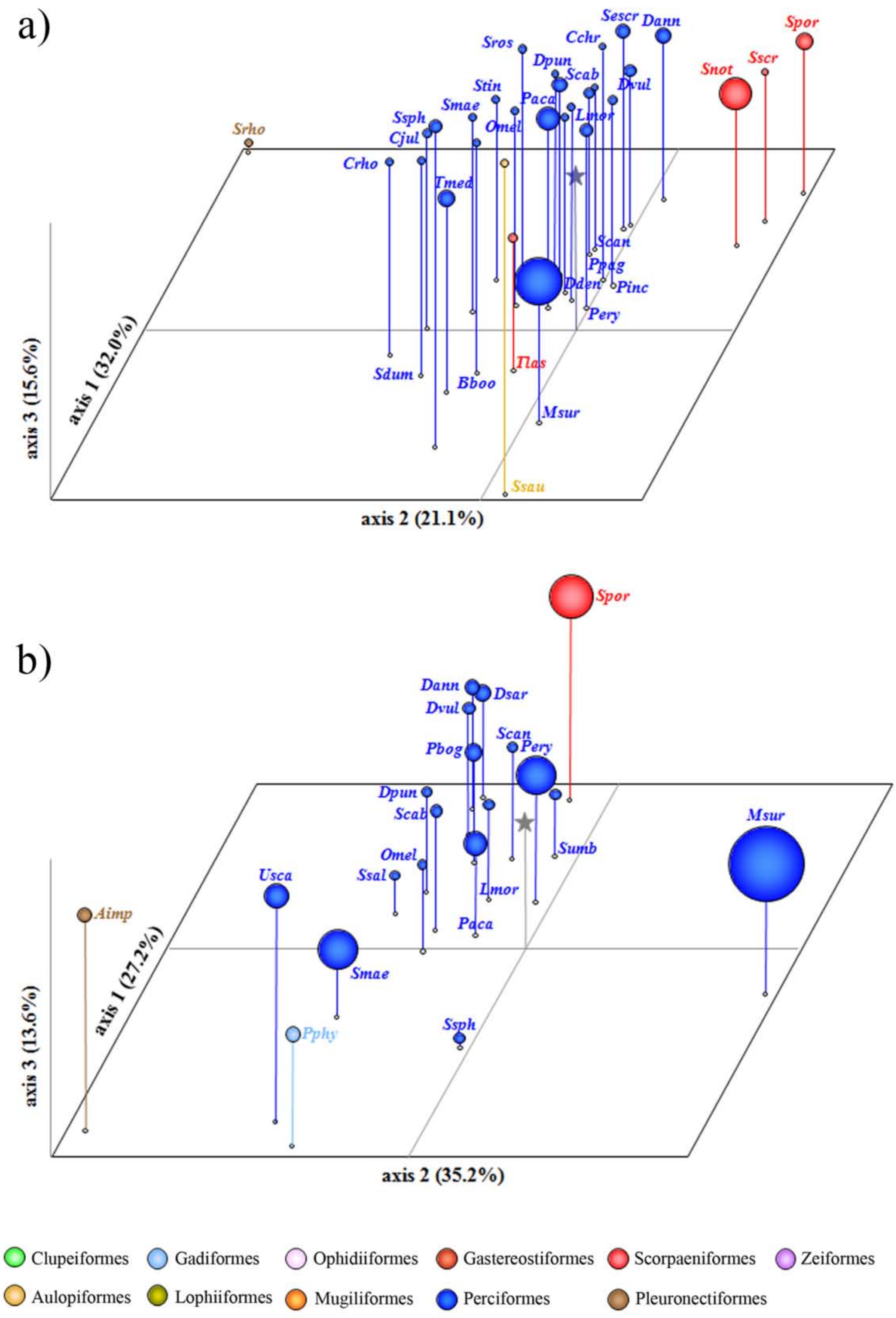


Figure S1. Representation of the fish morphospaces of rocky-seagrasses (*CSEA15*) (a) and gravel (*NG20*) (b) assemblages. The first three relative warps represent the three axis of the morphospace, providing each of them the corresponding percentage of total morphological variability. The size point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

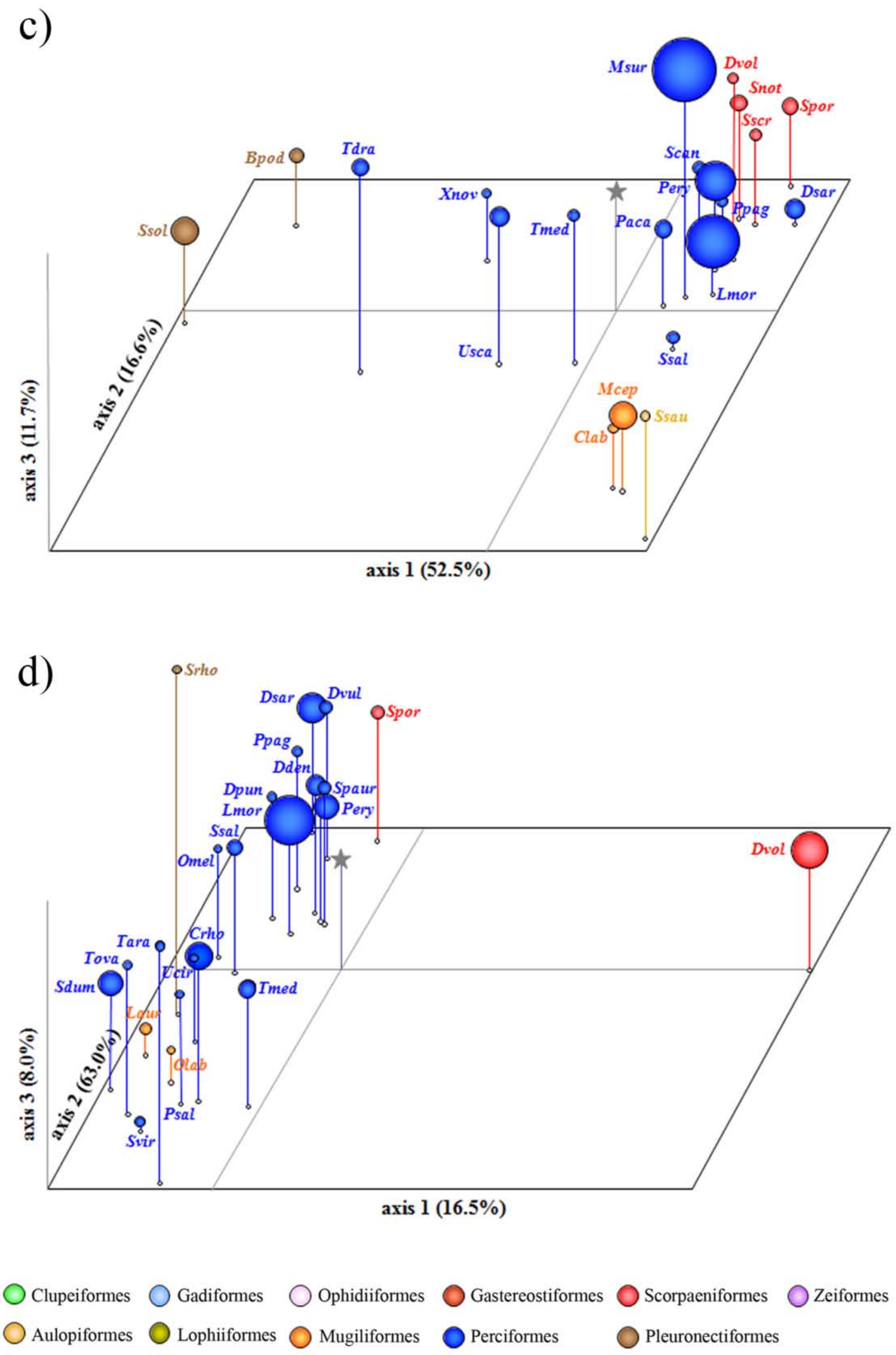


Figure S2. Representation of the fish morphospaces of sandy 10-20 m (*NS15*) (c) and sandy <10 m (*CS10*) (d) assemblages. The first three relative warps represent the three axis of the morphospace, providing each of them the corresponding percentage of total morphological variability. The size point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

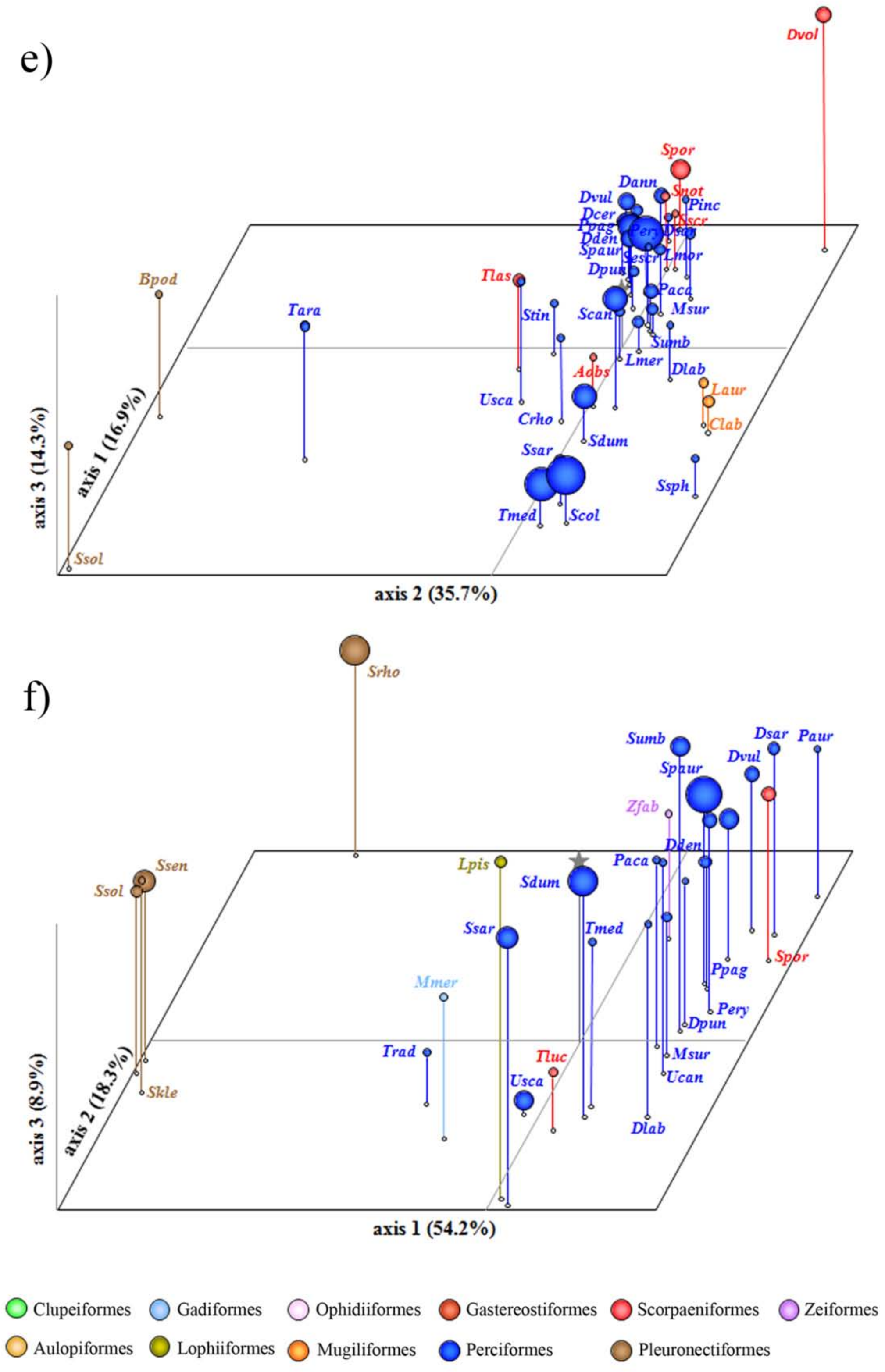


Figure S3. Representation of the fish morphospaces of sandy-rocky (*CS15*) (e) and sandy >20 m (*CS20*) (f) assemblages. The first three relative warps represent the three axis of the morphospace, providing each of them the corresponding percentage of total morphological variability. The size point of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

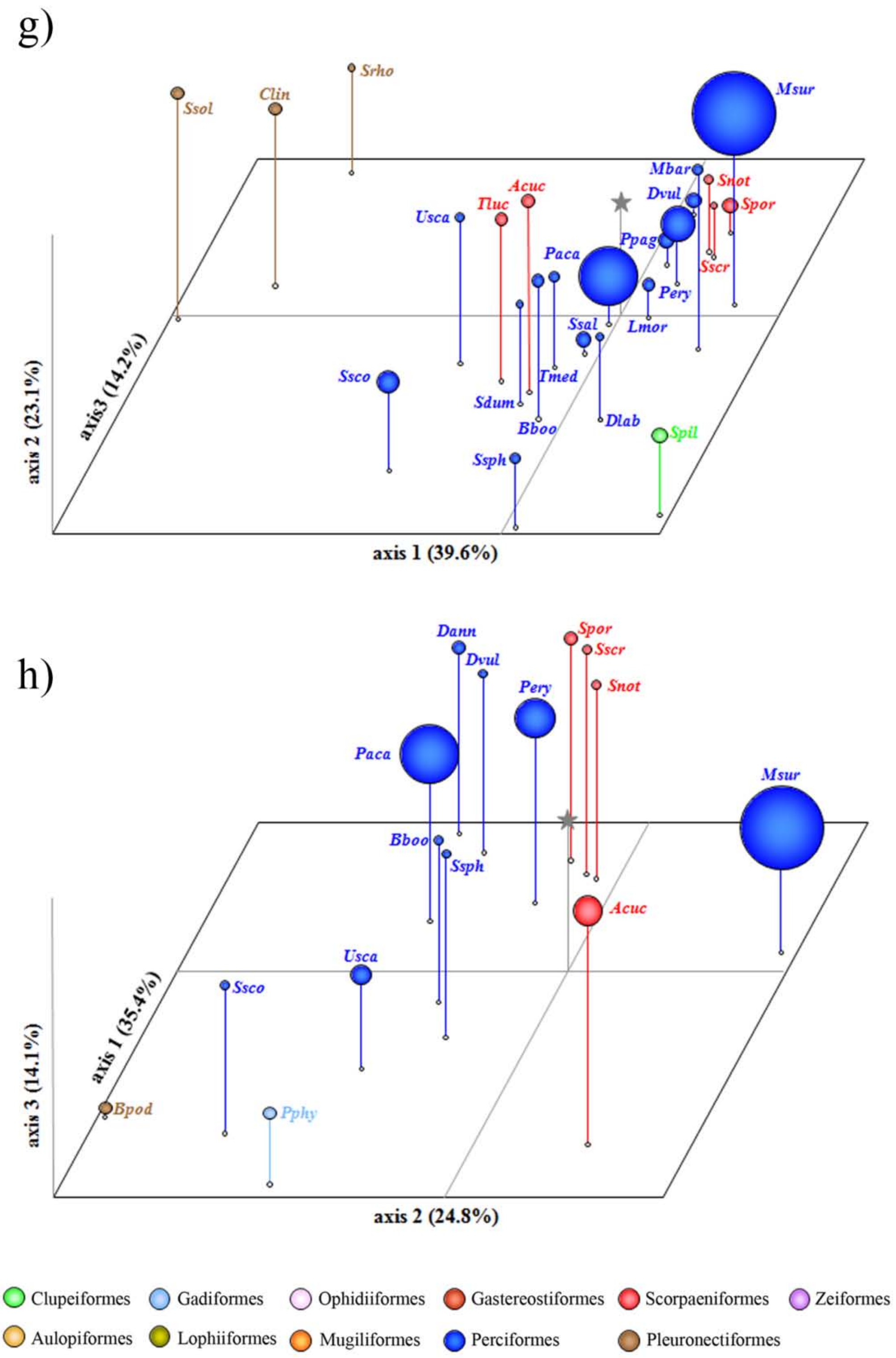


Figure S4. Representation of the fish morphospace of sandy-rocky >20 m (*NS20*) (g) and rocky (*NR15*) (h) assemblages. The first three relative warps represent the three axis of the morphospace, providing each of them the corresponding percentage of total morphological variability. The size point of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

