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THE FUNCTIONAL STRUCTURE OF MEDITERRANEAN SEAGRASS FISH ASSEMBLAGES WITH A GLIMPSE ON LOCAL FISHING EFFECTS

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RIASSUNTO

Le fanerogame marine sono specie chiave che formano praterie estese in aree costiere poco profonde e offrono molteplici servizi ecosistemici, tra cui il miglioramento della qualità dell'acqua, la protezione costiera e lo stoccaggio del carbonio. Creano inoltre ecosistemi altamente produttivi e diversificati in tutto il mondo e fungono da aree di alimentazione, rifugio e nursery per molte specie, inclusi pesci di interesse commerciale. Tuttavia, le fanerogame marine sono in forte declino a causa degli effetti diretti e indiretti delle attività antropiche, come la frammentazione e la contrazione dell'habitat causate dalla pesca a strascico, dall'inquinamento costiero e dal riscaldamento globale. Questo fenomeno è di interesse globale poiché il degrado degli habitat a fanerogame influenza direttamente le popolazioni ittiche, con possibili riduzioni nel reclutamento degli stadi giovanili dei pesci che potrebbero avere un impatto negativo sulle attività di pesca locali e globali.

Le comunità ittiche associate alle praterie di fanerogame marine sono generalmente caratterizzate da un alto livello di diversità, sia tassonomica che filogenetica e funzionale, ospitando una non trascurabile porzione (circa il 38%) di tutte le specie di pesci conosciute nel Mediterraneo, pur coprendo meno del 2% del fondale marino. Tuttavia, sebbene la diversità tassonomica delle comunità ittiche sia ampiamente documentata, la loro struttura funzionale e le relazioni con la complessità, la copertura e la distribuzione delle diverse fanerogame marine rappresentano aspetti spesso trascurati. Offrendo complessità strutturale e produttività primaria, le fanerogame marine sostengono diverse funzioni ecologiche, come il ciclo dei nutrienti e le interazioni trofiche, e sono essenziali per mantenere la resilienza e la funzionalità delle comunità ittiche in quanto forniscono habitat essenziali per l'alimentazione, la sopravvivenza e la riproduzione. Infatti, la stratificazione verticale delle praterie (i.e., porzione superiore, centrale e inferiore) offre diverse combinazioni di luce, cibo e rifugio, in grado di sostenere un'ampia varietà di specie, alcune delle quali utilizzano le praterie in ben determinati stadi vitali. Ne sono esempio i grandi predatori attivi che pattugliano le praterie e gli habitat circostanti alla ricerca di prede, la cui presenza sembra essere limitata alla fase adulta, come in alcune specie appartenenti alla famiglia Triakidae. Al contrario, molti pesci di piccole dimensioni utilizzano le fanerogame marine per tutto il ciclo vitale, trovando protezione dalla predazione e risorse alimentari, nutrendosi di epifiti, alghe microfite, macrofite ed invertebrati. Ne sono un esempio le specie appartenenti alle famiglie degli Sparidi e Gobidi o il pesce ago (*Syngnathus acus*), lo spinarello (*Gasterosteus aculeatus*), la perchia (*Serranus cabrilla*) e il grongo (*Conger conger*) tra le tante.

È interessante notare che in Mediterraneo i dati a sostegno delle diverse teorie sul ruolo delle fanerogame marine nel mantenere la diversità (sia tassonomica che funzionale) sono spesso limitati ad aree geografiche ristrette, non permettendo così una chiara interpretazione dei meccanismi alla

base della strutturazione delle comunità ittiche alla scala di bacino. Questo riduce la capacità di attuare strategie efficaci di conservazione e gestione. In questo quadro generale, la presente tesi di dottorato si è concentrata sull'indagine delle relazioni ecologiche tra le fanerogame marine mediterranee e la fauna ittica associata, con particolare attenzione alla diversità funzionale.

Al fine di rendere omogeneo il grande numero di informazioni troppo spesso frammentate a livello di bacino, è stato messo a punto un sistema per la revisione sistematica della letteratura scientifica semi-automatizzato, con ricerca tramite parole chiave e filtraggio basato su livelli soglia, al fine di fornire una sintesi completa delle specie ittiche presenti sugli habitat di fanerogame marine nel Mediterraneo, colmando le attuali lacune nella letteratura (Capitolo 1). Questo sforzo ha prodotto uno dei database più ampi ed aggiornati sulla presenza delle specie ittiche nelle principali fanerogame marine native del Mediterraneo, includendo informazioni geografiche (es. zone FAO, aree GFCM, coordinate dei siti), temporali (es. stagione e anno di campionamento), di campionamento (es. metodi, composizione dell'habitat) e bibliografiche, tra le altre, consentendo una sintesi narrativa della diversità ittica negli ecosistemi delle fanerogame marine.

In una fase successiva (Capitolo 2), il database è stato ampliato includendo informazioni sugli stadi vitali delle specie segnalate sulle diverse fanerogame marine, insieme a specifici tratti funzionali (riproduttivi, alimentari e modalità di predazione) associati all'uso potenziale dell'habitat da parte dei pesci. In particolare, la ricerca è stata incentrata sul verificare se le tre principali fanerogame marine native del Mediterraneo (*Posidonia oceanica*, *Cymodocea nodosa* e *Zostera marina*) ospitino e sostengano comunità di pesci con strategie funzionali simili, qui definite come specifiche combinazioni di tratti relativi alla riproduzione e all'alimentazione. Inoltre, sono stati utilizzati modelli lineari e modelli additivi generalizzati (GAM) per esplorare come le diverse strategie funzionali si relazionano agli stadi vitali delle specie, al fine di comprendere il legame tra strategie funzionali delle specie e utilizzo dell'habitat a fanerogame.

Nel Capitolo 3 sono stati approfonditi alcuni aspetti legati all'efficacia di specifiche pratiche di gestione e conservazione sulla composizione tassonomica e funzionale delle comunità ittiche associate ai posidonieti, utilizzando dati decennali relativi alla piccola pesca costiera. I dati sono stati raccolti a valle della messa in opera di una barriera antistrascico che ha impedito questa pratica di pesca illegale in due aree Natura 2000. I risultati hanno mostrato come le misure attive di conservazione delle praterie di *P. oceanica* abbiano portato ad un aumento delle dimensioni delle specie ittiche target per la piccola pesca costiera, indipendentemente dalle loro caratteristiche funzionali, anche se i tempi di recupero sono risultati diversi per le diverse categorie funzionali, con le specie di equilibrio (squali e razze) che hanno mostrato un ritardo nell'aumento della taglia rispetto alle altre.

Complessivamente, i risultati ottenuti in questa tesi hanno permesso di colmare lacune specifiche nello studio delle associazioni fanerogame/pesci, evidenziando al contempo aree di studio su cui focalizzare le ricerche future. L'identificazione di una "impronta funzionale" comune alle tre fanerogame indica un assemblaggio non casuale delle caratteristiche funzionali nelle comunità ittiche associate alle fanerogame del Mediterraneo, sostenendo l'ipotesi che la loro strutturazione dipenda in larga parte dal bilanciamento di diverse strategie riproduttive e alimentari, in grado di determinare l'uso ontogenetico dell'habitat, la strutturazione delle reti trofiche e il reclutamento delle specie, fondamentali per il mantenimento della biodiversità marina. I risultati ottenuti hanno importanti implicazioni, permettendo di identificare quelle che possono essere le potenziali risposte delle specie ai cambiamenti climatici e alla pressione della pesca, fornendo una base utile per comprendere come questi fattori influenzeranno le comunità ittiche nel prossimo futuro.