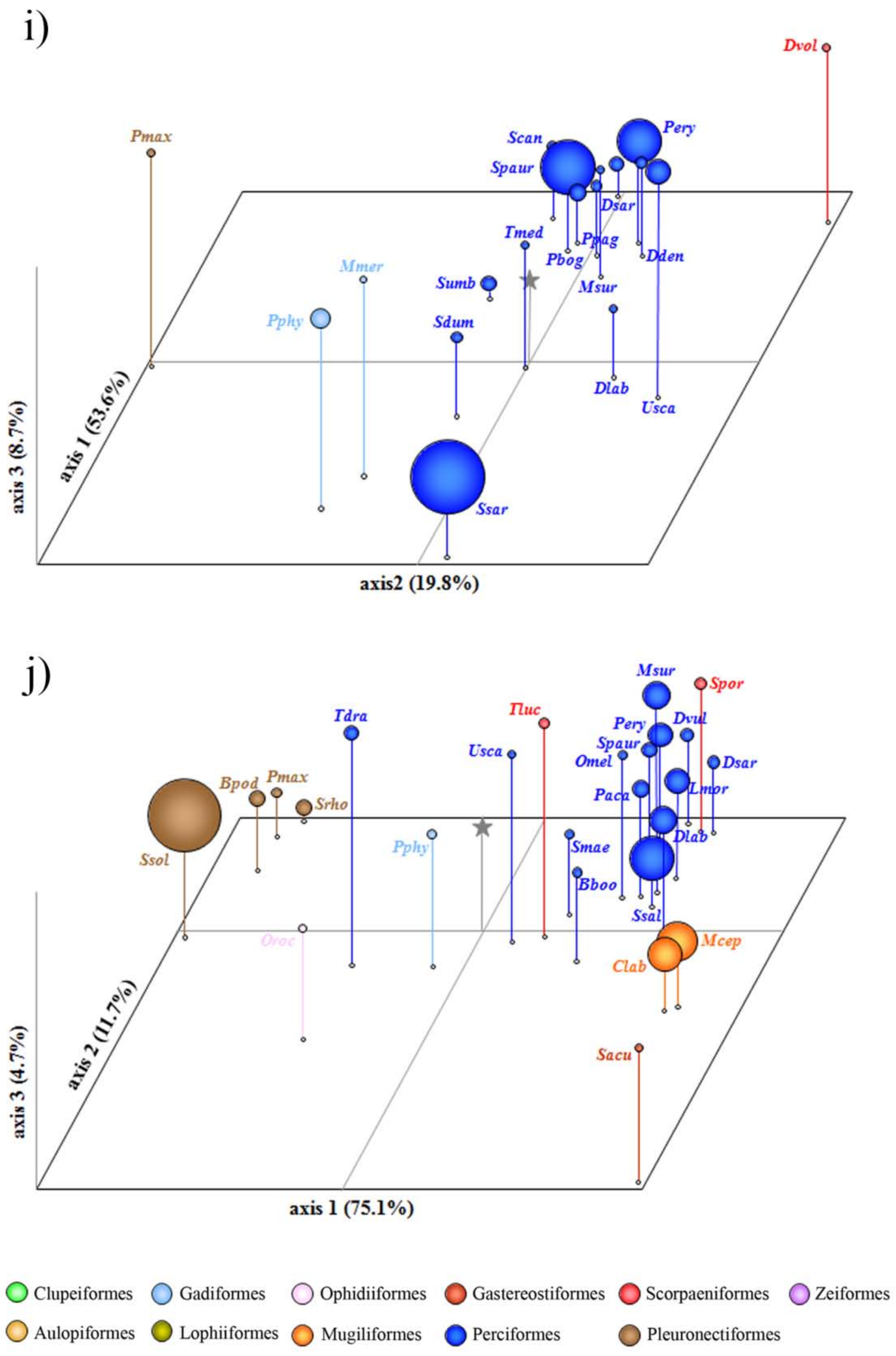


Figure S5. Representation of the fish morphospaces of muddy (*NM20*) (i) and sandy <10 m (*NS10*) (j) assemblages. The first three relative warps represent the three axis of the morphospace, providing each of them the corresponding percentage of total morphological variability. The size point of each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

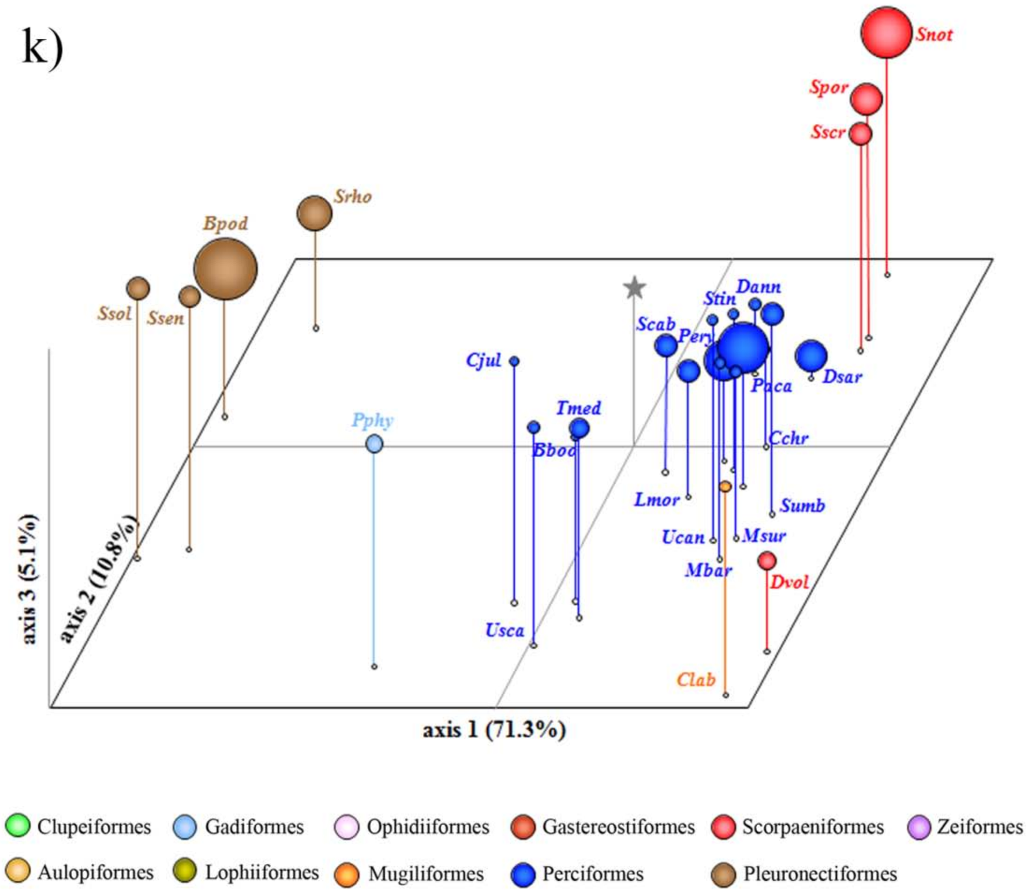


Figure S6. Representation of the fish morphospaces of rocky-sandy (*CR15*) (k) assemblage. The first three relative warps represent the three axis of the morphospace, providing each of them the corresponding percentage of total morphological variability. The size point of each species represents its 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^2) and number of total captured species for the different defined assamblages. Orders are listed alphabetically.

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

13. Appendix 1. Supplementary Material

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

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

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

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

				Assemblages					
Order	Family	Specie	Acronym	A (40-80m)	B (80-250m)	C (250-500m)	D (500-800m)	E (800-1400m)	F (1400-2200m)
Zeiformes	Zeidae	*Zeus faber*	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
Argentiniformes	Alepocephalidae	*Alepocephalus rostratus*	Aleros	Elo	Car	H	ML	BENTP	nmM
Aulopiformes	Paralepididae	*Arctozenus risso*	Arcris	Elo	Car	H	SM	MESP	mM
Argentiniformes	Argentinidae	*Argentina sphyraena*	Argsph	Elo	Car	R	SM	BENTP	nmM
Pleuronectiformes	Bothidae	*Arnoglossus imperialis*	Arnimp	Asy	Ang	S	SM	ENDB	NS
Pleuronectiformes	Bothidae	*Arnoglossus laterna*	Arnlat	Asy	Ang	S	S	ENDB	NS
Pleuronectiformes	Bothidae	*Arnoglossus rueppelii*	Arnrue	Asy	Ang	S	SM	ENDB	NS
Pleuronectiformes	Bothidae	*Arnoglossus thori*	Arntho	Asy	Ang	S	SM	ENDB	NS
Aulopiformes	Aulopidae	*Aulopus filamentosus*	Aulfil	Fus	Sub	R	M	EPIB	NS
Aulopiformes	Ipnopidae	*Bathypterois mediterraneus*	Batmed	Elo	Bat	S	SM	EPIB	NS
Pleuronectiformes	Soleidae	*Bathysolea profundicola*	Batpro	Asy	Ang	S	SM	ENDB	NS
Perciformes	Blenniidae	*Blennius ocellaris*	Bleoce	Obl	Dio	S	SM	EPIB	EPIB
Perciformes	Sparidae	*Boops boops*	Booboo	Fus	Car	H	SM	BENTP	nmM
Pleuronectiformes	Bothidae	*Bothus podas*	Botpod	Asy	Ang	S	SM	ENDB	EPIB
Perciformes	Callanthiidae	*Callanthias ruber*	Calrub	Fus	Car	R	SM	BENTP	nmM
Perciformes	Callionymidae	*Callionymus maculatus*	Calmac	Elo	Sub	S	SM	EPIB	EPIB
Perciformes	Caproidae	*Capros aper*	Capape	Ova	Bal	H	S	BENTP	nmM
Ophidiiformes	Carapidae	*Carapus acus*	Caracu	Ang	Ang	S	SM	EPIB	EPIB
Ophidiiformes	Bythitidae	*Cataetyx alleni*	Catall	Elo	Ang	R	SM	BENTP	NS
Ophidiiformes	Bythitidae	*Cataetyx laticeps*	Catlat	Elo	Ang	R	M	BENTP	NS
Perciformes	Centracanthidae	*Centracanthus cirrus*	Cencir	Fus	Car	H	SM	BENTP	nmM
Perciformes	Centrolophidae	*Centrolophus niger*	Cennig	Fus	Car	H	M	BENTP	nmM

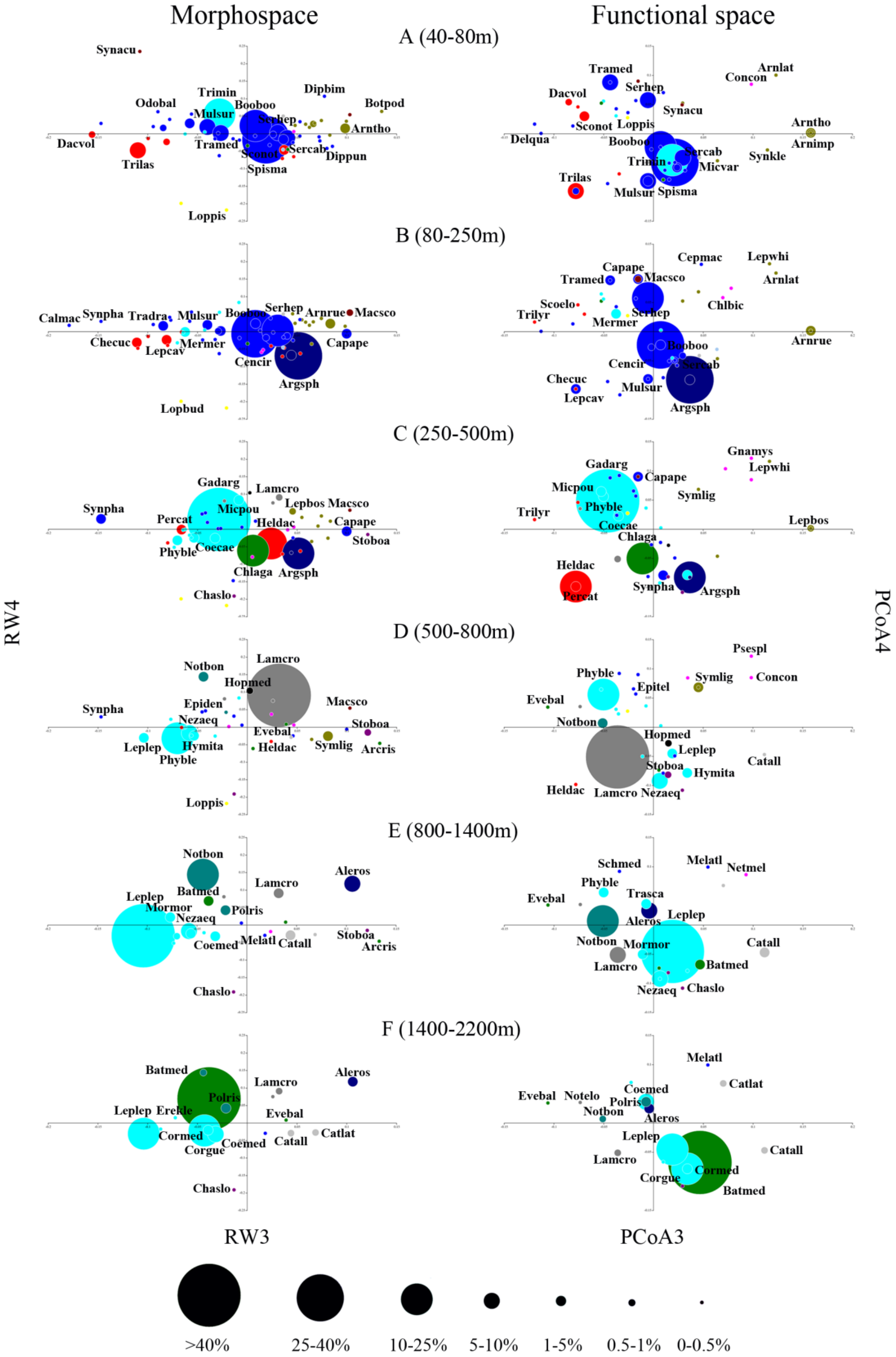
Order	Family	Specie	Acronym	Body shape	Swimming Type	Motility	Size	Vertical distribution	Diet
Perciformes	Cepolidae	*Cepola macrophthalma*	Cepmac	Ang	Ang	S	M	BENTP	nmM
Myctophiformes	Myctophidae	*Ceratoscopelus maderensis*	Cermad	Obl	Car	H	S	MESP	mM
Stomiiformes	Stomiidae	*Chauliodus sloani*	Chaslo	Elo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

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

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

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

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), 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.


Morphospace
Functional space
A (40-80m)
Synacu
Trimin
Dipbim
Odobal
Mulsur
Booboo
Botpod
Serhep
Arntho
Dacvol
Tramed
Sercab
Trilas
Sconot
Dippun
Spisma
Loppis
Tramed
Arnlat
Concon
Serhep
Dacvol
Synacu
Sconot
Loppis
Arntho
Delqua
Booboo
Arnimp
Sercab
Trimin
Micvar
Synkle
Trilas
Mulsur
Spisma
B (80-250m)
Calmac
Synpha
Tradra
Mulsur
Booboo
Serhep
Arnrue
Macsco
Checuc
Lepcav
Mermer
Capape
Cencir
Argsph
Lopbud
Cepmac
Lepwhi
Capape
Tramed
Macsco
Arnlat
Sceolo
Chlbic
Trilyr
Serhep
Mermer
Arnrue
Booboo
Cencir
Sercab
Checuc
Mulsur
Lepcav
Argsph
C (250-500m)
Gadarg
Lamcro
Synpha
Micpou
Lepbos
Macsco
Percat
Heldac
Capape
Stoboa
Phyble
Coecae
Chlaga
Argsph
Chaslo
Gnamys
Lepwhi
Gadarg
Capape
Micpou
Symlig
Phyble
Trilyr
Coecae
Lepbos
Chlaga
Heldac
Synpha
Argsph
Percat
D (500-800m)
Lamcro
Notbon
Hopmed
Macsco
Synpha
Epiden
Nezaeq
Stoboa
Evebal
Leplep
Hymita
Heldac
Symlig
Arcris
Phyble
Loppis
Psespl
Phyble
Symlig
Concon
Epitel
Evebal
Notbon
Hopmed
Leplep
Catall
Stoboa
Hymita
Heldac
Lamcro
Nezaeq
E (800-1400m)
Notbon
Aleros
Lamcro
Batmed
Leplep
Mormor
Polris
Nezaeq
Stoboa
Coemed
Melatl
Catall
Arcris
Chaslo
Schmed
Melatl
Netmel
Phyble
Evebal
Trasca
Leplep
Aleros
Notbon
Mormor
Catall
Batmed
Lamcro
Nezaeq
Chaslo
F (1400-2200m)
Batmed
Aleros
Lamcro
Polris
Leplep
Erekle
Evebal
Cormed
Catlat
Corgue
Coemed
Catall
Chaslo
Melatl
Catlat
Coemed
Evebal
Notelo
Polris
Notbon
Aleros
Leplep
Catall
Lamcro
Cormed
Corgue
Batmed
RW4
RW3
PCoA4
PCoA3
>40%
25-40%
10-25%
5-10%
1-5%
0.5-1%
0-0.5%

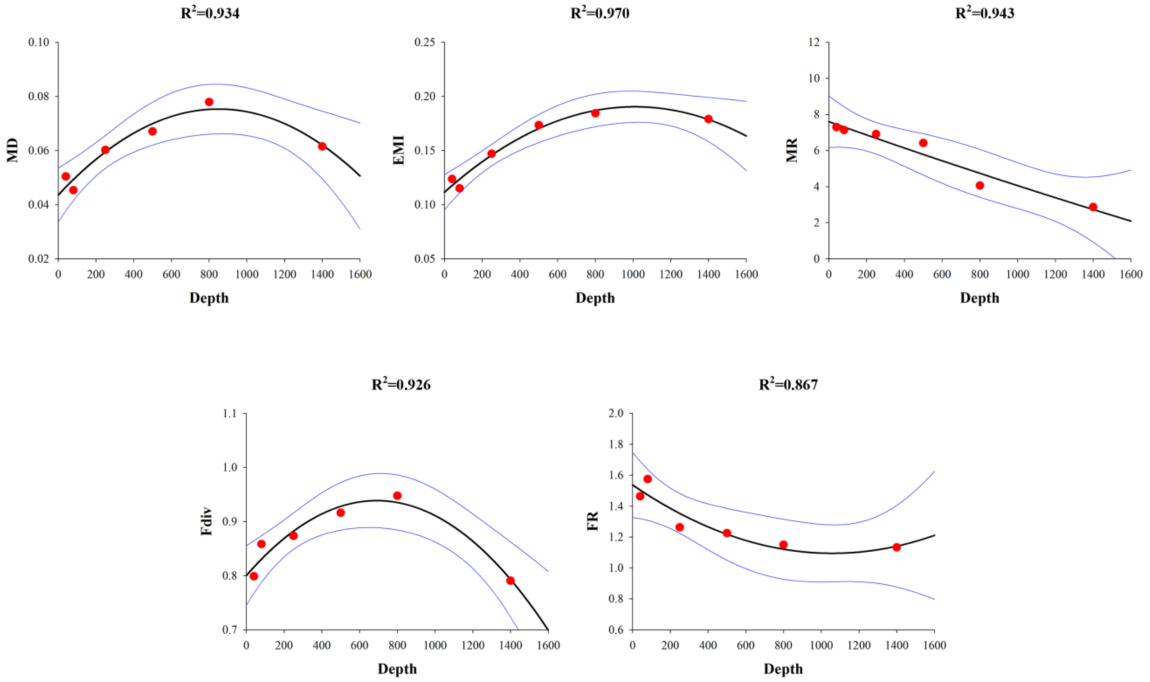


Figure S2. Bathymetric trends of the morphological and functional indices, with their respective second order polynomial regressions, of the different considered fish assemblages. Only the indices that followed a significant correlation with depth are shown (*MD*, *EMI*, *MR*, *Fdiv* and *FR*). In each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

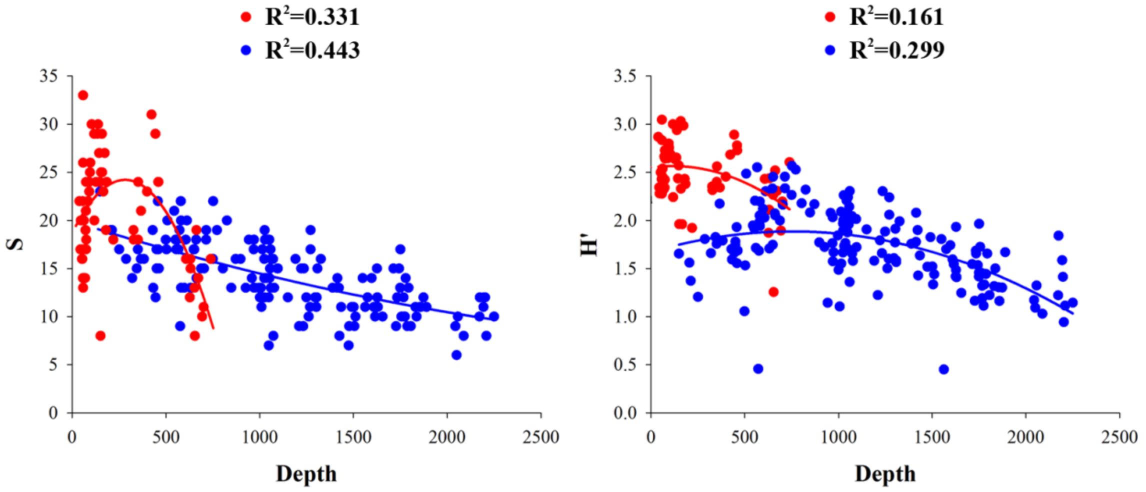


Figure S3. Bathymetric trends of the ecological diversity indices (*S* and *H'*), with their respective second order polynomial regressions, of the considered GOC73 (red points) and OTSB-14 hauls (blue points) separately. The blue and red lines represent the obtained tendency with depth. The value of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

14

Appendix 2

Publications

Ecological Indicators 29 (2013) 159–166

Contents lists available at SciVerse ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

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

Marc Farré, Victor M. Tuset*, Francesc Maynou, Laura Recasens, Antoni Lombarte

Institut de Ciències del Mar (CSIC), Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Catalonia, Spain

ARTICLE INFO

Article history:
Received 27 September 2012
Received in revised form 4 December 2012
Accepted 6 December 2012

Keywords:
Biodiversity
Morphological diversity
Geometrical morphology
Fish assemblages

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 characterized 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 analyzed. 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 analyze the evolution of fish assemblages over time from species checklists collected in experimental surveys from the late XIX century to the present.

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 (Lyashevska 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 'bathypteroiform' 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 (Echeinidae) 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), haddocks 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, 2003). 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

---

* Corresponding author. Tel.: +34 932 309 500; fax: +34 932 309 555.
E-mail address: vtuset@icm.csic.es (V.M. Tuset).

1470-160X/$ – see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.ecolind.2012.12.005

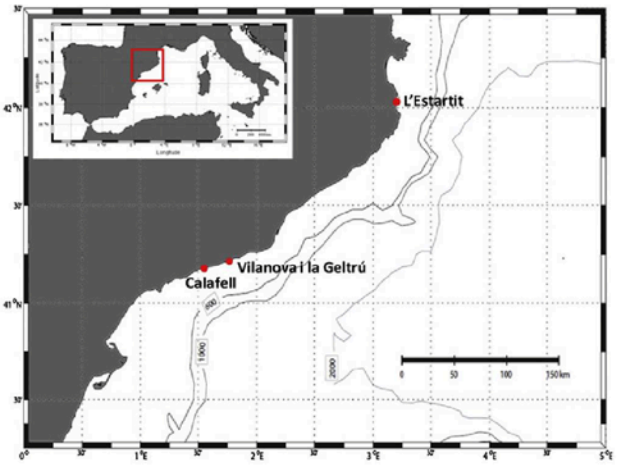


Fig. 1. Geographical localization of sampling.

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.

2. Materials and methods

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 analyzed 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).

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; and (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; and (f) Rocky-Seagrasses, 10–14 m.

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 (Δ), taxonomic distinctness (Δ^*), average taxonomic distinctness AvTD (Δ^+) and variation in taxonomic distinctness VarTD (Λ^+).

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

2.3. Geometric morphological indices

A total of 27 landmarks and semilandmarks (Fig. 2) with anatomical, ecological and taxonomical meaning were used

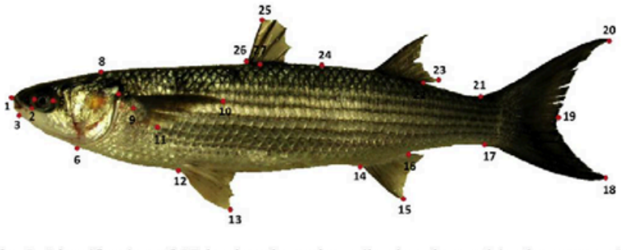


Fig. 2. Identification of 27 landmarks and semilandmarks used in the geometric morphological analysis.

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

(Recasens et al., 2006; Tables 2 and 3) for a specimen of each species from standardized images of the left side (using tpsDig, 2.16; Rohlf, 2001). After digitalising the metric maps of each species, they were rotated, scaled (to unit centroid size) and translated using a generalized least-square superimposition (GLS) procedure (generalized Procrustes) to remove scale and orientation distortions (using tpsRel 1.24; Rohlf, 2001). 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 visualized using relative warp analysis (Rohlf and Marcus, 2003). 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.

Relative warps were used to calculate morphological disparity, $MD = \sum_j RW_j^2/(N-1)$, 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, $EMI = \sum_j CC/(N-1)$, 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 (*MD*2, *MR*2 and *EMI*2). In the first case, the number of images analyzed per species was equivalent to the relative abundance in the samples. The species with abundance equal to or less than 1% were analyzed 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).

2.4. Comparison of indices

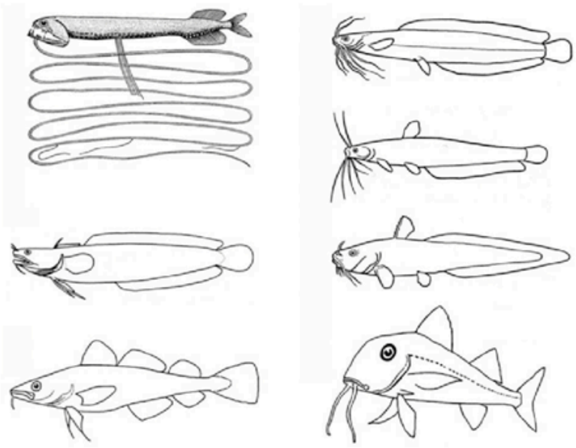
The comparison of diversity indices was performed using Spearman's correlation index and they were clustered in a dendrogram produced using the hierarchical method (Lyashevska and Farnsworth, 2012). It was carried out based on Euclidean distances, using Ward's aggregation algorithm. Previously, data were scaled using *Z*-score normalization because it is specially needed for distance metrics, such as Euclidean distance, which are sensitive to differences in the magnitude or scales of the attributes (Visalakshi and Thangavel, 2009).

3. Results

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

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)  	*Ecological meaning*: related to food acquisition
3	Differentiates among fishes with or without sensorial barbels on chin, and position and relative size of barbels (from Kasumyan, 2011)	*Ecological meaning*: extremely diverse, related to mode of life, behaviour and feeding strategies. *Taxonomic value*
4–5	Position and relative size of eye and its position respect to head and body size 	*Ecological meaning*: related to food acquisition and life strategies
6–8	Indicates the relative height and width of head respect to the body size	*Ecological meaning*: related to food acquisition and life strategies
24	Indicates the presence/absence of one or two dorsal fins	*Taxonomic value*
27	Defines the point of maximum height of the body shape	*Ecological meaning*: related to locomotion and life strategies

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 ($MD = 0.054$ *vs.* 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).

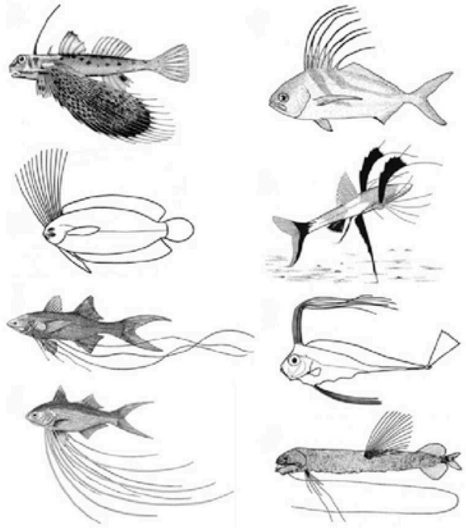
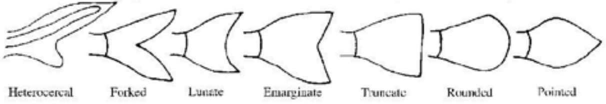
The mosphospace was determined by the peripheral morphology of fishes of each assemblage (Fig. 3). In the sandy sample, the morphology of these species was composed for flattened (Pleuronectiforms as *Bothus podas*, *Psetta maxima*, *S. solea* and *Scophtalmus rhombus*) and elongated shapes (Ophidiiforms as *Ophidion rochei*; Perciforms as *Trachinus draco*; and Syngnathiforms as *Syngnathus acus*), who bury in the sand or live on the sea bottom. Conversely, the more extreme shapes in the Rocky-Seagrasses corresponded with species living closer to surface (Clupeiforms as *Sardinella aurita*; and Beloniforms as *Belone belone*), typical of rocky-bottoms (Perciforms as *Diplodus annularis*, *Symphodus rostratus* and *Scorpaena scrofa*), and in lesser grade some flattened fishes (Pleuronectiforms as *Arnoglossus thori* and *S. 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).

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 (Δ) and taxonomic distinctness (Δ^*). Similarly to richness index, the Shannon diversity index was linked to morphological richness and functional diversity indices. Conversely, Pielou's evenness index (J')

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) 	*Ecological meaning*: related to swimming or walking over bottom, feeding and defensive strategies. *Taxonomic value*
12–13	Indicates pelvic fin shape and its relative position (see scheme before)	*Ecological meaning*: 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)	*Ecological meaning*: related to stability while swimming, walking over bottom and primary propulsion in some species. *Taxonomic value*
22–23	Defines where second dorsal fin finishes and its relative position (see scheme before)	*Ecological meaning*: related to stability while swimming and life strategies. *Taxonomic value*
25–26	Defines where first dorsal fin starts and its relative position (see scheme before)	*Ecological meaning*: related to stability while swimming, primary propulsion in some species, large fins as strucutres for the detection food or attracting preys or transformed in a suction cup type structure maintaining position. *Taxonomic value*
17–21	Defines shape of peduncle and caudal fin (from Bugas et al., 2009) 	*Ecological meaning*: related to locomotion

was weekly associated to that morpho-geometric diversity index (*EMI*) ($r_s = 0.561$) and morphological disparity (*MD*) ($r_s = 0.575$) obtained from abundance data. The taxonomical indices were correlated among them and with ecological and morphological disparity indices (*MD* and *MD*2), except for the variation in taxonomic distinctness (Λ^+). Morpho-geometric diversity indices were correlated between them and with the two unrelated indices; *EMI* with Pielou's evenness and *EMI*2 with the functional diversity. Finally, the functional diversity (*FD*) showed significant relation to some ecological and morphological richness indices, especially with specific richness (0.991) and morphological richness (*MR*2, 0.962) (Table 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*, *MR*2, *d*, *S* and *FD*), where morphology richness and functional diversity were related together and with specific richness; (b) a morpho-structural diversity group (*EMI*, *EMI*2 and *VarTD*), that measured the morphological and taxonomical distinctness of fishes within assemblages; and (c) a morpho-taxonomical diversity group (*MD*, *MD*2, *AvTD*, *DELT*, *DSTR*), where the morphological disparity depended on taxonomical groups.

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 (Lyashevska and Farnsworth, 2012), although it is, by far, the most common measure of biodiversity used by scientists, conservationists, and policy makers (Magurran, 1988; Gray, 2000; Wilsey et al., 2005; Flynn et al., 2009). Most studies reveal a

Table 4

Ecological, taxonomic, morphological and functional indices obtained for the localities considered. *d*, Margalef's richness index; *H′*, Shannon's diversity index; *S*, specific richness; *S′*, Simpson index; *J′*, Pielou's evenness index; Δ, taxonomic diversity; Δ^*, taxonomic distinctness; Δ^+, average taxonomic distinctness; Λ^+, variation in taxonomic distinctness; *EMI* and *EMI2*, morpho-geometric diversity; *MD* and *MD2*, morphological disparity; *MR* and *MR2*, morphological richness; *FD*, functional diversity.

Locality fish assemblages		Ecological					Taxonomic				Morphological						Functional
		S	*d*	*J′*	*H′*	*S′*	Δ	Δ^*	Δ^+	Λ^+	*EMI*	*MD*	*MR*	*EMI2*	*MD2*	*MR2*	*FD*
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	2.91	0.152	0.028	3.19	52.10
	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	2.76	0.206	0.037	3.09	41.50
	Sandy 10 m[a]	26	6.33	0.90	2.92	0.94	86.52	91.93	88.23	317.25	0.193	0.054	4.64	0.190	0.050	4.75	67.60
	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	3.84	0.204	0.044	4.08	53.00
	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	4.21	0.173	0.037	4.15	64.40
	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	4.22	0.206	0.041	4.33	61.50
	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	3.13	0.193	0.033	3.28	47.90
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	5.16	0.160	0.032	4.64	73.90
	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	4.68	0.169	0.031	6.60	96.40
	Sandy 20 m	27	6.79	0.92	3.02	0.95	79.93	83.90	85.26	339.96	0.209	0.045	5.83	0.182	0.043	6.59	68.90
	Rocky-Seagrass 10–14 m[a]	43	6.89	0.63	2.37	0.82	68.37	83.28	83.48	315.85	0.156	0.025	5.43	0.166	0.032	6.98	101.80
	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	4.41	0.171	0.107	5.99	84.20
	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	4.74	0.158	0.168	7.11	105.30

[a] It indicates the fish assemblages selected to as example to graphical illustration of morphospaces, its relation to morphological indices and the meaning of morphological indices.

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 (Lyashevska and Farnsworth, 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., 1995; 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 taxonomical 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 (Δ) were higher in sandy than

Table 5

Spearman's correlation among ecological, taxonomic, morphological and functional indices. *d*, Margalef's richness index; *H′*, Shannon's diversity index; *S*, specific richness; *S′*, Simpson index; *J′*, Pielou's evenness index; Δ, taxonomic diversity; Δ^*, taxonomic distinctness; Δ^+, average taxonomic distinctness; Λ^+, variation in taxonomic distinctness; *EMI* and *EMI2*, morpho-geometric diversity; *MD* and *MD2*, morphological disparity; *MR* and *MR2*, morphological richness; *FD*, functional diversity. In bold the variables significantly correlated.