ABSTRACT

Seagrasses are key habitat-forming species in shallow coastal areas and provide multiple ecosystem services including improved water quality, coastal protection and carbon sequestration, create highly productive and diverse ecosystems worldwide and serve as foraging, sheltering and nursery grounds for many species, including fish of commercial interest. Seagrasses are declining at an accelerating rate, due to the direct and indirect effects anthropogenic impacts, such as habitat fragmentation and contraction driven by trawling, coastal pollution and global warming. This is of global interest because seagrass habitats degradation directly influences fish populations, possibly resulting in a lower recruitment of juvenile fish that might impact local and global fisheries.

Fish communities associated with seagrass meadows are usually characterized by high level of diversity, either taxonomic, phylogenetic or functional, hosting a huge proportion (ca. 38%) of all known Mediterranean fish species despite covering less than 2% of the sea floor. However, if the taxonomic diversity of fish assemblages is widely documented, their functional structure and the relationships with the complexity, coverage and distribution of different seagrasses represent an often-neglected aspect. By offering structural complexity and primary productivity, seagrasses support diverse ecological functions, such as nutrient cycling and trophic interactions, and are essential for maintaining the resilience and functionality of fish communities as they provide essential habitat for feeding, survival and reproduction. Indeed, the vertical stratification of the canopy (i.e., upper, middle and lower portion) provides different combinations of light availability, food and shelter able to sustain a wide variety of species, some of which use the meadows at given life stages only. Examples are large active predators patrolling the meadows and surrounded habitats in search of prey, whose presence might be limited to their adult stage as to some species of Triakidae family. Conversely, many small-sized fish, such as species belonging to the family Sparidae and Gobiidae, or the greater pipefish (*Syngnathus acus*), three-spined stickleback (*Gasterosteus aculeatus*), comber (*Serranus cabrilla*) and conger (*Conger conger*) use the seagrasses during their entire their life cycle, finding protection against predation and food resources, feeding on a variety of epiphytic, micro- and macroalgae and invertebrates.

Interestingly, data supporting various theories about the role of seagrass in sustaining diversity (taxonomic and functional) are often restricted to specific geographic areas, thus not allowing a clear interpretation of the mechanisms behind the structuring of fish communities in the seagrass meadows of the Mediterranean basin, ultimately reducing the ability to implement effective conservation and management strategies. To answer these specific questions, my PhD thesis focused on the

investigation of the ecological relationships between Mediterranean seagrasses and the associated fish fauna, with a special focus on functional diversity.

With the aim of reconciling the excessive fragmentation of information with the need of data at the whole basin level, a semi-automated, threshold-based filtering pipeline for keyword-based searches has been implemented to provide a comprehensive synthesis of fish species inhabiting seagrass habitats across the Mediterranean Sea, addressing current gaps in the literature (Chapter 1). This effort produced one of the most up-to-date databases about the presence of fish species on the main native Mediterranean seagrasses, including geographic (e.g., FAO zone, GFCM area, site coordinates), temporal (e.g., sampling season and year), sampling (e.g., methods, habitat composition), and bibliographic information among others, enabling a narrative synthesis of fish diversity within seagrass habitats.

In a subsequent phase (Chapter 2), the database was expanded including information on the life stages at which species have been reported on different seagrasses, alongside specific functional traits related to reproductive, feeding, and predation mode that are known to be associated with the potential use of the habitat by fish. I broadened the focus by examining whether the three main seagrasses native of the Mediterranean (*Posidonia oceanica*, *Cymodocea nodosa* and *Zostera marina*) support similar functional strategies (i.e., specific combinations of life-history and feeding traits) of associated fish fauna. Moreover, linear and generalized additive models (GAMs) were employed to explore how different functional strategies relate to well-defined life stages at which species are most likely to be recorded. Finally (Chapter 3), I explored the effect of specific management and conservation strategies on fish community composition. Specifically, ten-years of data , collected after the ban of illegal trawling was enforced by the deployment of an artificial barrier, have been used to test changes in the taxonomic and functional composition of fish assemblages targeted by small-scale coastal fisheries. The findings showed that active conservation measures of *P. oceanica* meadows from illegal trawling resulted in increased sizes of target fish species, irrespective of their functional traits, but that the recovery time was delayed for species having an equilibrium life-history strategy.

Overall, the results obtained in this thesis allowed filling specific gaps in the study of seagrass/fish associations, highlighting at the same time study areas needing future researche. The identification of a 'functional fingerprint' indicates non-random trait assembly in fish communities across Mediterranean seagrasses, sustaining the hypothesis that fish assemblages on seagrasses mostly depend on the trade-off between different reproductive and feeding strategies, able to determine the ontogenetic habitat use and influencing the structuring of food webs and species recruitment, fundamental for the maintenance of marine biodiversity. This can have important consequences in

determining the responses of species to climate change and fishing pressure, providing a useful baseline to understand how these will affect fish assemblages in the next future.

INTRODUCTION

Seagrass meadows are relevant marine biodiversity hotspots, hosting a high richness of endemic species and being highly vulnerable to degradation and loss (Myers et al., 2000; Morrison et al., 2014). They also provide many ecosystem functions and services essential to both the good health of marine environments and the well-being of human populations (Unsworth et al. 2019).

Although seagrasses cover only a small portion of the ocean floor (~ 0.1%) and have a relatively low biomass compared to terrestrial ecosystems, they are able to create structurally complex and highly productive habitats known to play an important role in enhancing ecosystem stability and marine biodiversity (Duffy, 2006; Short et al., 2007; Sherwoord et al., 2017; Hyman et al., 2019). Seagrass habitats indeed support the resilience of coastal environments, improve water clarity by filtering pollutants and trapping fine sediments, reduce eutrophication and maintain a balanced nutrient load in coastal waters (particularly nitrogen and phosphorus) through carbon sequestration which contributes to the mitigation of climate change impacts (Hemminga & Duarte, 2000; Crooks et al., 2011; Duarte et al., 2013).

As to the functions and ecological services relevant to human well-being, seagrasses offer nature-based tourism and recreation and provide valuable nursery habitat for many species of commercial interest (Lilley & Unsworth, 2014; FAO, 2016; Nordlund et al., 2016). Indeed, they directly support industrial offshore and small-scale fisheries through the provision of fishing grounds for invertebrates and fish of subsistence and commercial value, such as the tiger prawn (e.g. *Penaeus esculentus*), conch (e.g. *Strombus gigas*), white spotted spinefoot (*Siganus canaliculatus*) and the walleye pollock (*Theragra chalcogramma*), one of the most landed species on the planet (Unsworth & Cullen, 2010; Lilley & Unsworth, 2014; Kritzer et al., 2016; McDevitt-Irwin et al., 2016; Nordlund et al., 2016). Moreover, seagrasses provide valuable nursery habitat and trophic subsidies for adjacent fisheries (Heck et al., 2008; Unsworth et al. 2019), as in the case of the Atlantic cod (*Gadus morhua*), which uses abundant food resources and shelter in seagrass during juvenile phase before migrating to deeper habitats where they are fished as adults (Lilley & Unsworth, 2014; Unsworth et al. 2019).

Seagrasses are monocotyledonous vascular flowering plants distributed in temperate and tropical shallow, coastal and estuarine waters, spreading across all continents except Antarctica (Short et al., 2011). Despite their global distribution, seagrasses have a low species diversity, as they count approximately 70 species belonging to 12 genera divided into four main families: Zosteraceae, Hydrocharitaceae, Posidoniaceae and Cymodoceaceae. All species typically grow in sandy or muddy substrates and are totally submerged modular plants composed of repeating units consisting of: i) a rhizome, which can extend horizontally below the sediment surface or vertically; ii) a bundle of long,

flattened, thin leaves attached to the rhizome by means of insertion points called nodes; iii) underground root system with stems buried within a soft substrate that stabilizes the sediments. In particular, rhizomes are flexible stems (excepted for *Posidonia oceanica* which has a highly lignified rhizome) that raise the leaves towards or above the sediment surface and are responsible for vegetative reproduction, as well as for connecting neighbouring ramets, thereby maintaining integration within the clone (Kendrick et al., 2005). The rhizome fragments between two nodes are called internodes, having a wide range in size among seagrass species, and the characteristics of leaves, nodes, internodes and roots determine the shape of the different meadows. Indeed, seagrasses can form extensive or patchy meadows and their size range from species with long flat blades that look like ribbons (*Cymodocea serrulata*) to fern-like leaves (*Halophila spinulosa*) or cylindrical blades (*Syringodium filiforme*) and with length ranging from few centimetres (*Halophila ovalis*) up to seven meters (*Zostera caulescens* in Japan; Aioi et al., 1998).

Regardless the species, a crucial characteristic of all seagrasses is their ability to stabilize the environment, resulting in important physical and biological support for associated vertebrate and invertebrate communities (Gillanders, 2006; Koch et al., 2006). They also add structural complexity to sediments, form the basis for complex food webs and create favourable conditions to support faunal assemblages with greater abundance and richness with respect to bare substrates (Williams and Heck, 2001; Jones et al., 2021; Yeager & Hovel, 2017; Heck and Orth 1980; Bell and Pollard 1989; Zubak et al. 2017). Indeed, recent works have shown how in the Indo-Pacific 746 species of fish utilize seagrass meadows, 486 in Australasia, 222 in the North-East Pacific, 313 in the Caribbean, and 297 in the North Atlantic (Unsworth et al., 2019).

Seagrass habitats support a wide range of organisms linked by trophic, mutualistic and competitive relationships, including species that inhabit the leaves such as epiphytes, bryozoans and gastropods, as well as species attached to stems and rhizomes, like sessile polychaetes and tubicolous amphipods, and mobile species that dwell beneath the leaf canopy, such as crabs and fishes (Kikuchi and Peres, 1977). Many of these organisms utilize seagrass habitats at different stages of their life cycle, deriving distinct benefits from this unique ecosystem. As suggested by Kalogirou and co-authors (2010), species linked at various degree to seagrasses can be divided into: i) seagrass residents, i.e., species which are stationary and highly dependent on seagrass meadows (such as sea turtles, dugong and manatee); ii) seagrass migrants, i.e., species which visit seagrasses in a peculiar stage, usually as adults for spawning or feeding or as juveniles for nursery ground (such as cod, haddock, and snapper); iii) occasional visitors, species that feed on large areas spanning different marine habitats, including seagrasses and so appearing in low association with this habitat (Ginsburg and Lowenstam 1958; Thayer et al., 1975; Orth 1977). Indeed, many marine organisms often undergo changes in the diet,

feeding strategies, or even social behaviour as they develop, leading to an ontogenetic shift in their use of habitats (Fobert et al., 2020; Polte et al., 2017). The above-mentioned *G. morhua*, is one such example. Other species are characterized by specific combinations of traits that give them a stronger tendency to have the same reproductive and feeding modalities throughout their entire lifetime (Lattanzi et al., 2024). This is particularly evident in habitats like seagrasses, where their structural complexity might determine how species perceive and use them. Such interactions are often related to their peculiar adaptations related to morphology, ecological requirements, trophic ecology and behaviour and suggest that species assemble non-randomly along gradients of structural complexity, reflecting the interplay between habitat features and organismal traits (Ferreira et al., 2023; Sanabria-Fernández et al., 2024).

Overall, the structuring of fish fauna on seagrass habitats might depend on different mechanisms, as the species assemblage can be the result of dispersal limitation, biotic interactions, and environmental filtering (Moreira-Saporiti et al., 2023; McGill et al., 2006; Weiher et al., 2011; Grime and Pierce, 2012). Structurally complex habitats (such as seagrass meadows) might exert a strong environmental filtering, leading to local assemblages similar in terms of functional traits composition (Sutton et al., 2021; Kraft et al., 2015). Although seagrasses support biodiversity and fisheries by providing food supplies for fish and waterfowl and shelter from predation (Bertness & Callaway, 1994; Bulleri et al., 2018), differences in their characteristics would determine the structural complexity of the meadows (e.g., canopy height, number of leaves per shoot, length and width of the leaves), potentially limiting the similarity between associated fish assemblages in terms of both taxonomic and functional diversity. Indeed, seagrass habitats host both generalist species placed at intermediate to low trophic levels and large active top predators, thanks to their ability to provide protection against predation by reducing prey visibility and impeding predator movement (Shultz et al., 2009). This suggests a lower risk of predation mortality than surrounding open habitats (i.e., the so called 'seagrass superiority hypothesis'). On the other hand, they may provide foraging opportunities for predators due to either the high prey density moving in and out from the meadows if they are transient species, or the many hideaways if they are ambushing residents (Heck and Orth, 1980). In both cases, predators take on the role of structuring fish communities in seagrass meadows, as postulated by the "Predation Mode Hypothesis" (Heck & Orth, 1980; Bell and Pollard 1989; Zubak et al., 2017; Schultz et al., 2009; Fouzai et al., 2019).

Despite their importance, seagrass ecosystems are threatened worldwide and are being lost rapidly (Short et al., 2006). Indeed, only recently the socio-ecological value of seagrass ecosystem services has received recognition and, since the beginning of the 20th century, the widespread loss of seagrass meadows has been estimated at 0.9% yr^{-1} due to a variety of anthropogenic stressors (e.g., trawling,

dredging and indirect anthropogenic stressors such as pollution and eutrophication) that affect the distribution, diversity and health of these habitats and associated species and communities (Strydom et al., 2023; Hall et al., 1999; Short et al., 2011; Strydom et al., 2020; Waycott et al., 2009; Ralph, 2007).