Indices	Ecological					Taxonomic				Morphological						
	S	*d*	*J′*	*H′*	*S′*	Δ	Δ^*	Δ^+	Λ^+	*EMI*	*MD*	*MR*	*EMI2*	*MD2*	*MR2*	
Ecological	*S*	1														
	d	**0.821**	1													
	J′	0.063	0.292	1												
	H′	**0.601**	**0.726**	**0.815**	1											
	S′	0.448	**0.618**	**0.905**	**0.974**	1										
Taxonomic	Δ	0.385	0.456	**0.831**	**0.842**	**0.894**	1									
	Δ^*	0.393	0.363	0.525	**0.572**	**0.632**	**0.879**	1								
	Δ^+	0.237	0.231	0.473	0.443	0.458	**0.665**	**0.637**	1							
	Λ^+	-0.311	-0.258	-0.182	-0.316	-0.302	-0.423	-0.357	-0.324	1						
Morphological	*EMI*	-0.505	-0.275	**0.561**	0.074	0.254	0.264	0.126	0.379	0.038	1					
	MD	0.061	0.055	**0.575**	0.435	0.505	**0.632**	**0.571**	**0.797**	-0.099	0.522	1				
	MR	**0.825**	**0.907**	0.327	**0.669**	**0.604**	0.473	0.407	0.192	-0.297	-0.088	0.154	1			
	EMI2	**-0.693**	-0.468	0.344	-0.132	0.030	0.083	-0.058	0.297	-0.077	**0.839**	0.308	-0.410	1		
	MD2	0.124	0.052	0.425	0.353	0.409	**0.573**	**0.567**	**0.802**	-0.168	0.441	**0.953**	0.135	0.299	1	
	MR2	**0.941**	**0.934**	0.259	**0.724**	**0.615**	0.533	0.478	0.385	-0.481	-0.280	0.214	**0.885**	0.454	0.278	1
Functional	*FD*	**0.991**	**0.901**	0.113	**0.630**	0.498	0.423	0.401	0.308	-0.346	-0.451	0.115	**0.846**	**-0.605**	0.193	**0.962**

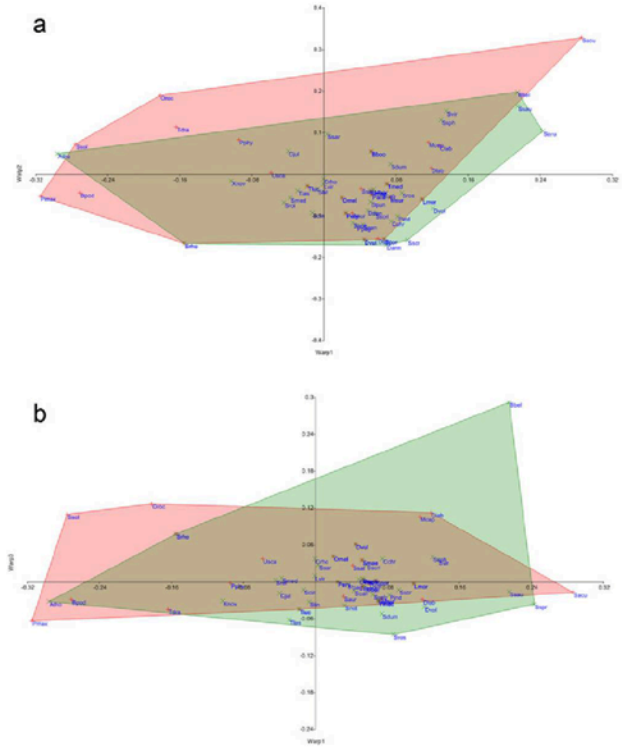


Fig. 3. Morphospaces of two fish assemblages selected, sand <10 m (pink) and Rocky-Seagrasses (green), using relative warps 1–2 (a) and 1–3 (b). In blue the acronyms of fishes.

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).

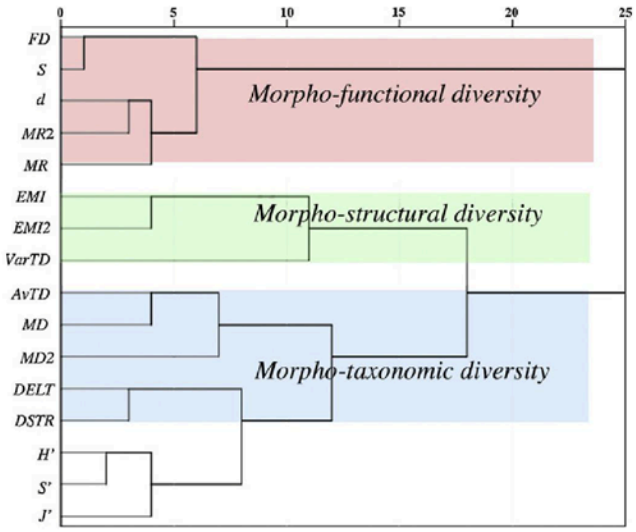


Fig. 4. Hierarchical clustering of biodiversity indices using Ward distance indicating several clusters: (1) morpho-functional diversity; (2) morpho-structural diversity; and (3) morpho-taxonomical diversity.

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 that 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 analyze 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.

Acknowledgements

Data of this study were financed by project "ESCAL 1" (Ref. PCC30004/99), "ESCAL 2" (Ref. 02P30015) of the DG Fisheries of the Government of Catalonia, "CONFLICT" (Ref. CGL2008-00047) of the Spanish National Research Plans and "EMPAFISH" (E.U. DG MARE project Ref. 006539). Marc Farré Foix acknowledges a pre-doctoral grant from the Government of Andorra, ATC010-AND, academic year: 2012–2013. Dr. Victor Tuset is a worker of CSIC within the modality "JAE-Postdoc" of Programme "Junta para la Ampliación de Estudios" co-funded by the European Social Foundation (FSE).

References

Albouy, C., Guilhaumon, F., Villéger, S., Mouchet, M., Mercier, L., Culioli, J.M., Tomasini, J.A., Le Loc'h, F., Mouillot, D., 2011. Predicting trophic guild and diet overlap from functional traits: statistics, opportunities, and limitations for marine ecology. Mar. Ecol. Prog. Ser. 436, 17–28.
Antonucci, F., Costa, C., Aguzzi, J., Cautadella, S., 2009. Ecomorphology of morpho-functional relationships in the family of Sparidae: a quantitative statistic approach. J. Morphol. 270, 843–855.
Bellwood, D.R., Wainwright, P.C., Fulton, C.J., Hoey, A.S., 2006. Functional versatility supports coral reef biodiversity. Proc. R. Soc. B 273, 101–107.
Bookstein, F.L., 1991. Morphometric Tools for Landmark Data. Geometry and Biology. Cambridge University Press, New York.
Bugas Jr., P.E., Copeland, J.R., Murphy, B. (Eds.), 2009. Virginia Master Naturist Training Manual. Virginia.
Campbell, N., Neat, F., Burns, F., Kunzlik, P., 2011. Species richness, taxonomic diversity, and taxonomic distinctness of the deep-water demersal fish community on the Northeast Atlantic continental slope (ICES Subdivision VIa). ICES J. Mar. Sci. 68, 365–376.
Ciampaglio, C.N., Kemp, M., Mcshea, D.W., 2001. Detecting changes in morphospace occupation patterns in the fossil record: characterization and analysis of measures of disparity. Paleobiology 27, 695–715.
Clabaut, C., Bunje, P.M., Salzburger, W., Meyer, A., 2007. Geometric morphometric analyses provide evidence for the adaptive character of the Tanganyikan cichlid fish radiations. Evolution 61 (3), 560–578.
Clarke, K.R., Warwick, R.M., 1998. A taxonomic distinctness index and its statistical properties. J. Appl. Ecol. 35, 523–531.
Clarke, K.R., Warwick, R.M., 2001. A further biodiversity index applicable to species lists, variation in taxonomic distinctness. Mar. Ecol. Prog. Ser. 216, 265–278.

Colgate, J.E., Lynch, K.M., 2004. Mechanics and control of swimming: a review. IEEE J. Ocean. Engineering 29 (3), 660–673.

Cornwell, W.K., Schwilk, D.W., Ackerly, D., 2006. A trait-based test for habitat filtering: convex hull volume. Ecology 87 (6), 1465–1471.

Davis, M.P., Chakrabarty, P., 2011. Tripodfih (Aulopiformes: *Bathypterois*) locomotion and landing behaviour from video observation at bathypelagic depths in the Campos Basin of Brazil. Mar. Biol. Res. 7 (3), 297–303.

Dumay, O., Tari, P.S., Tomasini, J.A., Mouillot, D., 2004. Functional groups of lagoon fish species in Languedoc Roussillon, southern France. J. Fish Biol. 64, 970–983.

Ernst, R., Linsenmair, K.E., Rodel, M.O., 2006. Diversity erosion beyond the species level: dramatic loss of functional diversity after selective logging in two tropical amphibian communities. Biol. Conserv. 133, 143–155.

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M., DeClerck, F., 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecol. Lett. 12, 22–33.

Foote, M., 1993. Discordance and concordance between morphological and taxonomic diversity. Paleobiology 19, 185–204.

Froese, R., Pauly, D. (Eds.), 2011. FishBase. World Wide Web electronic publication, www.fishbase.org

Fulton, C.J., Bellwood, D.R., Wainwright, P.C., 2001. The relationship between swimming ability and habitat use in wrasses (Labridae). Mar. Biol. 139, 25–33.

Gerber, S., Eble, G.J., Neige, P., 2008. Allometric space and allometric disparity: a developmental perspective in the macroevolutionary analysis of morphological disparity. Evolution 62, 1450–1457.

Gray, J.S., 2000. The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. J. Exp. Mar. Biol. Ecol. 250, 23–49.

Gosline, W.A., 1994. Function and structure in the paired fins of scorpaeniform fishes. Environ. Biol. Fish. 40, 219–226.

Halpern, B.S., Floeter, S.R., 2008. Functional diversity responses to changing species richness in reef fish communities. Mar. Ecol. Prog. Ser. 364, 147–156.

Heino, J., Soininen, J., Lappalainen, J., Virtanen, R., 2005. The relationship between species richness and taxonomic distinctness in firewater organisms. Limnol. Oceanogr. 50 (3), 978–986.

Helfman, G.S., Collette, B.B., Facey, D.E., 1997. The Diversity of Fishes. Blackwell Science, Oxford.

Jenkins, R.E., Burkhead, N.M., 1993. Freshwater Fishes of Virginia. American Fisheries Society, Bethesda, Maryland.

Kasumyan, A.O., 2011. Tactile reception and behavior of fish. J. Ichthyol. 51 (11), 1035–1103.

Langerhans, R.B., Layman, C.A., Shokrollahi, A.M., DeWitt, T.J., 2004. Predator-driven phenotypic diversification in *Gambusia affinis*. Evolution 58, 2305–2318.

Lombarte, A., Aguirre, H., 1997. Quantitative differences in the chemoreceptors systems in the barbels of two species of Mullidae (*Mullus surmuletus* and *M. barbatus*) with different bottom habitats. Mar. Ecol. Prog. Ser. 150, 57–64.

Lombarte, A., Olaso, I., Bozzano, A., 2003. Ecomorphological trends in Artedidraconidae (Pisces: Perciformes: Notothenioidei) of the Weddell Sea. Antartic Sci. 15, 211–218.

Lombarte, A., Palmer, M., Matallanas, J., Gómez-Zurita, J., Morales-Nin, B., 2010. Ecomorphological trends and phylogenetic inertia of otolith sagittae in Nototheniidae. Environ. Biol. Fish. 89, 607–618.

Lombarte, A., Gordoa, A., Whitfield, A.K., James, N.C., Tuset, V.M., 2012. Ecomorphological analysis as a complementary tool to detect changes in fish communities following major perturbations in two South African estuarine systems. Environ. Biol. Fish. 94 (4), 601–614.

Lyashevska, O., Farnsworth, K.D., 2012. How many dimensions of diversity do we need? Ecol. Indic. 18, 485–492.

McClain, C.R., Johnson, N.A., Rex, M.A., 2004. Morphological disparity as a biodiversity metric in lower bathyal and abyssal gastropod assemblages. Evolution 58 (2), 338–348.

Magurran, A.E., 1988. Ecological Diversity and Its Measurement. Princeton University Press, New Jersey.

Margalef, R., 1958. Information theory in ecology. Gen. Syst. 3, 36–71.

Mason, N.W.H., Lanoiselee, C., Mouillot, D., Irz, P., Argillier, C., 2007. Functional characters combined with null models reveal inconsistency in mechanisms of species turnover in lacustrine fish communities. Oecologia 153, 441–452.

Martín, P., Maynou, F., Stelzenmüller, V., Sacanell, M., 2012. A small scale fishery near a rocky littoral marine reserve in the northwestern Mediterranean (Medes Islands): yield (catches?) after two decades of fishing prohibition. Sci. Mar. 76 (3), 607–618.

Maynou, F., Recasens, L., Lombarte, A., 2011. Fishing tactics dynamics of a Mediterranean small-scale coastal fishery. Aquat. Living Resour. 24, 149–159.

Mercader, L., Lloris, D., Rucabado, J.A., 2001. Tots els peixos del mar Catalá: Diagnosis i claus d'identificació. Institut d'Estudis Catalans, Barcelona.

Micheli, F., Halpern, B.S., 2005. Low functional redundancy in coastal marine assemblages. Ecol. Lett. 8, 391–400.

Motta, P.J., Clifton, K., Hernandez, P., Eggold, B.T., 1995. Ecomorphological correlates in ten species of subtropical seagrass fishes: diet and microhabitat utilization. Environ. Biol. Fish. 44, 37–60.

Mouillot, D., Gaillard, S., Aliaume, C., Verlanque, M., Belsher, T., Troussellier, M., Do Chi, T., 2005. Ability of taxonomy diversity indices to discriminate coastal lagoon environments based on macrophyte communities. Ecol. Indic. 5, 1–17.

Muss, B.J., Nielsen, J.G., 1999. Sea Fish. Scandinavian Fishing Year Book, Hedehusene.

Neige, P., 2003. Spatial patterns of disparity and diversity of the recent cuttlefishes (Cephalopoda) across the Old World. J. Biogeogr. 30, 1125–1137.

Nelson, J.S., 2006. Fishes of the World, fourth ed. Wiley and Sons, New Jersey.

Olden, J.D., Poff, N.L., Bestgen, K.R., 2008. Trait synergisms and the rarity, extirpation, and extinction risk of desert fishes. Ecology 89, 847–856.

Pavoine, S., Vallet, J., Dufour, A.-B., Gachet, S., Daniel, H., 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. Oikos 118, 391–402.

Pease, A.A., Ginzález-Díaz, A.A., Rodiles-Hernández, R., Winemiller, K.O., 2012. Functional diversity and trait-environment relationships of stream fish assemblages in a large tropical catchment. Fresh. Res. 57 (5), 1060–1075.

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758.

Pielou, E.C., 1975. Ecological Diversity. Wiley, New York.

Price, S.A., Holzman, R., Near, T.J., Wainwright, P.C., 2011. Coral reefs promote the evolution of morphological diversity and ecological novelty in labrid fishes. Ecol. Lett. 14, 462–469.

Recasens, L., Lombarte, A., Sánchez, P., 2006. Teleostean fish composition and structure of an artificial reef and a natural rocky area in Catalonia (North Western Mediterranean). Bull. Mar. Sci. 78, 71–82.

Ricklefs, R.E., 2010. Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. Proc. Natl. Acad. Sci. U.S.A. 107 (4), 1265–1272.

Rohlf, F.J., 2001. TPS Dig 1.31 and TPS Relative Wards Software. State University of New York at Stony Brook.

Rohlf, F.J., Marcus, L.F., 2003. A revolution in morphometrics. Trends Ecol. Evol. 8, 129–132.

Roy, K., Foote, M., 1997. Morphological approaches to measuring biodiversity. Trends Ecol. Evol. 12, 277–281.

Roy, K., Balch, D.P., Helberg, M.E., 2001. Spatial patterns of morphological diversity across the Indo-Pacific: analyses using strombid gastropods. Proc. R. Soc. Lond. B. 268, 2503–2508.

Schoener, T.W., 1974. Resource partitioning in ecological communities. Science 185, 27–39.

Shannon, C.E., Weaver, W., 1949. The Mathematical Theory of Communication. University of Illinois Press, Illinois.

Simpson, E.H., 1949. Measurement of species diversity. Nature 163, 688.

Somerfield, P.J., Clarke, R., Warwick, R.M., Dulvy, N.K., 2008. Average functional distinctness as a measure of the composition of assemblages. ICES J. Mar. Sci. 65, 1462–1468.

Stelzenmüller, V., Maynou, F., Martín, P., 2009. Patterns of species and functional diversity around a coastal marine reserve: a fisheries perspective. Aquat. Conserv. Mar. Fresh. Ecosyst. 19, 554–565.

Villéger, S., Ramos Miranda, J., Flores Hernandez, D., Mouillot, D., 2010. Contrasted changes in taxonomic and functional diversity of tropical fish communities after habitat degradation. Ecol. Appl. 20, 1512–1522.

Villéger, S., Novack-Gottshall, P.M., Mouillot, D., 2011. The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. Ecol. Lett. 14, 561–568.

Visalakshi, N.K., Thangavel, K., 2009. Impact of normalization in distributed K-means clustering. Inter. J. Soft Comput. 4, 168–172.

Wagner, C.E., McIntyre, P.B., Buels, K.S., Gilbert, D.M., Michel, E., 2009. Diet predicts intestine length in Lake Tanganyika's cichlid fishes. Funct. Ecol. 23, 1122–1131.

Wainwright, P.C., Richard, B.A., 1995. Predicting patterns of prey use from morphology of fishes. Environ. Biol. Fish. 44, 97–113.

Wainwright, P.C., Bellwood, D.R., Westneat, M.W., 2002. Ecomorphology of locomotion in labrid fishes. Environ. Biol. Fish. 65, 47–62.