One of the main indirect anthropogenic impacts is global climate change, which is likely to have direct and indirect effects by decreasing the distributional range of seagrass habitats, shifting suitable habitats for seagrass associated species in the coming decades and increasing the risks of invasion by alien species (Short and Neckles, 1999; Saunders et al., 2013; Valle et al., 2014). For instance, the invasion of *Halophila stipulacea* from the Red Sea into the Mediterranean after the opening of the Suez Canal has led to a widespread distribution in the eastern Mediterranean, extending as far west as Sicily and, probably, to the Caribbean due to boat traffic (Ruiz and Ballantine, 2004). The disappearance of endemic seagrass species, or their replacement with invasive ones, produces a change in the habitat with consequences in the taxonomic and functional diversity of associated assemblages as the morphological characteristics and the structural complexity of seagrass meadows have great influence in regulating fish assemblages (Gullström et al., 2008).

Compared to unvegetated habitats, seagrass meadows show not only higher fish abundance and species richness but also higher growth and survival rates (Heck et al., 2003; Larkum et al., 1989; Connolly 1994). Similarly, the composition (e.g., pure and/or mixed) and three-dimensional structure of meadows determine the taxonomic and functional diversity of associated fish assemblages (Hori et al., 2009). Meadows characterized by high diversity in terms of seagrass species (e.g., mixed meadows), high three-dimensional structure and intermediate biomass levels, positively influence fish taxonomic diversity, while their effect on the functional structure differed among fish functional groups (Hori et al., 2009). For instance, fish inhabiting the surface of the meadows usually prefer low biomass levels and high three-dimensional structure, those inside the canopy high biomass levels and high three-dimensional structure, while those at the bottom of the canopy low biomass levels and three-dimensional structure (Hori et al., 2009). Such pattern relies on species-specific functional strategies of fish that could be altered by the effect of seagrass loss, degradation and replacement by invasive and structurally less complex species as *H. stipulacea* in the Mediterranean Sea (Olinger et al., 2017). Therefore, to improve conservation efforts and management practices, it is pivotal to focus on the study of both taxonomic and functional diversity (alongside phylogenetic diversity), as a clear understanding of the extent to which different seagrasses are able to structure fish fauna would help peculiar functional strategies more at risk in the face of anthropogenic pressures (e.g., fishery), or provide important information about how global change (e.g., increasing sea temperatures) will reshape seagrass biodiversity (Zhang et al., 2019).

Despite biodiversity is a multidimensional concept (Purvis and Hector, 2000; Franklin,1988; Noss,1990; Noss and Cooperrider, 1994), management approaches often overlook the study and conservation of functional diversity, which is one of the main drivers of ecological processes regulating ecosystem functioning (Zhang et al., 2024; Mouillot et al., 2011). Indeed, the composition and diversity of functional traits determine how individuals interact with the environment, which consequently will select certain combinations of physiological–ecological adaptations (Dézerald et al., 2015; Violle et al., 2014; Jarzyna and Jetz, 2016; Mouillot et al., 2011; Schmera et al., 2017). By definition, functional traits are any measurable morphological (e.g., body size, body shape), physiological (e.g., drought tolerance in plants, and metabolic rate in animals), phenological (e.g., lifespan, age of sexual maturity) characteristics expressed by an organism, that strongly influences individual fitness (i.e., growth, reproduction and survival, Violle et al., 2007; McGill et al., 2006) and determine the responses of species to environmental conditions, disturbance, and biotic interactions, as well as their effects on ecosystem processes (Mouillot et al., 2013; Adler et al., 2014). Functional traits can be classified into response traits (how species respond to environmental conditions) and effect traits (how species influence ecosystem processes). Looking at traits variability within the species belonging to a given community allows identifying possible mechanisms determining the distribution of species, their population dynamics, species coexistence and ecosystem functioning (Cadotte et al., 2017; González-Suárez & Revilla, 2013; Laughlin & Messier, 2015; Moles, 2018; Schneider et al., 2019, Díaz, et al., 2007).

While the study of taxonomic diversity focuses on the analysis of information from species richness (i.e. the number of different species occur in a given area), species evenness (i.e. the distribution of individuals among these different species) and diversity indices that combine both, the study of functional diversity describes the diversity and relative abundance of species based on the ecological roles, functions and interactions that they perform within the ecosystem (Chalmandrier et al., 2015; Violle et al., 2012). The functional structure of a community consists in the composition and diversity of species functional traits and is usually represented in a multivariate space (i.e., "functional space") (Mouillot et al., 2013). The probabilistic hypervolumes and Kernel density estimates (Blonder et al., 2014; Blonder et al., 2018) may be used to delineate the shape and volume of this multidimensional space, providing a tool to map how densely or sparsely species occupy various regions of the functional space (Carmona et al., 2016; Laughlin et al 2015). From the analysis of this multivariate space it is possible to obtain three primary components of functional diversity that describe the functional structure of each assemblage, indicate different facets of functional diversity across multiple scales and show niche overlap in diverse communities: i) Functional Richness (FRic); ii) Functional Evenness (FEve); iii) Functional Divergence (FDiv) (Carmona et al., 2016; Mason et

al., 2005; Villèger et al., 2008; Díaz et al., 2016 ; Carmona et al., 2021). Functional richness represents the volume of the functional space occupied by the species, strongly related to local taxonomic richness being unweighted respect to the abundance (Villéger et al., 2008). Functional evenness indicates whether mean species traits are distributed regularly within the occupied trait space in terms of both equal distances between nearest neighbors and equal abundances (Villéger et al., 2008). The functional divergence indicates the variance of species' functions and how species abundances diverge from the center of the functional space (Villéger et al., 2008). Furthermore, the identification of areas of particularly dense species occupation in the traits' space, called "functional hotspots", can be measured as the smallest portion of functional space including 50% of the species, representing the core of functional strategies within the community of interest (Carmona et al., 2016; Mason et al., 2005; Villèger et al., 2008; Díaz et al., 2016; Carmona et al., 2021).

The application of functional diversity indices based on traits often explains ecosystem functioning better than species richness and/or evenness (Hooper et al., 2000; Danovaro et al., 2008), also because functional traits help understanding specific stressors that are ignored in taxonomic data analysis, which species are irreplaceable due to unique roles and predict ecosystem responses by evaluating which functions might be disrupted or supported (Zhang et al., 2019). This is of global interest because seagrass habitats degradation directly influences fish populations that rely on them for nurseries, feeding and protection, possibly resulting in a reduced recruitment of juvenile fish and leading to smaller fish populations in nearby ecosystems (Jones et al., 2021). Reductions of biodiversity and fish maturity might impact local and global fisheries making populations and fisheries more vulnerable to environmental change (Bianchi et al., 2008).

Nonetheless, how specific functional strategies determine the way with which fish use seagrasses during their life cycle and the mechanisms involved in their structuring still remain unclear (Jones et al., 2021). Knowledge gaps also concern the role of habitat heterogeneity and fish life stages in determining the presence and the potential use of seagrasses by species both at a local and broader geographical scale. As a result, partial and fragmented data are obtained, which do not allow a correct understanding of the mechanisms behind the structuring of fish communities, with consequences also for the management and conservation of these resources at local and global level.

Based on composition and distributional ranges of different seagrass species, it is possible to identify six global bioregions (Short et al., 2007), with the Mediterranean region (which includes Mediterranean Sea, Black, Caspian and Aral Seas and north-west Africa) being the smallest one. The Mediterranean Sea is a semi-enclosed oligotrophic small basin recognized as a one of the world's major hotspots of biodiversity with an exceptionally high species diversity and endemism rate (Coll et al. 2010; Myers et al., 2000; Thompson, 2020). It covers only 0.32% of the global oceanic volume

but it is considered one of the most significant marine and coastal biodiversity reservoirs sheltering around 11% of all known marine species (Bianchi and Morri,2000).

Among all the species detected in the Mediterranean Sea, 28% of flora and nearly 10% of fish are endemic (Heywood, 1995; Quignard & Tomasini, 2000). The three main seagrass species the Mediterranean Sea are *P. oceanica, C. nodosa, Z. marina*. *P. oceanica*, the only endemic seagrass of the Mediterranean, forms meadows from the surface down to a depth of about 35 meters and represent the most important shallow water coastal habitat in the region (Abadie et al., 2018). *P. oceanica* is characterized by ribboned leaves, with rounded tips and arranged fan-shaped in clusters of about 6 or 7 that can reach more than 1 m long, a higher shoot density and a dense root system. The roots can grow to 70 cm beneath the surface of sediment and their vertical development leads to a progressive raising of the soil, which creates a typical formation called matte consisting of interlaced remnants of roots, several layers of rhizomes and entangled sediment. This structure exerts a shading effect on the substrate and create dense meadows where a high number of organisms find shelter, food resources and nursery ground (Ceccherelli and Cinelli, 1999; Colombini et al., 2009; Duarte et al., 2013; Hyman et al., 2019). *C. nodosa* is the main seagrass species of the subtidal zones and is distributed across the Mediterranean and the adjacent Atlantic Ocean, including southern Portugal, Mauritania, the Canary Islands, and Madeira (Navarro-Mayoral et al., 2023; Tuya et al., 2006; Masucci et al., 2012). This seagrass forms extensive but often fragmented subtidal meadows characterized by denticulate leaves smaller in size than *P. oceanica*, which can reach 40 cm and are only 3-4 mm wide. Furthermore, unlike *P. oceanica*, the rhizomes of *C. nodosa* do not grow in an orthotropic sense and this prevents the formation of a real matte so that the meadows consist of a "turf": a layer of superficial sediment containing sparse and low plant growth, including a compact root network.

It should be noticed that *C. nodosa* through its higher thermal resilience may act as a pioneer species, influencing environmental conditions by stabilizing the substrata and facilitating the establishment of *P. oceanica*. Moreover, in the presence of its ongoing regression, *C. nodosa* acts as an opportunistic species, forming mixed meadows and partially reducing the decline rate of *P. oceanica* meadows (Llabres et al., 2023; Den Hartong, 1970; Infantes et al., 2011). *Z. marina* is one of the world's most widespread marine plant species and in the Mediterranean Sea its distribution is more limited and in gradual decline. Indeed, *Z. marina* is predominantly subtidal, growing down to 10-15 meters depth depending on water clarity and prefers cold and slightly saline waters, which in the Mediterranean are now found only in the northernmost areas of the Aegean Sea and the Adriatic, as well as along some stretches of the French and Spanish coasts. The structure of *Z. marina* meadows is similar to that of *P. oceanica* with the difference in the length of the leaves and the density of the shoots: the shoots of *Z. marina* have an average of 4 leaves which width varies between 4 mm and 10

mm and length is usually 30 to 60 cm long, forming dense and extensive meadows (Borum et al., 2004).

In relation to the EU KNOWSEAS project, it has been shown that seagrass decline carries a substantial economic cost: in the Mediterranean basin, for recreational fishing, seagrass contributed an estimated €58.3 million to €91.5 million annually from 2006 to with an average annual contribution of €77.7 million, which was approximately 4% of the value of all seafood caught (Jackson et al., 2015). Certain species would have a significant economic impact for commercial fishing if seagrass were to further decline, such as cuttlefish (Sepiidae, Sepiolidae), scorpion fish (Scorpaenidae) and octopus (Octopodidae) among others (Jackson et al., 2015). Despite their relevance in terms of both biodiversity conservation and fisheries support, the Mediterranean Sea is highly impacted by climate change and anthropogenic activities (Halpern et al., 2015; Costello et al., 2010).

Fish geographic distributions are clustered in the Mediterranean Sea, according to the temperature and salinity longitudinal gradient that characterize the sea: subtropical species occur in the south-eastern area, where water temperatures are higher than average (Theocharis et al., 1993), and cold-adapted species inhabit northern areas (Bianchi and Morri, 2000). As a result of global warming, species that were typically found in the warm waters of the southern areas have been observed more frequently in the north, where waters are becoming warmer (Astraldi et al., 1995; Bianchi and Morri, 2000; Sabatés al.,2006). Because changes in thermal conditions drive the reorganization of fish assemblages and their geographical distribution, climate change is strongly affecting Mediterranean marine biota and ecosystems due to substantial temperature increases (Rahel and Hubert, 1991; Sabatés et al., 2006; Ben Rais Lasram & Mouillot, 2009; Lejeusne et al., 2010; Givan et al., 2018; Nykjaer, L. 2009; Shaltout, M. & Omstedt, 2014). Over the last 30-40 years, the water temperature of the western Mediterranean Sea has increased both at depth and at the surface (Bethoux et al., 1990; Rixen et al., 2005; Diaz-Almela et al., 2007), driving the “meridionalization” of the northern and “tropicalization” of the southern sectors of the Mediterranean Sea, mainly due to the northward migration of native species and the introduction of alien species through the Suez Canal and the Strait of Gibraltar (Goren & Galil, 2005; Bianchi et al., 2013). In this scenario, cold-temperate species will move towards the coldest parts of the Mediterranean Sea. However, as warming intensifies, these species may become confined to limited reservoir areas leading to a "trapping effect" that exposes endemic species to a critical threat and increases their risk of extinction (Ben Rais Lasram et al., 2010). Beyond species geographic range shifts, climate warming may also induce the fragmentation of suitable habitats resulting in a loss of both population abundance and genetic diversity (Gibbs,

2001) besides an increase in population vulnerability to extreme events and disturbances (Piessens et al., 2009).

The Mediterranean is also a global hotspot of alien species (Edelist et al., 2013; Molnar et al., 2008; Costello et al., 2010) with over 775 Lessepsian alien species established across the basin (Zenetos, 2022). Indeed, non-indigenous species (NIS) reach the Mediterranean through active (i.e. invasion) or passive (aquaculture activities and fouling on ship hulls or ballast tanks) dispersal and in the eastern basin their invasion is mainly due to the opening and continuous enlargement of the Suez Canal (Katsanevakis et al.,2014; Galil et al., 2015). Their growing presence and abundance negatively impact activities as fishing, shipping, public health and tourism, as well as the equilibrium of the ecosystem (Zenetos et al., 2002). For instance, the tropical alga *Caulerpa taxifolia*, first reported in the western Mediterranean in 1984, is found to replace the native endemic *P. oceanica*, and moreover contains a toxin able of hindering the growth of other organisms, leading to a higher rate of fragmentation of seagrass meadows (Montefalcone et al., 2010).