Warwick, R.M., Clarke, K.R., 1995. New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. Mar. Ecol. Prog. Ser. 129, 301–305.

Webb, P.W., 1984. Body form, locomotion and foraging in aquatic vertebrates. Am. Zool. 24, 107–120.

Winemiller, K.O., 1991. Ecomorphological diversification in lowland fresh-water fish assemblages from 5 biotic regions. Ecol. Monogr. 61, 343–365.

Willis, S.C., Winemiller, K.O., Lopez-Fernandez, H., 2005. Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river. Oecologia 142, 284–295.

Wilsey, B.J., Chalcraft, D.R., Bowles, C.M., Willig, M.R., 2005. Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. Ecology 86 (5), 1178–1184.

Zelditch, M.L., Sheets, H.D., Fink, W.L., 2003. The ontogenic dynamics of shape disparity. Paleobiology 29, 139–156.

Ichthyol Res (2014) 61:152–158
DOI 10.1007/s10228-014-0390-2

FULL PAPER

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

Víctor M. Tuset · Marc Farré · Antoni Lombarte ·
Fernando Bordes · Rupert Wienerroither ·
Pilar Olivar

Received: 5 October 2013 / Revised: 5 December 2013 / Accepted: 10 January 2014

Abstract The morphology of fishes plays a very important role in the ecosystem biodiversity to show 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 the 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

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 the organisms have 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 (Tyszka 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 2001; Rohlf and Marcus 2003). 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 space (Fig. 1), also called patterning. Recently, morphological studies have used the quadrant analysis as an approach to describe this patterning (Shen et al. 2008; Goatley et al. 2010; Ricklefs 2012; Werdelin and Lewis 2013).

Electronic supplementary material The online version of this article (doi:10.1007/s10228-014-0390-2) contains supplementary material, which is available to authorized users.

V. M. Tuset (✉) · M. Farré · A. Lombarte · P. Olivar
Institute of Marine Science, Passeig Marítim 37-49,
08003 Barcelona, Spain
e-mail: vtuset@icm.csic.es

F. Bordes
Department of Fisheries Resources, Canarian Institute of Marine Science (ICCM ACIISI), P.O. Box. 56,
35200 Telde (Las Palmas), Canary Islands, Spain

R. Wienerroither
Institute of Marine Research, P.O. Box 1870, Nordnes,
5817 Bergen, Norway

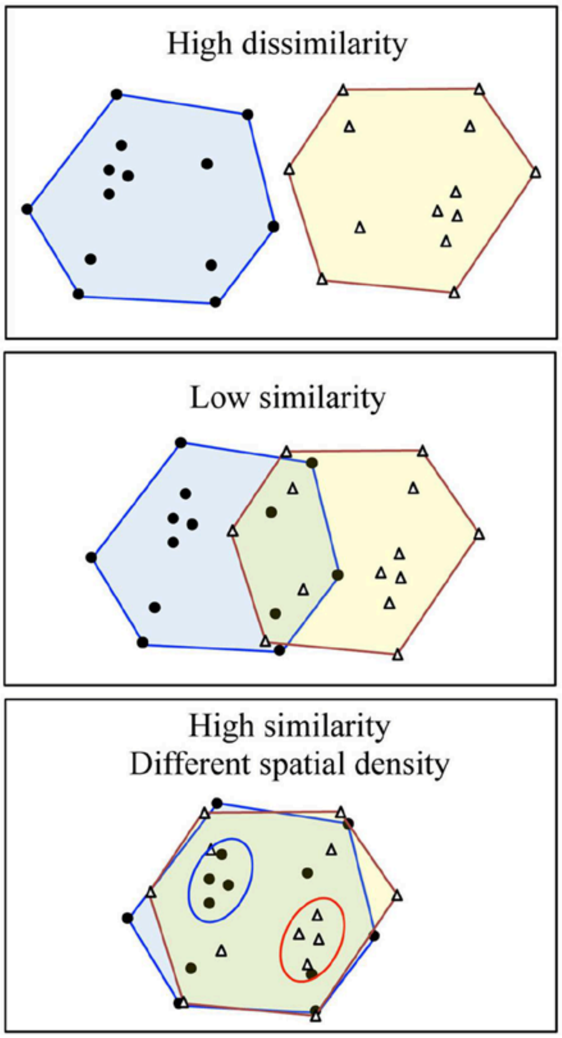


Fig. 1 Similarity between theoretical spaces showing spatial distribution variation in the set data (*coloured circles*)

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 also true that in some species, fins and other sensorial organs ("singular structures") are also key factors in behaviours (Colgate and Lynch 2004; Yamanoue 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 for "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 success 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 (Wienerroither 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.

Materials and methods

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 [Electronic supplementary material (ESM) Table S1]. 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) (ESM Fig. S1): "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 (09:45–17:45) and nighttime (20:10–02:00). 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).

Morphospace analysis. The changes in fish shapes were quantified using geometric morphometric techniques (Bookstein 1991; Rohlf and Marcus 2003). Due to the special morphology of many deep fishes, we decided to use semi-landmarks 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 semi-landmarks (ESM Fig. S2) were digitalised with tpsDig 2.16 (Rohlf 2001) 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 (GLS) procedure (generalised Procrustes) to remove scale and orientation distortions using tpsRew 1.24 (Rohlf 2001). Changes in fish shape were visualised using relative warp analysis of superimposed landmark coordinates (Rohlf and Marcus 2003). 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 a 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 (MDS). 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 are 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 MDS. All statistical calculations were carried out using the PRIMER V6.1.13 computer program (Clarke and Gorley 2006) and PAST ver. 2.10 (Hammer and Harper 2006).

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).

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 sensorial barbels (Stomiidae, Stomiiformes), high body and big head (Sternoptychidae, Stomiiformes), big head and narrow caudal peduncle (Stephanoberyciformes), and high 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 the absence of "non-typical shapes" (ESM Fig. S3). 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%) (ESM Fig. S3). In the remaining assemblages, only the LMD assemblage had Lophiiformes, which clearly conditioned its

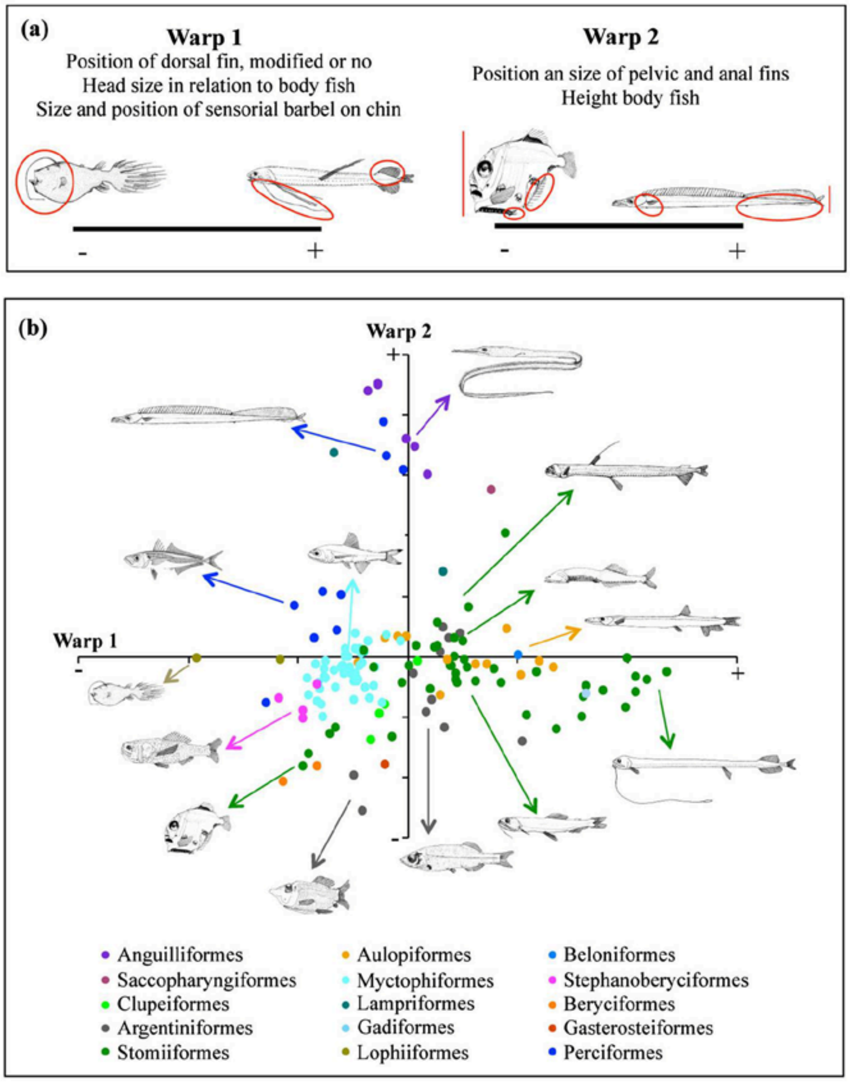


Fig. 2 Morphological meaning of warps 1 and 2 (**a**), and plot representing all species in the morphospace helping to its comprehension (**b**)

similarity with the other assemblages (25.4–33.3%) (Fig. S3). The cluster and MDS analyses grouped the upper mesopelagic assemblages with LMN and then with LMD (ESM Fig. S4a). This is a consequence of the spatial distribution of *Oneirodes anisacanthus* (Lophiiformes) on the *x*-axis, improving the convex hull and dissimilarity among these assemblages.

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 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 (ESM Fig. S4b). 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 (ESM Fig. S4b).

Discussion

The morphological diversity within an assemblage depends on which mechanism is acting to promote species coexistence

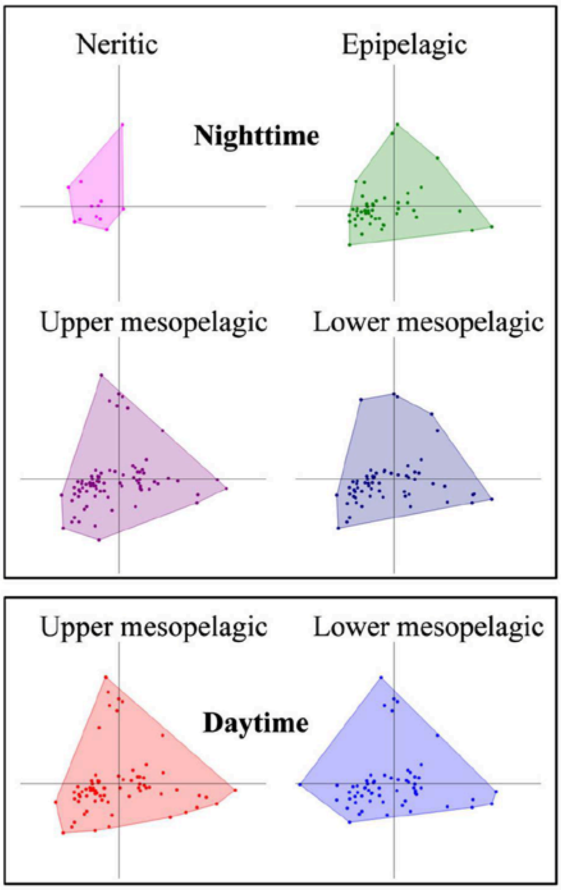


Fig. 3 Warp plot with convex hull delineating the morphospace realised by mesopelagic fish assemblages

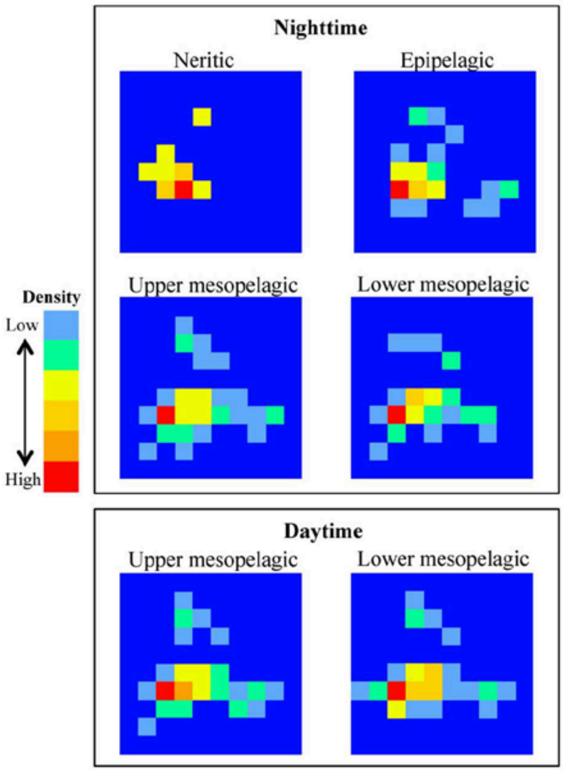


Fig. 4 Warp plot with patterning of morphospace realized by mesopelagic fish assemblages. *Colours scale* indicates the density of species in each cell

(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 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 (De Witt 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. 2009). 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 to distinguish and feed on other preys lesser visible, such as polychaetes and gelatinous organisms (Mauchile 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.

At the centre of the morphospace, the active piscivore foragers have well-muscled bodies, well-developed eyes

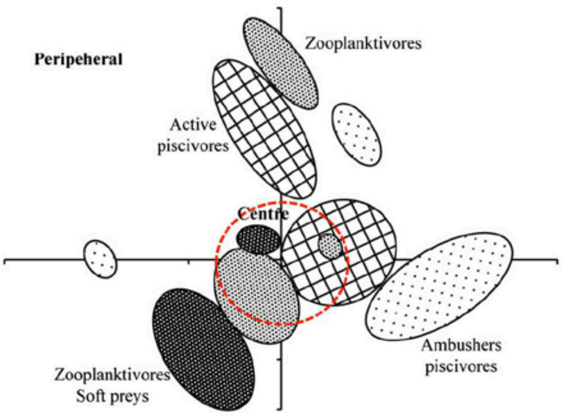


Fig. 5 Warp plot with feeding groups of mesopelagic fishes

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

Acknowledgments The surveys were carried out in projects supported by the Viceconsejería de Pesca del Gobierno de Canarias. We especially thank Mrs. Isabel Bordes Cabrera for the fish drawings in this paper by allowing its reproduction from the book "Catálogo de especies meso y batipelágicas. Peces, moluscos y crustáceos. Colectadas con arrastre en las Islas Canarias durante las campañas realizadasa bordo del B/E "La Bocaina". ICCM-Gobierno de Canarias. This research has been partially sponsored by the Spanish projects CTM2008-04489-C03-03 and CTM2012-39587-C04-03. Marc Farré Foix acknowledges a pre-doctoral grant from the Government of Andorra, ATC010-AND, academic year: 2012–2013.

References

Barlow KA, Sutton T (2008) Ecology of the midwater fish family Melamphaidae over the Mid-Atlantic Ridge. ICES CM 2008/C 17:1–10

Bookstein FL (1991) Morphometric tools for landmark data: geometry and biology. Cambridge University Press, New York

Bordes F, Wienerroither R, Uiblein F, Moreno T, Bordes I, Hernàndez V, Caballero C (2009) Catálogo con las especies meso y batipelágicas. Peces, moluscos y crustáceos. Colectadas con arrastre en las islas Canarias durante las campañas a bordo del B/E "La Bocaina". ICCM-ASCII-Gobierno de Canarias. Las Palmas, Spain

Cartes JE, Hidalgo M, Papiol V, Massuti E, Moranta J (2009) Changes in the diet and feeding of the hake *Merluccius merluccius* at the shelf-break of the Balearic Islands: influence of the mesopelagic-boundary community. Deep-Sea Res I 56:344–365

Clarke KR, Gorley RN (2006) PRIMER v6: user manual/ tutorial. PRIMER-E, Plymouth, UK

Colgate JE, Lynch KM (2004) Mechanics and control of swimming: a review. IEEE J Ocean Engin 29:660–673

Collin SP, Partridge JC (2006) Retinal specializations in the eyes of deep-sea teleost. J Fish Biol 49:157–174

Davis MP, Chakrabarty P (2011) Tripodfish (Aulopiformes: *Bathypterois*) locomotion and landing behaviour from video observation at bathypelagic depths in the Campos Basin of Brazil. Mar Biol Res 7:297–303

De Witt FA, Cailliet GM (1972) Feeding habits of two bristlemouth fishes, *Cyclothone acclidens* and *C. signata* (Gonostomatidae). Copeia 3:868–871

Drew JA, Buxman CL, Holmes DD, Mandecki JL, Mungkaje AJ, Richardson AC, Westneat MW (2012) Biodiversity inventories and conservation of the marine fishes of Bootless Bay, Papua New Guinea. BMC Ecol 12:15

Farré M, Tuset VM, Maynou F, Recasens L, Lombarte A (2013) Geometric morphology as an alternative for measuring the diversity of fish assemblages. Ecol Indic 29:159–166

Foote M (1997) The evolution of morphological diversity. Annu Rev Ecol Evol Syst 28:129–152

Gartner JV, Crabtree RE, Sulak KJ (1997) Feeding at depth. In: Randal DJ, Farrel AP (eds) Deep-sea fishes. Academic Press, New York, pp 115–93

Goatley CHR, Bellwood DR, Bellwood O (2010) Fishes on coral reefs: changing roles over the past 240 million years. Paleobiol 36:415–427

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4:379–391

Gosline WA (1994) Function and structure in the paired fins of scorpaeniform fishes. Environ Biol Fish 40:219–226

Haddock SHD, Moline MA, Case JF (2010) Bioluminescence in the Sea. Annu Rev Mar Sci 2:443–493

Hammer Ø, Harper DAT (2006) Paleontological data analysis. Blackwell Publishing, Oxford

Hopkins TL, Sutton TT, Lancarft TM (1996) The trophic structure and predation impact of a low latitude midwater fish assemblage. Prog Oceanogr 38:205–239

Kassam DD, Adams DC, Ambali AJD, Yamaoka K (2003) Body shape variation in relation to resource partitioning within cichlid trophic guilds coexisting along the rocky shore of Lake Malawi. Anim Biol 53:59–70

Kneitel JM, Chase JM (2004) Trade-offs in community ecology: linking spatial scales and species coexistence. Ecol Lett 7:69–80

Lavin PA, Mcphail JD (1985) The evolution of freshwater diversity in threespine stickleback (*Gasterosteus aculeatus*): site-specific differentiation of trophic morphology. Can J Zool 63:2632–2638

Layman CA, Langerhans RB, Winemiller KO (2005) Body size, not other morphological traits, characterizes cascading effects in fish assemblage composition following commercial netting. Can J Fish Aquat Sci 62:2802–2810

Lombarte A, Aguirre H (1997) Quantitative differences in the chemoreceptor systems in the barbels of two species of Mullidae (*Mullus surmuletus* and *M. barbatus*) with different bottom habitats. Mar Biol Prog Ser 150:57–64

Lombarte A, Gordoa A, Whitfield AK, James NC, Tuset VM (2012) Ecomorphological analysis as a complementary tool to detect changes in fish communities following major perturbations in two South African estuarine systems. Environ Biol Fish 94:601–614

McClain CR, Johnson NA, Rex MA (2004) Morphological disparity as a biodiversity metric in lower bathyal and abyssal gastropod assemblages. Evol 58:338–348

Mauchile J, Gordon JDM (1986) Foraging strategies of deep-sea fish. Mar Ecol Prog Ser 27:227–238

Muss BJ, Nielsen JG (1999) Sea fish. Scandinavian Fishing Year Book. Hedehusene, Denmark

Olivar MP, Bernal A, Molí B, Peña M, Balbín R, Castellón A, Miquel J, Massutí E (2012) Vertical distribution, diversity and assemblages of mesopelagic fishes in the western Mediterranean. Deep-Sea Res I 62:53–69

Pierce SE, Angielczyk KD, Rayfield EJ (2009) Morphospace occupation in thalattosuchian crocodylomorphs: skull shape variation, species delineation and temporal patterns. Paleontol 52:1057–1097

Pusch C, Beckmann A, Porteiro FM, Westernhagen von H (2004) The influence of seamounts on mesopelagic fish communities. Arch Fish Mar Res 51:165–186

Recasens L, Lombarte A, Sánchez P (2006) Teleostean fish composition and structure of an artificial reef and a natural rocky area in Catalonia (North Western Mediterranean). Bull Mar Sci 78:71–82

Ricklefs RE (1990) Ecology, 3rd edition. W.H. Freeman, New York

Ricklefs RE (2012) Species richness and morphological diversity of passerine birds. Proc Natl Acad Sci 109:14482–14487

Rohlf FJ (2001) TPS Dig 1.31 and TPS relative wards software. State University of New York at Stony Brook, New York

Rohlf FJ, Marcus LF (2003) A revolution in morphometrics. Trends Ecol Evol 8:129–132

Ross SW, Quattrini AM, Roa-Varón AY, McClain JP (2010) Species composition and distributions of mesopelagic fishes over the slope of the north-central Gulf of Mexico. Deep-Sea Res II 57:1926–1956

Roy K, Foote M (1997) Morphological approaches to measuring biodiversity. Trends Ecol Evol 12:277–281

Salvanes AGV, Kristoffersen JB (2001) Mesopelagic Fishes. In: Steel J, Thorpe S, Turekian K (eds) Encyclopedia of Ocean Sciences. Academic Press, San Diego. pp 1711-1717

Shen B, Dong L, Xiao S, Kowalewski M (2008) The Avalon explosion: evolution of Ediacara morphospace. Science 319:81–84

Shimazaki M, Nakaya K (2004) Functional anatomy of the luring apparatus of the deep-sea ceratioid anglerfish *Cryptopsaras couesii* (Lophiiformes: Ceratiidae). Ichthyol Res 51:33–37

Sutton TT, Hopkins TL (1996) The species composition, abundance and vertical distribution of the stomiid (Pisces: Stomiiformes) fish assemblage of the Gulf of Mexico. Bull Mar Sci 59:530–542

Tyszka J (2006) Morphospace of foraminiferal shells: results from the moving reference model. Lethaia 39:1–12

Uiblein F, Bordes F (1999) Complex trophic interactions around ocean islands. Ocean Challenge 9:15–16

Villéger S, Novack-Gottshall PM, Mouillot D (2011) The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. Ecol Lett 14:561–568

Walker JA (2010) An integrative model of evolutionary covariance: a symposium on body shape in fishes. Integr Comp Biol 50:1051–1056

Ward AB, Mehta RS (2010) Axial elongation if fishes: using morphological approaches to elucidate developmental mechanisms in studying body shape. Integr Comp Biol 50:1091–1105

Werdelin L, Lewis ME (2013) Temporal change in functional richness and evenness in the Eastern African Plio-Pleistocene carnivoran guild. PLoSONE 8: e57944

Wienerroither R, Uiblein F, Bordes F, Moreno T (2009) Composition, distribution, and diversity of pelagic fishes around the Canary Islands, Eastern Central Atlantic. Mar Biol 5:328–344

Yamanoue Y, Setiamarga DHE, Matsuura K (2010) Pelvic fins in teleosts: structure, function and evolution. J Fish Biol 77: 1173–1208

Journal of Sea Research 99 (2015) 107–117

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Habitat influence in the morphological diversity of coastal fish assemblages

Marc Farré *, Antoni Lombarte, Laura Recasens, Francesc Maynou, Victor M. Tuset

Institut de Ciències del Mar (ICM-CSIC), Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Catalonia, Spain

ARTICLE INFO

Article history:
Received 9 December 2014
Received in revised form 9 February 2015
Accepted 7 March 2015
Available online 14 March 2015

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

ABSTRACT

Ecological diversity based on quantitative data is widely used to characterize 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.

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., 2007), 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 behaviours 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 behaviours (Almany, 2004; Pitcher, 1986), and locomotion (Blake, 2004; Yamanoue 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, is

---

* Corresponding author. Tel.: +34 932 309 500; fax: +34 932 309 555.
E-mail address: farre@icm.csic.es (M. Farré).

http://dx.doi.org/10.1016/j.seares.2015.03.002
1385-1101/© 2015 Elsevier B.V. All rights reserved.

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.

2. Material and methods

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; Gordoa, 2009; Macpherson et al., 2000, 2002).

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).

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 characterized 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).

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

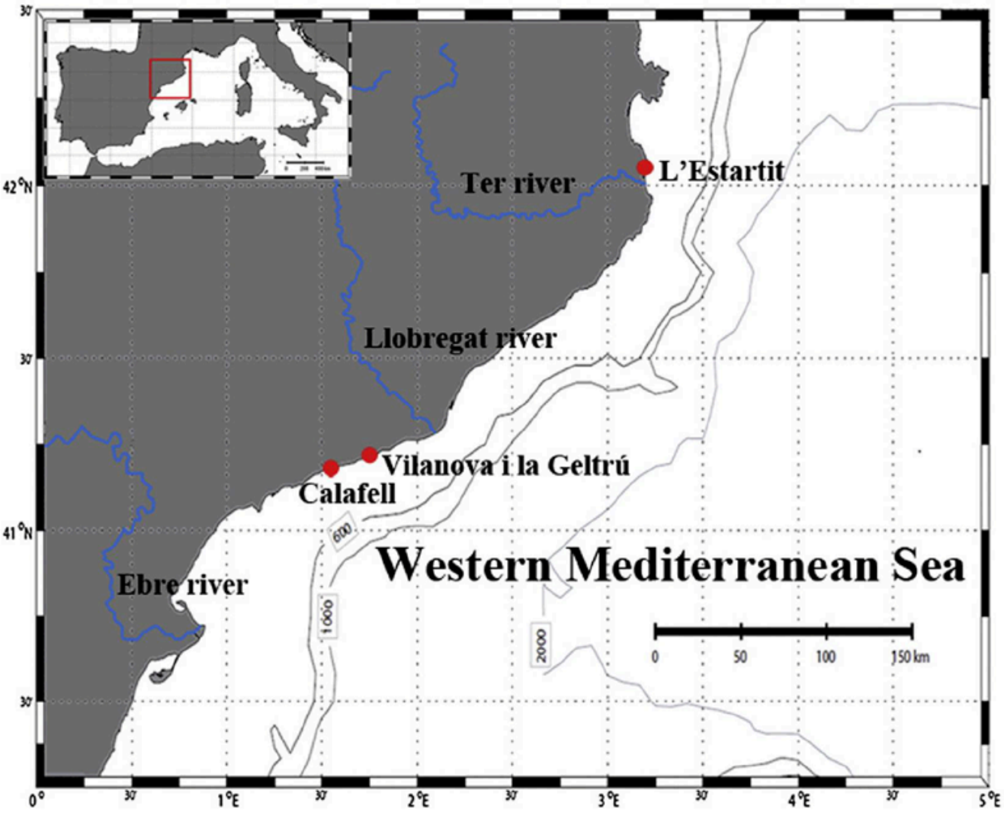


Fig. 1. Geographical localization of study areas: Vilanova i la Geltrú-Calafell or Central zone and L'Estartit or Northern zone.

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 the 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 the Supplementary Materials). 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 (*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).

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., 2007).

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 Fig. 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 standardized 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).

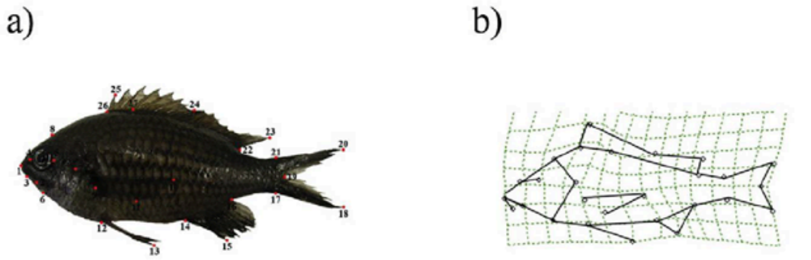
Landmarks and semilandmarks were digitised using tpsDig v. 2.16 (Rohlf, 2001a), and their record included body shape, fins position and size and other sensory organs that are key traits in behaviours such as locomotion, feeding, spawning or defence against predation (Gosline, 1994; Yamanoue et al., 2010). 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 tpsRel v. 1.49 (Rohlf, 2001c), 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).

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, 2001b). 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 standardize 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.

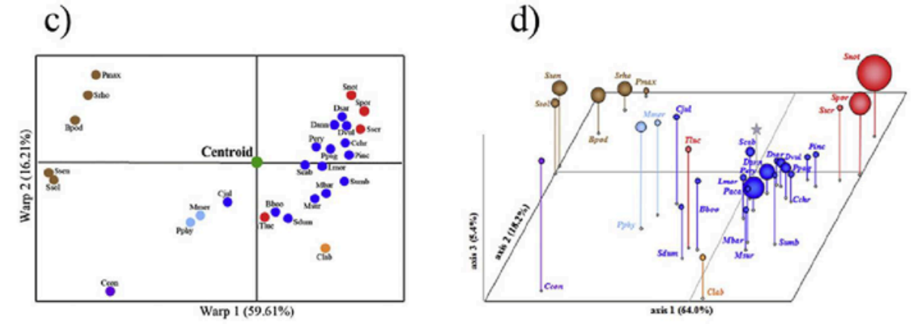
2.5. Environmental effect study

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



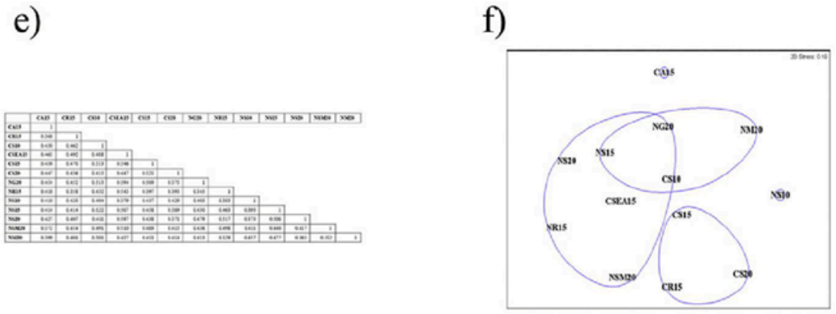
Selection of 27 landmarks
TPS Dig v. 2.16 (Rohlf 2001a)

Deformation grid
for each species



GLS procedure and thin-plate spline approach
Obtention consensus configuration and relative warps
TPS Relw v. 1.49 (Rohlf 2001c)

Construction of morphospaces using three first axes
Relative abundance data for each species (point sizes)



Comparison between morphospaces
Correlation matrix
TPS Pls v. 1.18 (Rohlf 2001b)

nMDS of morphospaces

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

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).

3. Results

3.1. Structure of fish assemblages

A high variability in specific composition and richness was noted among the different assemblages (see Table S1 in the Supplementary Materials). 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), *P. acarne* and *P. erythrinus* (Sparidae) especially in the assemblages containing hard substratum (*NG20*, *NR15* and *NS20*), whereas the assemblages from sandy bottoms (*NS10* and *NS15*) were also characterized 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, characterized by typical species of soft substrates such as *Sparus aurata* (Sparidae), *Sarda sarda* (Scombridae) or *Uranoscopus scaber* (Uranoscopidae).

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

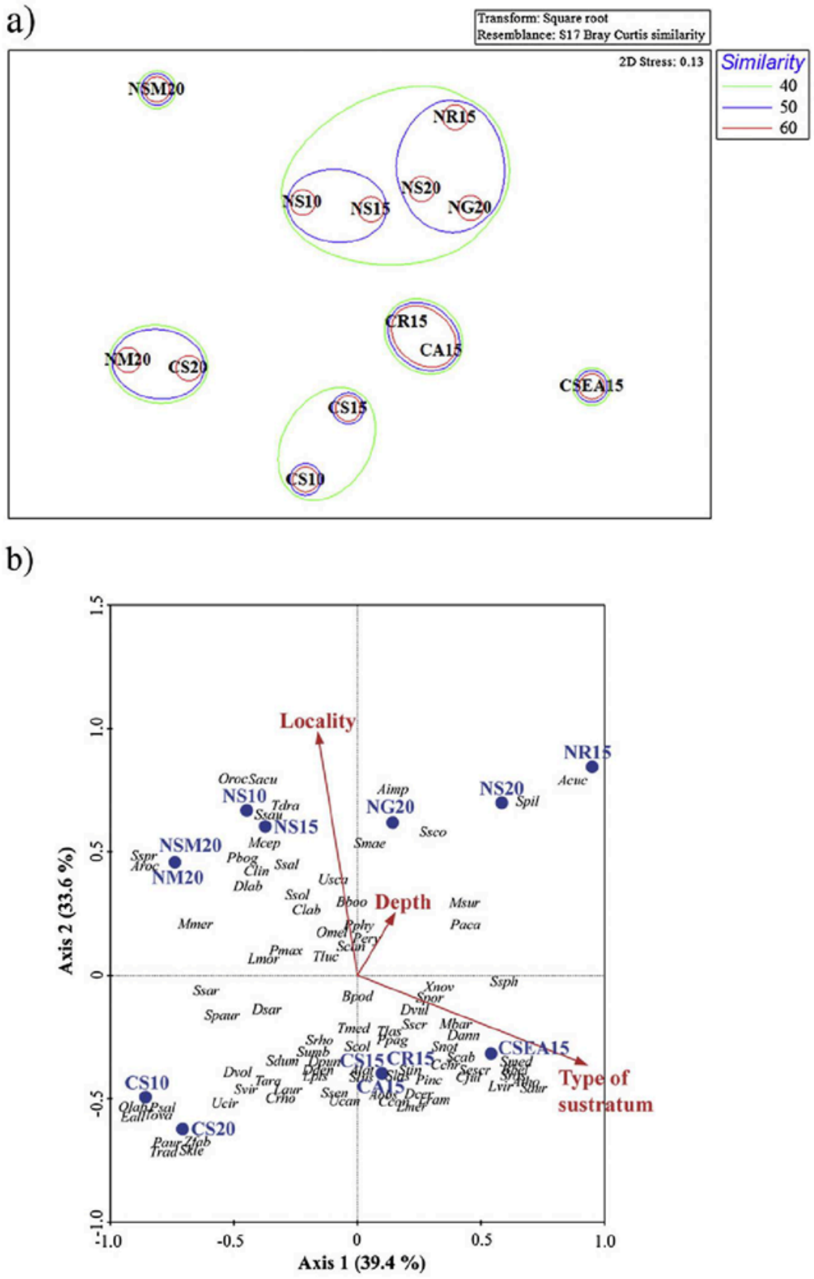


Fig. 3. Non-metric multidimensional scaling ordination (nMDS) from abundance data of the assemblages using the Bray–Curtis similarity (a) and correspondence canonical analysis (CCA) based on specific abundances, with the communities represented by points and environmental variables by vectors (b). The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

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.

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.