Among many, seagrass and associated organisms represent some of the most impacted habitat by the effect of global climate change and other anthropogenic activities (Vasilakopoulos et al., 2014; Tsikliras et al., 2015). In particular, more than 1.2 million hectares of Mediterranean Sea host seven species of seagrass (Telesca et al., 2015): the only endemic seagrass of the Mediterranean Sea, *P. oceanica* (Boudouresque et Verlaque, 2008); the natives *Cymodocea nodosa*, *Zostera marina* and *Zostera noltei*; *Ruppia maritima* typical of brackish lagoons and salt marshes (Shili et al., 2007) ; the lessepsian species *Halophila stipulacea* and the introduced species via ballast water *Halophila decipiens* (Gerakrais et al., 2020; Winters et al., 2020).

Overall, they support a high number of epiphytic algal species (Reyes and Sansón, 1997), providing food and shelter for diverse organisms and influencing local and regional fish abundance, diversity (e.g., taxonomic and functional diversity) and structure (Tuya et al., 2001, 2006; Espino et al., 2011; Manez-Crespo et al., 2022). Indeed, each species of seagrass is characterized by different structure and can be viewed at various levels, from within-meadow architectural features to gross meadow morphology as it consists of shoot density, canopy height, biomass, leaf size, growth form, depth tolerance and patch fragmentation (Abadie et al., 2018). The structure of seagrass affects differently habitat complexity which, in association with environmental conditions, landscape context, and species interactions within and around meadows, can influence the composition and abundance of associated biota (Thistle et al. 2010; Iacarella et al. 2018; Whippo et al. 2018; Wong and Kay 2019; Stark et al. 2020).

The vertical stratification of the canopy (i.e., upper, middle and lower portion) supports different species assemblages, such as epiphytic assemblages on leaves, pelagic assemblages within and above

the canopy, benthic assemblages on or near the sediment, and infaunal assemblages within the root and rhizome system (Murphy et al., 2021; Schmidt et al. 2011; Whippo et al., 2018) and the dense and different three-dimensional structure of seagrasses creates a particular habitat which is mainly responsible for the presence of some organisms rather than others and their abundance. Meadows with complex canopy structures (higher canopy, longer and wider leaves, greater numbers of leaves per shoot) increase the availability of food resources and reduce predation pressure (Hovel et al., 2002; Vonk et al., 2010): seagrasses with narrow leaves (e.g., *Cymodocea nodosa*) are easier to manipulate for smaller bodied fish (Prado and Heck, 2011), while broad and tapeform seagrass leaves (e.g., *P. oceanica*) can form denser meadows and host larger fishes (Lattanzi et al. 2024).

Despite the crucial role of seagrasses in fisheries and biodiversity of the Mediterranean Sea, a thorough and up to date synthesis of fish species observed in different seagrass habitats is still lacking at whole basin scale (Lattanzi et al., 2024). This might hinder a clear understanding of the mechanisms involved in the structuring processes of fish communities and the role of seagrass structural complexity and extension (Jones et al., 2021; Lürig et al., 2016; McDevitt-Irwin et al., 2016) in determining fish taxonomic and functional (bio)diversity, useful for establishing up-to-date conservation and management practices able to contrast the effects of direct (e.g., fishery) and indirect (e.g., global warming) anthropogenic impacts.

THESIS STRUCTURE

The presents thesis is divided into three main chapters, which aim to answer specific questions raised by the current knowledge gap:

Chapter 1. In this chapter, a semi-automated, threshold-based filtering pipeline was implemented to perform a systematic review of the current literature about the presence of fish on seagrasses across the whole Mediterranean basin. This allowed us to build up one of the most up-to-date datasets concerning all fish species reported in native Mediterranean seagrasses, including specific functional traits known to be involved with the potential use of seagrasses by fish. The dataset allowed to: i) provide an overall view of fish diversity in Mediterranean seagrasses; ii) analyse the distribution of fish life stages across various seagrass habitats; iii) test the role of species-specific traits associated with the potential use of seagrass by fish in determining the presence of species on different seagrass habitats at a given life stage; iv) identify key findings and knowledge gaps for future research.

This chapter has been published in the journal *Reviews in Fish Biology and Fisheries*:
Lattanzi, A., Bellisario, B. & Cimmaruta, R. A review of fish diversity in Mediterranean seagrass habitats, with a focus on functional traits. Rev Fish Biol Fisheries 34, 1329–1349 (2024). https://doi.org/10.1007/s11160-024-09876-w

Chapter 2. In this second chapter, the functional characteristics of fish assemblages in three main native seagrasses of the Mediterranean Sea (*P. oceanica*, *C. nodosa* and *Z. marina*) have been analysed. The results are discussed in view of the inherent differences of seagrasses in terms of structural complexity, coverage and distribution, with the aim of understanding the extent to which fish assemblages show convergent or divergent functional strategies in native Mediterranean seagrasses. The role of species-specific traits associated with the potential use of seagrass by fish in determining the presence of species at a given life stage (i.e., juveniles only, juveniles and adults, adults only) was also explored.

In this chapter, we identified a common ‘fingerprint' in the functional strategies of seagrasses-associated fish, characterized a *r-like* strategy including small size, low trophic level and fast growth rate. Seagrasses seem to differ in their ability to support higher trophic level species (e.g., large active and ambush predators), likely using this habitat almost exclusively as foraging grounds during their adult life stage. We discuss our findings in the light of future climate scenarios, providing a useful baseline to understand the effect of multiple threats on marine biodiversity as, for instance, the

expansion of small, fast-growing non-native seagrass species (*Halophila stipulacea*) with respect to long-lived, large and slow-growing species, such as *P. oceanica*.

This chapter is presently under review in *Functional Ecology* (Manuscript ID, FE-2025-00067).

Chapter 3. In this third chapter, the results of active protection of seagrass meadows (*P. oceanica*) against illegal trawling artificial reefs were explored based on data from three different fishing campaigns carried out over a 10 years period in two SACs (Special Area of Conservation) located in the NW of the Latium Region (Tyrrhenian Sea). The functional composition of fish assemblages was explored per SAC and per year, considering species-specific information regarding life-history traits, reflecting reproductive, growth and feeding modes. Data were used to characterize and analyse spatial and temporal changes in both taxonomic and functional structure of fish assemblages during a decade after the deployment of artificial reefs enforcing the ban of illegal trawling. The findings showed that the species could be decomposed into a continuum of three life-history strategies (opportunistic, periodic and equilibrium) and that the protection of *P. oceanica* meadows from illegal trawling resulted in increased sizes of target fish species, irrespective of their functional traits, underscoring the importance of conservation measures.

This chapter is presently in preparation as a scientific paper

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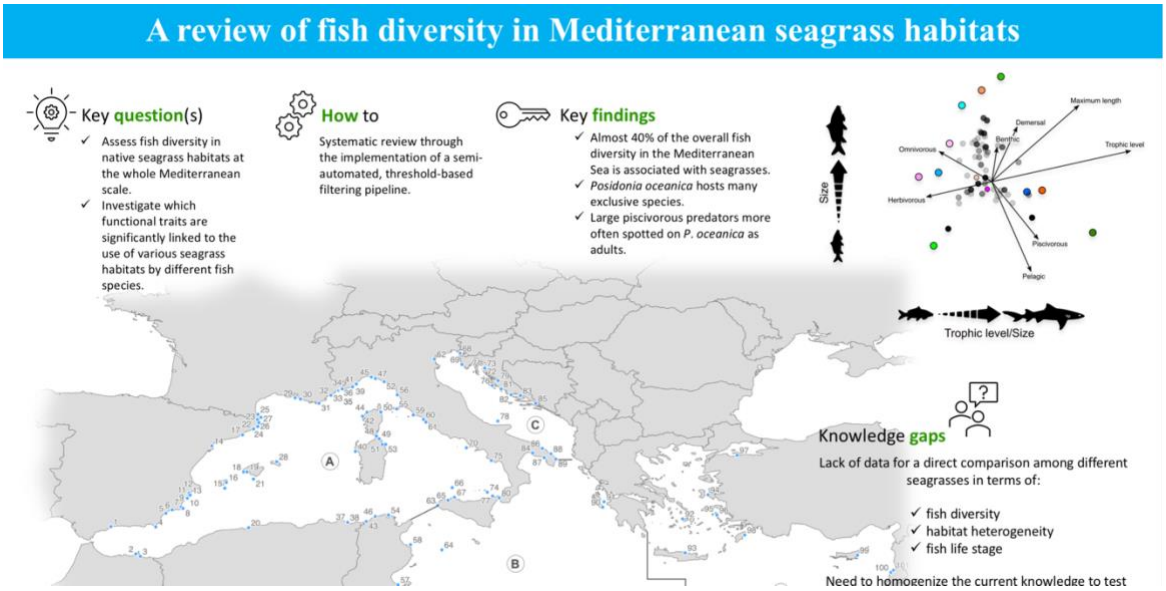
CHAPTER 1

A REVIEW OF FISH DIVERSITY IN MEDITERRANEAN SEAGRASS HABITATS, WITH A FOCUS ON FUNCTIONAL TRAITS

Lattanzi, A., Bellisario, B. & Cimmaruta, R. A review of fish diversity in Mediterranean seagrass habitats, with a focus on functional traits. *Rev Fish Biol Fisheries* 34, 1329–1349 (2024). https://doi.org/10.1007/s11160-024-09876-w



Abstract

Besides providing key ecosystem services, including improved water quality, coastal protection, and carbon sequestration, seagrasses are highly productive habitat-forming species essential in supporting fish diversity at the global level. In the Mediterranean Sea, seagrasses represent the main component of the sublittoral marine environment hosting a huge number of fish species that use this habitat for reproduction, foraging and/or refuge from predation. However, a complete synthesis of fish species observed in different seagrass habitats is still lacking at the whole Mediterranean basin scale, so hindering a thorough understanding of the main mechanisms involved in determining fish diversity patterns. We performed a systematic review by implementing a semi-automated, threshold-based filtering pipeline that allowed building up a dataset concerning all fish species reported in native Mediterranean seagrasses, including specific functional traits known to be involved with the potential use of seagrasses by fish. These data allowed to carry on a narrative synthesis on fish diversity in seagrass habitats, providing support to several assumptions repeatedly stated in literature but so far sustained mainly by local and fragmented data. Our findings suggested the onset of a general pattern in the occurrence of species, mostly based on life history and driven by body size and feeding habits.

We evidenced unexpected knowledge gaps on the role of habitat heterogeneity and fish life stages in determining the presence and the potential use of seagrasses by species. In depth studies are therefore needed to better understand the mechanisms behind the structuring of fish communities, fundamental for the maintenance of marine biodiversity.

Keywords: fish-seagrass association; native Mediterranean seagrass; trophic level; life stage; predator-prey segregation; threshold-based literature searching

Introduction

Seagrasses represent a key habitat in the marine environment, playing a crucial role in maintaining marine biodiversity, besides their strategic importance in supporting many commercially and socially important fish species (Unsworth and Cullen 2010). In the Mediterranean Sea, a small oligotrophic basin recognized as a main hotspot of biodiversity (Coll et al. 2010), a significant number of fish use seagrass habitats to forage, from herbivorous grazers to omnivores and predators that may feed upon animals living in the canopy where the shaded and colder waters provide shelter for species at different life stages (Terrados and Duarte 2000; Boudouresque 2004). Moreover, even large predators usually not directly associated with seagrasses may benefit indirectly from these habitats, by preying on specimens moving between different environmental patches (Kalogirou et al. 2010; Kruschel and Schultz 2020). Seagrass beds are also important nursery habitats for several species of fish that here spawn or settle as juveniles, either spending their entire life cycle in the meadows or moving to other ecosystems as they mature (Ren et al. 2022).

Within this framework, it is not surprising that Mediterranean seagrasses are widely studied and that systematic literature reviews are frequently carried out to summarise the state of the art, to evaluate their natural capital value or to identify future research directions (Romero et al. 2016; Boudouresque et al. 2021; Catucci et al. 2023; Procaccini et al. 2023). Despite their relevance in terms of both biodiversity conservation and fisheries support, a thorough and up to date synthesis of fish species observed in different seagrass habitats is still lacking at whole Mediterranean basin scale. Indeed, many studies are often carried out in restricted geographic areas, using unstandardized methods and pursuing different objectives, making it difficult to extract clear and comparable data. Another reason for this gap is due to the high number of papers produced over the years, preventing to apply an expert opinion and making difficult to carry on exhaustive systematic literature reviews, usually performed to answer specific questions and therefore working on a reasonable number of papers to be filtered (Kastner et al. 2012). The subject has been therefore addressed in terms of either worldwide pattern using selected case studies (e.g., Unsworth et al. 2018), Mediterranean sub-basins (e.g., Koutsidi et al. 2020), or within specific contexts of Mediterranean fisheries or Marine Protected Areas management without a specific focus on seagrass substrates (e.g., Piroddi et al. 2020; Fraschetti et al. 2022). The lack of a comprehensive view of fish distribution in different seagrasses at the Mediterranean scale may also hinder a complete understanding of the role played by both functional traits and adaptive or behavioural mechanisms that may account for fish diversity patterns in seagrass habitats.

In this paper, we tried to fill this gap by performing a systematic review through the implementation of a semi-automated, threshold-based filtering pipeline rooted into the approaches of the JBI methodology (Joanna Briggs Institute; Peters et al. 2020) and PRISMA statement (Preferred Reporting Items for Systematic Reviews and Meta-Analyses; Moher et al. 2009; Page et al. 2021). Our primary goal was to produce exhaustive and comparable information on fish species that use native seagrass habitats across the entire Mediterranean Sea. To this end, we performed a systematic review and used the retrieved data to build up a dataset including all fish species reported in seagrasses with associated metadata, alongside specific functional traits known to be involved with the potential use of seagrasses by fish. The implemented dataset was then used to reach the following objectives: 1) provide an overall view of fish diversity in Mediterranean seagrasses; 2) analyse the distribution of fish life stages across various seagrass habitats; 3) test the role of species-specific traits associated with the potential use of seagrass by fish in determining the presence of species on different seagrass habitats at a given life stage; 4) identify key findings and knowledge gaps for future research.