The morphological structure of the assemblages (two illustrative examples were selected and are shown in Fig. 6; for the remaining assemblages, see the Supplementary Materials, Fig. S1–S6) showed

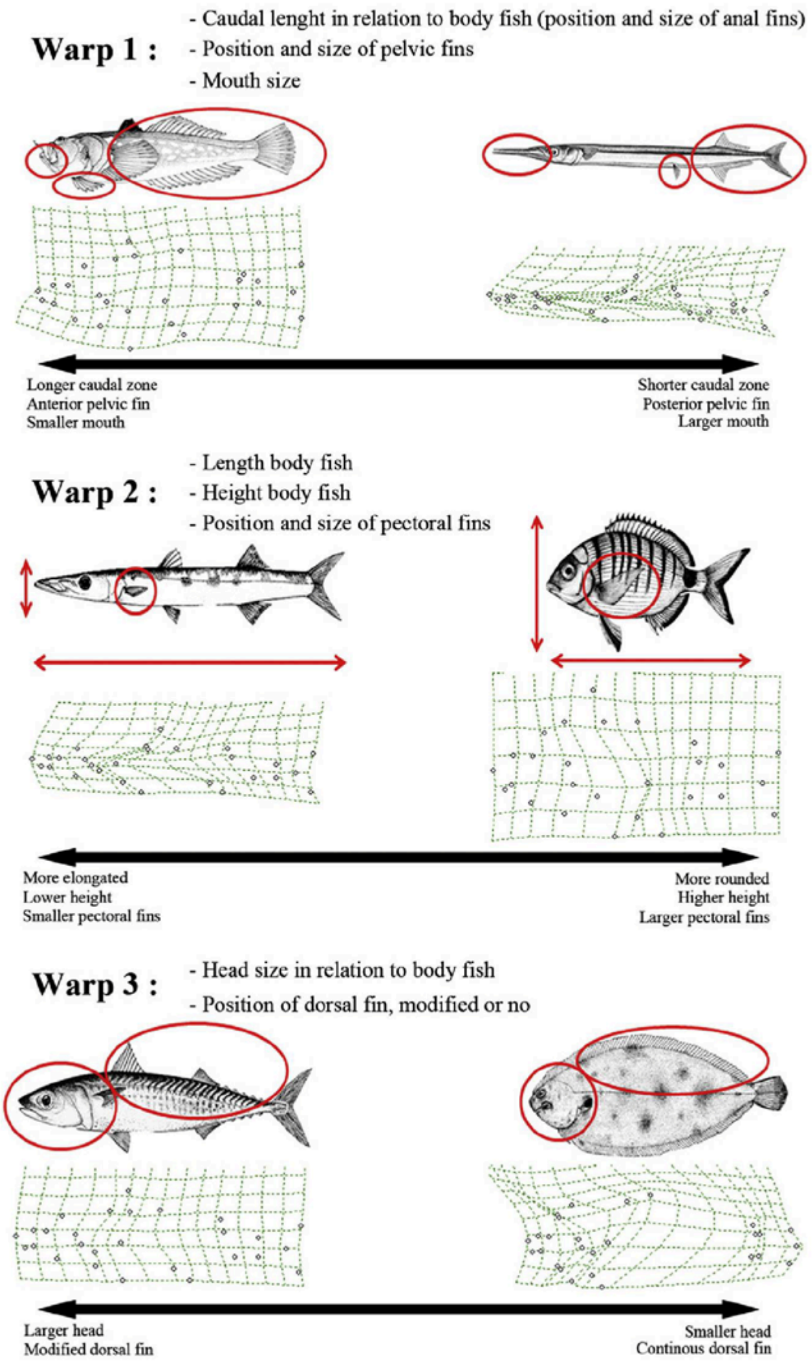


Fig. 4. Scheme representing the main morphological characteristics defined by the three axes of the morphospace, coinciding with the first three relative warps.

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*, *S. 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 *M. 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.

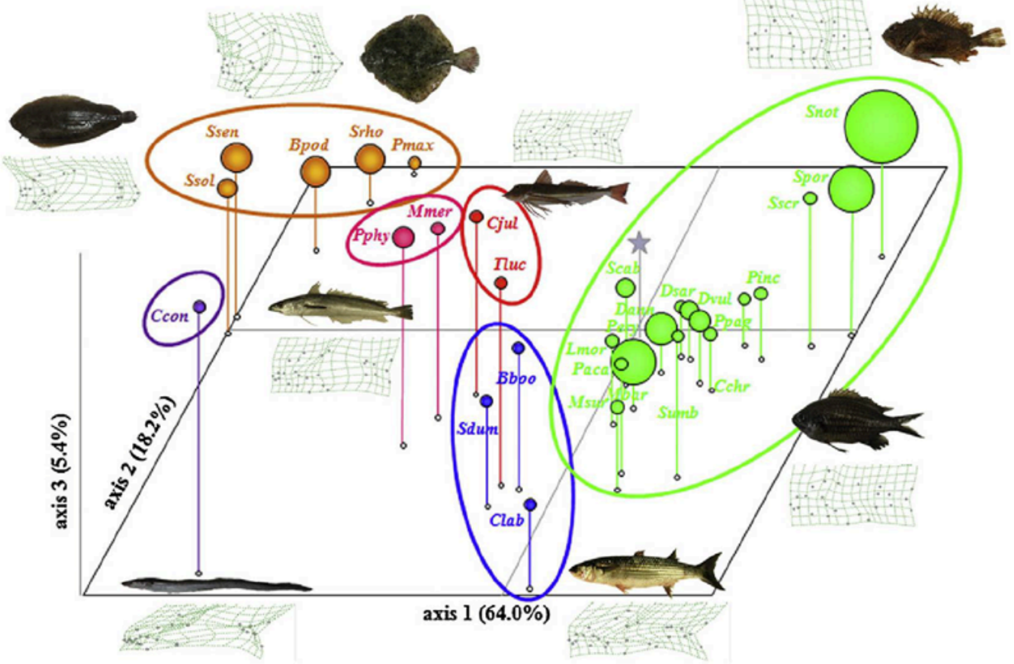


Fig. 5. Example of the main morphological groups differentiated within the morphospaces, each of them represented by different colours. Deformation grids indicating shapes found within each group are provided, as well as images of the represented species.

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 *M. cephalus, Synapturichthys kleinii, S. acus, Merluccius merluccius* or *Trachinus* spp.; to hard bottoms (*CSEA15, NG20, NR15*) and 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 *C. 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, A. imperialis, S. acus, Trachinus draco* or *A. 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.

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 (*C. 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 characterized 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

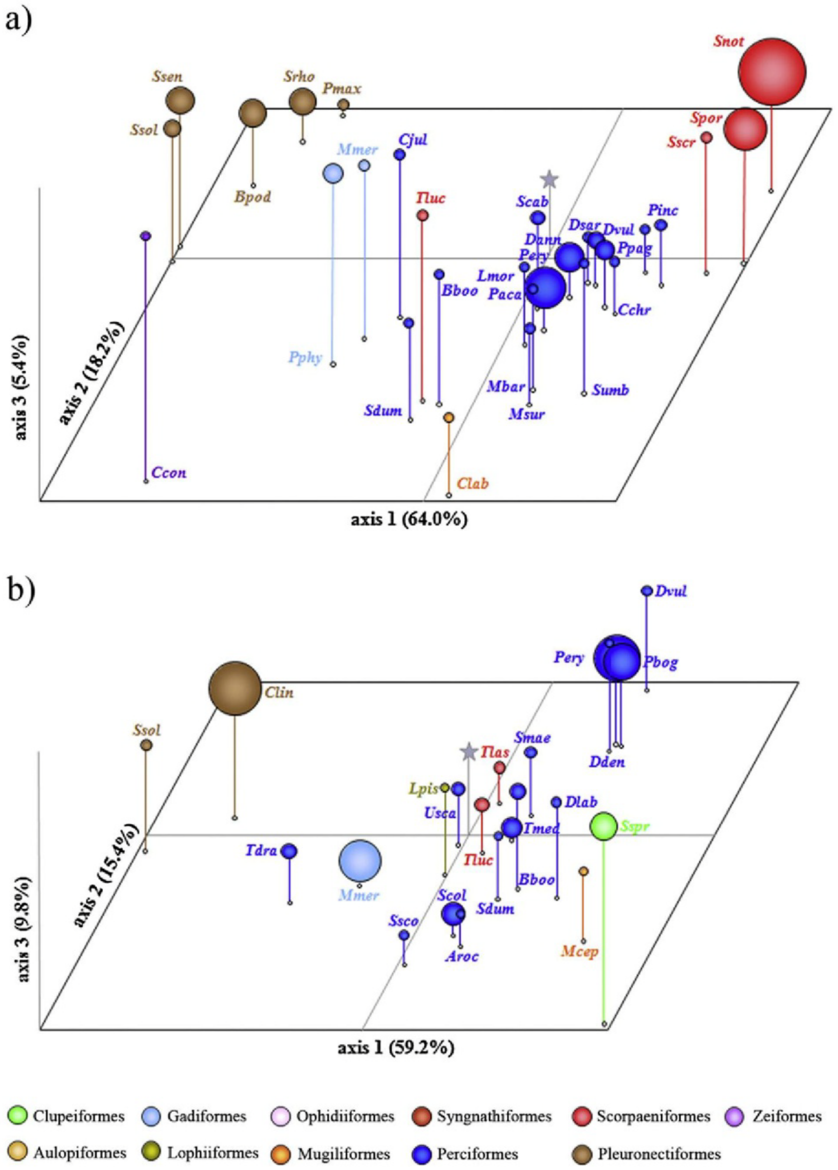


Fig. 6. Representation of the morphospaces of two fish assemblages: artificial reef assemblage (*CA15*) (a) and sandy–muddy assemblage (*NSM20*) (b). The first three relative warps represent the three axes of the morphospace, providing each of them the corresponding percentage of total morphological 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.

Table 1
Average correlation values among assemblages based on the PLS analysis (tps Pls v. 1.18; Rohlf, 2001b). Bold values indicate correlations > 0.45.

		Central zone						Northern zone						
Locality	Assemblages	CA15	CR15	CS10	CSEA15	CS15	CS20	NG20	NR15	NS10	NS15	NS20	NSM20	NM20
Central zone	CA15	1												
	CR15	0.368	1											
	CS10	0.430	**0.462**	1										
	CSEA15	**0.465**	**0.492**	**0.488**	1									
	CS15	0.439	**0.470**	**0.513**	**0.546**	1								
	CS20	0.447	0.436	0.415	0.447	**0.521**	1							
Northern zone	NG20	**0.454**	**0.452**	**0.513**	**0.594**	**0.509**	0.375	1						
	NR15	0.418	0.358	0.432	**0.543**	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	**0.522**	**0.507**	**0.458**	0.389	0.430	**0.463**	0.393	1			
	NS20	0.427	0.407	0.411	**0.597**	0.438	0.371	**0.479**	**0.517**	0.373	**0.508**	1		
	NSM20	0.372	**0.454**	**0.491**	**0.510**	**0.489**	0.415	0.436	**0.498**	0.411	0.440	0.417	1	
	NM20	0.399	0.401	**0.501**	0.427	**0.451**	0.414	0.413	0.329	**0.457**	**0.477**	0.365	0.352	1

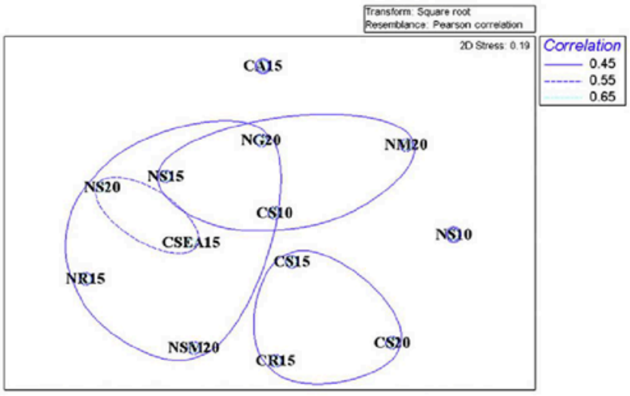


Fig. 7. Non-metric multidimensional scaling ordination (nMDS) from the average correlation matrix between morphospaces using Pearson's correlation.

different times during the year (Maynou et al., 2011). Moreover, the fishing area is larger and the fishing effort is widely distributed, which favours a lower impact on biodiversity and composition of assemblages. Besides, the introduction in this area in the 90s 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 these 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). 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., *C. conger*). That was also noted in the *NS10* assemblage as consequence of species such as *O. rochei* and *S. 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.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.seares.2015.03.002.

Acknowledgements

Data of this study were financed by project "ESCAL 1" (Ref. PCC30004/99), "ESCAL 2" (Ref. 02P30015) of the DG Fisheries of the Government of Catalonia, "CONFLICT" (Ref. CGL2008-00047) of the Spanish National Research Plans and "EMPAFISH" (E.U. DG MARE project Ref. 006539). Marc Farré Foix acknowledges a pre-doctoral grant from the Government of Andorra, ATC010-AND, academic years: 2012–2013 and 2013–2014. Dr. Victor Tuset was worker of CSIC (2010–2013) within the modality "JAE-Postdoc" of Programme "Junta para la Ampliación de Estudios" co-funded by the European Social Foundation (FSE).

References

Adams, D.C., 1999. Methods for shape analysis of landmark data from articulated structures. Evol. Ecol. Res. 1, 959–970.

Akin, S., Buhan, E., Winemiller, K.O., Yilmaz, H., 2005. Fish assemblage structure of Koycegiz Lagoon-Estuary, Turkey: spatial and temporal distribution patterns in relation to environmental variation. Estuar. Coast. Shelf Sci. 64, 671–684.

Albouy, C., Guilhaumon, F., Villéger, S., Mouchet, M., Mercier, L., Culioli, J.M., Tomasini, J.A., Le Loc'h, F., Mouillot, D., 2011. Predicting trophic guild and diet overlap from functional traits: statistics, opportunities, and limitations for marine ecology. Mar. Ecol. Prog. Ser. 436, 17–28.

Almany, G.R., 2004. Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? Oikos 106, 275–284.

Angeles, A.D.J., Gorospe, J.G., Torres, M.A.J., Demayo, C.G., 2014. Length–weight relationship, body shape variation and asymmetry in body morphology of *Siganus guttatus* from selected areas in five Mindanao bays. Int. J. Aquat. Sci. 5 (1), 40–57.

Azzurro, E., Tuset, V.M., Lombarte, A., Maynou, F., Simberloff, D., Rodríguez-Pérez, A., Solé, R.V., 2014. External morphology explains the success of biological invasions. Ecol. Lett. 17, 1455–1463.

Barros, F., Underwood, A.J., Lindegarth, M., 2001. The influence of rocky reefs on structure of benthic macrofauna in nearby soft-sediments. Estuar. Coast. Shelf Sci. 52, 191–199.

Blake, R.W., 2004. Fish functional design and swimming performance. J. Fish Biol. 65, 1193–1222.

Bookstein, F.L., 1991. Morphometric Tools for Landmark Data. Geometry and Biology. Cambridge University Press, New York.

Charbonnel, E., Serre, C., Ruitton, S., Harmelin, J.G., Jensen, A., 2002. Effects of increased habitat complexity on fish assemblages associated with large artificial reef units (French Mediterranean coast). ICES J. Mar. Sci. 59, 208–213.

Clarke, K.R., Warwick, R.M., 2001. A further biodiversity index applicable to species lists, variation in taxonomic distinctness. Mar. Ecol. Prog. Ser. 216, 265–278.

Claudet, J., Pelletier, D., Jouvenel, J.Y., Bachet, F., Galzin, R., 2006. Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: identifying community-based indicators. Biol. Conserv. 130, 349–369.

Claudet, J., García-Charton, J.A., Lenfant, P., 2011. Combined effects of levels of protection and environmental variables at different spatial resolutions on fish assemblages in a marine protected area. Conserv. Biol. 25 (1), 105–114.

Consoli, P., Romeo, T., Ferraro, M., Sarà, G., Andaloro, F., 2013. Factors affecting fish assemblages associated with gas platforms in the Mediterranean Sea. J. Sea Res. 77, 45–52.

Cooper, W.J., Westneat, M.W., 2009. Form and function of damselfish skulls: rapid and repeated evolution into a limited number of trophic niches. BMC Evol. Biol. 9, 24.

Costa, C., Cataudella, S., 2007. Relationship between shape and trophic ecology of selected species of Sparids of the Caprolace coastal lagoon (Central Tyrrhenian sea). Environ. Biol. Fish 78, 115–123.

Demestre, M., Sánchez, P., Abelló, P., 2000. Demersal fish assemblages and habitat characteristics on the continental shelf and upper slope on the north-western Mediterranean. J. Mar. Biol. Assoc. UK 80, 981–988.

Eklöv, P., Svanbäck, R., 2006. Predation risk influences adaptive morphological variation in fish populations. Am. Nat. 167 (3), 440–452.

Farré, M., Tuset, V.M., Maynou, F., Recasens, L., Lombarte, A., 2013. Geometric morphology as an alternative for measuring the diversity of fish assemblages. Ecol. Indic. 29, 159–166.

Félix-Hackradt, F.C., Hackradt, C.W., Treviño-Otón, J., Pérez-Ruzafa, A., García-Charton, J.A., 2014. Habitat use and ontogenetic shifts of fish life stages at rocky reefs in South-western Mediterranean Sea. J. Sea Res. 88, 67–77.

Foote, M., 1997. The evolution of morphological diversity. Annu. Rev. Ecol. Syst. 28, 129–152.

Franco, A., Franzoi, P., Malavasi, S., Riccato, F., Torricelli, P., Mainardi, D., 2006. Use of shallow water habitats by fish assemblages in a Mediterranean coastal lagoon. Estuar. Coast. Shelf Sci. 66, 67–83.

Fraschetti, S., Terlizzi, A., Bussotti, S., Guarnieri, G., D'Ambrosio, P., Boero, F., 2005. Conservation of Mediterranean seascapes: analyses of existing protection schemes. Mar. Environ. Res. 59, 309–332.

Friedman, M., 2010. Explosive morphological diversification of spiny-finned teleost fishes in the aftermath of the end-Cretaceous extinction. Proc. R. Soc. B 277, 1675–1683.

Gaertner, J.C., Mazouni, N., Sabatier, R., Millet, B., 1999. Spatial structure and habitat associations of demersal assemblages in the Gulf of Lions: a multicompartmental approach. Mar. Biol. 135, 199–208.

Gaertner, J.C., Bertrand, J.A., Gil de Sola, L., Durbec, J.P., Ferrandis, E., Souplet, A., 2005. Large spatial scale variation of demersal fish assemblage structure on the continental shelf of the NW Mediterranean Sea. Mar. Ecol. Prog. Ser. 297, 245–257.

García-Charton, J.A., Pérez-Ruzafa, A., 2001. Spatial pattern and the habitat structure of a Mediterranean rocky reef fish local assemblage. Mar. Biol. 138, 917–934.

García-Charton, J.A., Pérez-Ruzafa, A., Marcos, C., Claudet, J., Badalamenti, F., Benedetti-Cecchi, L., Falcón, J.M., Milazzo, M., Schembri, P.J., Stobart, B., Vandeperre, F., Brito, A., Chemello, R., Dimech, M., Domenici, P., Guala, I., Le Diréac'h, L., Maggi, E., Planes, S., 2008. Effectiveness of European Atlanto-Mediterranean MPAs: do they accomplish the expected effects on populations, communities and ecosystems? J. Nat. Conserv. 16, 193–221.

García-Rubies, A., 1999. Effects of fishing on community structure and on selected populations of Mediterranean coastal reef fish. Nat. Sicil. 23, 59–81 (supplement).

García-Rubies, A., Zabala, M., 1990. Effects of total fishing prohibition on the rocky fish assemblages of Medes Islands marine reserve (NW Mediterranean). Sci. Mar. 54, 317–328.

Gatz Jr., A.J., 1979. Community organization in fishes as indicated by morphological features. Ecology 60 (4), 711–718.

Gili, J.M., Ros, J., 1985. Study and cartography of the benthic communities of Medes Islands (NE Spain). PSZN I: Mar. Ecol. 6, 219–238.

Gordoa, A., 2009. Characterization of the infralittoral system along the north-east Spanish coast based on sport shore-based fishing tournament catches. Estuar. Coast. Shelf Sci. 82, 41–49.

Gosline, W.A., 1994. Function and structure in the paired fins of scorpaeniform fishes. Environ. Biol. Fish 40, 219–226.

Gratwicke, B., Speight, M.R., 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. J. Fish Biol. 66, 650–667.

Guidetti, P., 2000. Differences among fish assemblages associated with nearshore *Posidonia oceanica* seagrass beds, rocky–algal reefs and unvegetated sand habitats in the Adriatic Sea. Estuar. Coast. Shelf Sci. 50, 515–529.

Harmelin-Vivien, M., Le Diréac'h, L., Bayle-Sempere, J., Charbonnel, E., García-Charton, J.A., Ody, D., Pérez-Ruzafa, A., Reñones, O., Sánchez-Jerez, P., Valle, C., 2008. Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: evidence of fish spillover? Biol. Conserv. 141, 1829–1839.

Humphries, A.T., La Peyre, M.K., Kimball, M.E., Rozas, L.P., 2011. Testing the effect of habitat structure and complexity on nekton assemblages using experimental oyster reefs. J. Exp. Mar. Biol. Ecol. 409, 172–179.

Karr, J.R., James, F.C., 1975. Eco-morphological configurations and convergent evolution of species and communities. In: Cody, M.L., Diamond, J.M. (Eds.), Ecology and Evolution of Communities. Harvard University Press, Cambridge, pp. 258–291.

Kassam, D.D., Sato, T., Yamaoka, K., 2002. Landmark-based morphometric analysis of the body shape of two sympatric species, *Ctenopharynx pictus* and *Otopharynx* sp. "heterodon nankhumba" (Teleostei: Cichlidae), from Lake Malawi. Ichthyol. Res. 49, 340–345.

Kassam, D.D., Adams, D.C., Ambali, A.J.D., Yamaoka, K., 2003. Body shape variation in relation to resource partitioning within cichlid trophic guilds coexisting along the rocky shore of Lake Malawi. Anim. Biol. 53 (1), 59–70.

Kovalenko, K.E., Thomaz, S.M., Warfe, D.M., 2012. Habitat complexity: approaches and future directions. Hydrobiologia 685, 1–17.

La Mesa, G., Molinari, A., Gambaccini, S., Tunesi, L., 2010. Spatial pattern of coastal fish assemblages in different habitats in North-western Mediterranean. Mar. Ecol. 32, 104–114.

Labropoulou, M., Eleftheriou, A., 1997. The foraging ecology of two pairs of congeneric demersal fish species: importance of morphological characteristics in prey selection. J. Fish Biol. 50, 324–340.

Langerhans, R.B., Layman, C.A., Langerhans, A.K., Dewitt, T.J., 2003. Habitat-associated morphological divergence in two Neotropical fish species. Biol. J. Linn. Soc. 80, 689–698.

Langerhans, R.B., Chapman, L.J., DeWitt, T.J., 2007. Complex phenotype–environment associations revealed in an East African cyprinid. J. Evol. Biol. 20 (3), 1171–1181.

Layman, C.A., Langerhans, R.B., Winemiller, K.O., 2005. Body size, not other morphological traits, characterizes cascading effects in fish assemblage composition following commercial netting. Can. J. Fish. Aquat. Sci. 62, 2802–2810.

Letourneur, Y., Darnaude, A., Salen-Picard, C., Harmelin-Vivien, M., 2001. Spatial and temporal variations of fish assemblages in a shallow Mediterranean soft bottom area (Gulf of Fos, France). Oceanol. Acta 24, 273–285.

Lombarte, A., Gordoa, A., Whitfield, A.K., James, N.C., Tuset, V.M., 2012. Ecomorphological analysis as a complementary tool to detect changes in fish communities following major perturbations in two South African estuarine systems. Environ. Biol. Fish 94 (4), 601–614.

Maci, S., Basset, A., 2009. Composition, structural characteristics and temporal patterns of fish assemblages in non-tidal Mediterranean lagoons: a case study. Estuar. Coast. Shelf Sci. 83, 602–612.

Macpherson, E., 1994. Substrate utilisation in a Mediterranean littoral fish community. Mar. Ecol. Prog. Ser. 114, 211–218.

Macpherson, E., García-Rubies, A., Gordoa, A., 2000. Direct estimation of natural mortality rates for littoral marine fishes using populational data from a marine reserve. Mar. Biol. 137, 1067–1076.

Macpherson, E., Gordoa, A., García-Rubies, A., 2002. Biomass size spectra in littoral fishes in protected and unprotected areas in the NW Mediterranean. Estuar. Coast. Shelf Sci. 55, 777–788.

Martín, P., Maynou, F., Stelzenmüller, V., Sacanell, M., 2012. A small scale fishery near a rocky littoral marine reserve in the northwestern Mediterranean (Medes Islands) after two decades of fishing prohibition. Sci. Mar. 76 (3), 607–618.

Martins, G.M., Faria, J., Rubal, M., Neto, A.I., 2013. Linkages between rocky reefs and soft-bottom habitats: effects of predation and granulometry on sandy macrofaunal assemblages. J. Sea Res. 81, 1–9.

Maynou, F., Recasens, L., Lombarte, A., 2011. Fishing tactics dynamics of a Mediterranean small-scale coastal fishery. Aquat. Living Resour. 24, 149–159.

McClain, C.R., Johnson, N.A., Rex, M.A., 2004. Morphological disparity as a biodiversity metric in lower bathyal and abyssal gastropod assemblages. Evolution 58 (2), 338–348.

McCormick, M.I., 1994. Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. Mar. Ecol. Prog. Ser. 112, 87–96.

Menezes, G.M., Sigler, M.F., Silva, H.M., Pinho, M.R., 2006. Structure and zonation of demersal fish assemblages off the Azores Archipelago (mid-Atlantic). Mar. Ecol. Prog. Ser. 324, 241–260.

Mercader, L., Lloris, D., Rucabado, J.A., 2001. Tots els peixos del mar Català: Diagnosis i claus d'identificació. Institut d'Estudis Catalans, Barcelona.

Mérigot, B., Bertrand, J.A., Mazouni, N., Manté, C., Durbec, J.P., Gaertner, J.C., 2007. A multi-component analysis of species diversity of groundfish assemblages on the continental shelf of the Gulf of Lions (north-western Mediterranean Sea). Estuar. Coast. Shelf Sci. 73, 123–136.

Montaña, C.G., Winemiller, K.O., 2010. Local-scale habitat influences morphological diversity of species assemblages of cichlid fishes in a tropical floodplain river. Ecol. Freshw. Fish 19, 216–227.

Montaña, C.G., Winemiller, K.O., Sutton, A., 2014. Intercontinental comparison of fish ecomorphology: null model tests of community assembly at the patch scale in rivers. Ecol. Monogr. 84 (1), 91–107.

Mouillot, D., Gaillard, S., Aliaume, C., Verlaque, M., Belsher, T., Troussellier, M., Chi, T.D., 2005. Ability of taxonomic diversity indices to discriminate coastal lagoon environments based on macrophyte communities. Ecol. Indic. 5 (1), 1–17.

Nelson, J.S., 2006. Fishes of the World. Fourth ed. Wiley and Sons, New Jersey.

Norton, S.F., 1995. A functional approach to ecomorphological patterns of feeding in cottid fishes. Environ. Biol. Fish 44, 61–78.

Peres-Neto, P.R., 2004. Patterns in the co-occurrence of fish species in streams: the role of site suitability, morphology and phylogeny versus species interactions. Oecologia 140, 352–360.

Pessanha Pais, M., Henriques, S., Murta, A.G., Azevedo, M., Costa, M.J., Cabral, H.N., 2010. Identifying functional homogeneity in a dynamic environment: application to soft-substrate fish assemblages off the Portuguese coast. J. Sea Res. 89, 30–43.

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758.

Pinault, M., Bissery, C., Gassiole, G., Magalon, H., Quod, J.P., Galzin, R., 2014. Fish community structure in relation to environmental variation in coastal volcanic habitats. J. Exp. Mar. Biol. Ecol. 460, 62–71.

Pitcher, T.J., 1986. Functions of shoaling behaviour in teleosts. In: Pitcher, T.J. (Ed.), The Behaviour of Teleost Fishes. Springer, US, pp. 294–337.

Price, S.A., Holzman, R., Near, T.J., Wainwright, P.C., 2011. Coral reefs promote the evolution of morphological diversity and ecological novelty in labrid fishes. Ecol. Lett. 14, 462–469.

Recasens, L., Lombarte, A., Sánchez, P., 2006. Teleostean fish composition and structure of an artificial reef and a natural rocky area in Catalonia (North Western Mediterranean). Bull. Mar. Sci. 78, 71–82.

Ricklefs, R.E., 2010. Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. Proc. Natl. Acad. Sci. U. S. A. 107 (4), 1265–1272.

Rohlf, F.J., 2001a. TPS Dig 2.16 and TPS Relative Warps Software. State University of New York at Stony Brook.

Rohlf, F.J., 2001b. TPS Pls 1.18 and TPS Relative Warps Software. State University of New York at Stony Brook.

Rohlf, F.J., 2001c. TPS Relw Version 1.49 and TPS Relative Warps Software. State University of New York at Stony Brook.

Rohlf, F.J., Corti, M., 2000. Use of two-block partial least-squares to study covariation in shape. Syst. Biol. 49 (4), 740–753.
Rohlf, F.J., Marcus, L.F., 1993. A revolution in morphometrics. Trends Ecol. Evol. 8 (4), 129–132.
Ruitton, S., Francour, P., Boudouresque, C.F., 2000. Relationships between algae, benthic herbivorous invertebrates and fishes in rocky sublittoral communities of a Temperate Sea (Mediterranean). Estuar. Coast. Shelf Sci. 50, 217–230.
Selleslagh, J., Amara, R., 2008. Environmental factors structuring fish composition and assemblages in a small macrotidal estuary (eastern English Channel). Estuar. Coast. Shelf Sci. 79, 507–517.
Somerfield, P.J., Clarke, R., Warwick, R.M., Dulvy, N.K., 2008. Average functional distinctness as a measure of the composition of assemblages. ICES J. Mar. Sci. 65, 1462–1468.
Stelzenmüller, V., Maynou, F., Martín, P., 2007. Spatial assessment of benefits of a coastal Mediterranean Marine Protected Area. Biol. Conserv. 136, 571–583.
Stelzenmüller, V., Maynou, F., Martín, P., 2009. Patterns of species and functional diversity around a coastal marine reserve: a fisheries perspective. Aquat. Conserv. Mar. Freshwat. Ecosyst. 19, 554–565.
Svanbäck, R., Eklöv, P., 2002. Effects of habitat and food resources on morphology and ontogenetic growth trajectories in perch. Oecologia 131, 61–70.
ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 65 (7), 1167–1179.
ter Braak, C.J.F., Šmilauer, P., 2002. CANOCO Reference Manual and CANODRAW for Windows User's Guide: Software for Canonical Community Ordination, Version 4.5. Microcomputer Power, Ithaca, New York.
Tunesi, L., Molinari, A., Salvati, E., 2006. Fish assemblage of the marine protected area of Cinque Terre (NW Mediterranean Sea): first characterization and assessment by visual census. Chem. Ecol. 22 (1), 245–253.
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). Ichthyol. Res. 61, 152–158.
Tuya, F., Boyra, A., Sanchez-Jerez, P., Haroun, R.J., 2005. Multivariate analysis of the bentho-demersal ichthyofauna along soft bottoms of the Eastern Atlantic: comparison between unvegetated substrates, seagrass meadows and sandy bottoms beneath sea-cage fish farms. Mar. Biol. 147, 1229–1237.
Villéger, S., Ramos Miranda, J., Flores Hernandez, D., Mouillot, D., 2010. Contrasted changes in taxonomic and functional diversity of tropical fish communities after habitat degradation. Ecol. Appl. 20 (6), 1512–1522.
Wainwright, P.C., Belwood, D.R., Westneat, M.W., Grubich, J.R., Hoey, A.S., 2004. A functional morphospace for the skull of labrid fishes: patterns of diversity in a complex biomechanical system. Biol. J. Linn. Soc. 82, 1–25.
Wedding, L.M., Friedlander, A.M., McGranaghan, M., Yost, R.S., Monaco, M.E., 2008. Using bathymetric Lidar to define nearshore benthic habitat complexity: implications for management of reef fish assemblages in Hawaii. Remote Sens. Environ. 112, 4159–4165.
Willis, S.C., Winemiller, K.O., Lopez-Fernandez, H., 2005. Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river. Oecologia 142, 284–295.
Winemiller, K.O., 1991. Ecomorphological diversification in lowland fresh-water fish assemblages from five biotic regions. Ecol. Monogr. 61, 343–365.
Yamanoue, Y., Setiamarga, D.H.E., Matsuura, K., 2010. Pelvic fins in teleosts: structure, function and evolution. J. Fish Biol. 77, 1173–1208.
Zelditch, M.L., Sheets, H.D., Fink, W.L., 2003. The ontogenic dynamics of shape disparity. Paleobiology 29, 139–156.

15

Glossary

15.1 General concepts

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

15.2 Biodiversity concepts

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

15.3 Fish assemblages

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

15.4 Statistical and analytical methods

CCA	Correspondence Canonical Analysis
GPA / GLS	General Procrustes Analyses / General Least-square Superimposition procedure
***K-S* test**	Kolmogorov-Smirnov test
MANOVA	Multivariate ANalysis of VAriance
nMDS	non-metric MultiDimensional Scaling analysis
OLS	Ordinary Least Square method
PCA	Principal Components Analysis
PCoA	Principal Coordinates Analysis
PCoA1	Axis nº 1 of the PCoA
PCoA2	Axis nº 2 of the PCoA
PCoA3	Axis nº 3 of the PCoA
PCoA4	Axis nº 4 of the PCoA
PCoA*x*	Axis nº *x* of the PCoA
PLS	Partial Least Square method
QSOR	Sum of range of the middle two quartiles
r	Clark-Evans nearest neighbor
$\mathbf{R^2}$	Coefficient of determination
RDA	Redundancy Analysis
RDA1	Axis nº 1 of the RDA
RDA2	Axis nº 2 of the RDA
RW1	Axis represented by the Relative Warp nº 1
RW2	Axis represented by the Relative Warp nº 2
RW3	Axis represented by the Relative Warp nº 3
RW4	Axis represented by the Relative Warp nº 4
SOV	Sum of Variance
UPGMA	Unweighted Pair Group Method with Arithmetic mean
VMR	Variance-to-Mean Ratio