Materials and methods

Systematic Review protocol

We followed the nine steps proposed by the JBI (Joanna Briggs Institute) methodology (Peters et al. 2020) and PRISMA statement (Preferred Reporting Items for Systematic Reviews and Meta-Analyses; Moher et al. 2009; Page et al. 2021), to collect all available information about the presence of fish species on different seagrasses of the Mediterranean Sea. Many additions were however implemented to the protocol, mainly regarding the screening phase, to cope with the high number of papers recovered by searching databases (see Supplementary Information). The inclusion criteria for the review were developed in according to the PCC framework (Population (or participants)/Concept/Context), which is highly recommended for constructing a clear and meaningful title, review question, and inclusion criteria by applying the PRISMA flow diagram for the systematic search and review (Cronin et al. 2008; Moher et al. 2009; Peters et al. 2020; Foo et al. 2021; Page et al. 2021).

We made some implementations to the screening phase of the PRISMA guidelines, with the aim of conducting an exhaustive survey of the academic literature to list all the fish species using seagrass habitats across different regions of the Mediterranean Sea and to build up an associated dataset. All types of documents were considered, and studies published in English, French, Spanish and Italian were included in the review. Grey literature was considered at the later stage of the backward and

forward analysis because of the high duplication of data due to frequent grey reporting, followed by indexed publication of the same data. According to PRISMA guidelines, the survey was carried out by implementing a semi-automatic pipeline of three sequential steps, as summarized below. Detailed information for each step of the analysis is reported in Supplementary Information.

Step 1 – Identification - Searching the libraries

We conducted a keyword-based search within six different databases (Dimension, Mendeley, ScienceDirect, Scopus, Web of Science and Wiley Online Library, last access on June 30, 2023) by selecting 69 keywords identifying the three main fields of the research objective (Mediterranean Sea, seagrass, and fish fauna), linked by 68 *OR* and three *AND* Boolean operators (Supplementary Figure S1). No restrictions were applied for publication year.

The pipeline of papers filtering is reported step by step in Fig. 1. Advanced searches were therefore carried out in each of the possible research fields (Title, Abstract, Author Keywords, Text and References) of the six bibliographic databases using a different query for each library due to both their different query limits and years of coverage (Supplementary Table S1). Results have been exported as an Excel file containing the abstract, the Authors' keywords and the title of each paper (sub-Step 1.1 in Fig. 1), which represents the basis of subsequent searches. We removed from the paper list those records having partial searchable information (i.e., literature without abstract) and duplicate papers (sub-Step 1.2 in Fig. 1), by using both Microsoft Excel and the function *removes.duplicates* in the package 'litsearchr' of R (Grames et al. 2019; R Core Team 2022).

We set up a scoring method for the listed papers to apply several successive filters to automatically identify and discard those not containing suitable information. We therefore scored the papers by setting a higher, more specific and exhaustive set of 193 key-terms about the four key-subject groups of the research: Group S – key-terms related to the seagrasses and habitat targets; Group F – key-terms related to fish biology; Group A – key-terms related to sampling, i.e., for either the methods or fish target assemblages; Group G – key-terms related to the Mediterranean basin and geographic localities (Supplementary Table S2). The presence/absence of these key-terms was assessed using the function *str_detect* in the package 'stringr' of R (Wickham 2019).

Step 2 – Screening - Scoring and filtering papers

We assigned a score to each group of key-terms to calculate a Relevance Score (RS) for each paper. This allowed identifying papers likely containing a high amount of relevant information (higher RS)

and to rate the type of information, i.e., concerning seagrass habitat, and/or fish assemblages, and/or sampling methods and/or geographic locality (sub-Step 2.1 in Fig. 1). A detailed protocol is described in the Supplementary Information and Supplementary Table S3.

Once obtained a RS for each paper, we performed a sequential filtering to keep only those papers able to provide information suitable to build up the final dataset. Each filter was applied on the remaining papers after the previous filtration step. Filter 1 allowed excluding papers with a score lower than a threshold value based on the comparison of the representativeness of each of the four key-subject groups in papers with high *vs*. low RS (sub-Step 2.2 in Fig. 1 and Supplementary Tables S4 and S5). Filter 2 allowed dropping papers with a low RS (sub-Step 2.2 in Fig. 1). Filter 3 was based on both the 'Most Frequent Keywords' (MFK, identifying recurring and relevant keywords) and 'Negative Keywords' (NK, whose presence indicates that the paper does not focus on Mediterranean seagrass and/or fish communities although mentioning them, for instance for comparison purposes). This last filter allowed removing: i) all papers containing one or more Negative Keyword within their Most Frequent Keywords; ii) all papers with a low key-terms/MFK ratio; iii) all papers that do not have any keyword related to Group S (Seagrass) or F (Fish) in their Most Frequent Keywords (sub-Step 2.3 in Fig. 1). The pipeline of filtering steps is described in detail in Supplementary Information.

Step 3 – Eligibility and inclusion – Data extraction and refining

Once obtained the short list of papers likely containing useful information, we read all the abstracts to further select by expert opinion those of interest, that is, papers providing information on fish presence in seagrass habitats across the Mediterranean Sea (sub-Step 3.1 in Fig. 1). The selection process was based on the 'team approach', as recommended by Levac et al. (2010). As the selected libraries could miss studies of interest, during the full text reading we searched for useful papers absent from the six libraries but listed in their references by carrying on a backward search based on the Reference papers and, similarly, forward research with the aim of integrating as much data as possible in case of partial data in the papers within our list (sub-Step 3.2 in Fig. 1).

To obtain complete and comparable data, we carried out a manual extraction of data concerning each recorded fish species, along with the source reference paper. The fish species list was finally refined by discarding singletons, thus retaining only those species recorded in at least two separate research studies (in accordance with Unsworth et al. 2014). However, among the singletons detected, we kept Lessepsian species, frequently being listed as a unique record (sub-Step 3.2 in Fig. 1). The resulting dataset provided a full list of the fish species recorded on seagrasses by the present literature,

by reporting each observation associated with: 1) Mediterranean ecoregion, 2) the reference FAO zone, 3) GFCM (General Fisheries Commission for the Mediterranean) Area, 4) site, 5) geographic location, 6) season, 7) year, 8) sampling method, 9) habitat composition, 10) substrate, 11) life stage, 12) latitude, 13) longitude of each location and 14) bibliographic information (see Data Availability Statement).

Patterns of fish diversity

A curve slope analysis was used to illustrate differences in the frequency of records among the 248 fish species reported in literature. To this end, we performed a piecewise regression between the number of records of listed species and the number of localities, comparing the goodness of fit with the equivalent linear regressions by the Akaike Information Criterion (AIC, Burnham and Anderson 1998) and best model was expressed by AIC differences, $\Delta AIC = AIC - \min(AIC)$ and Akaike model weights. All computations were performed by using the 'segmented' package of R (Muggeo 2008). A bipartite (or two-mode) network projection was used to visually explore the observed pattern of fish diversity, with nodes representing two disjoint and independent sets of data (fish and seagrasses) whose connections here represent the recorded presence of a given species in each seagrass. The network visualization was performed using the Visone software system (Baur et al. 2001).

We also performed a series of analyses to understand how fish species distribute over different seagrasses according to their life stage and which traits were mostly associated with the patterns detected. We first started by aggregating data contained in the 'Habitat' field of the dataset to homogenate the over 30 different types of seagrass and seagrass/seaweeds/coralligenous/*Ruppia* combinations found in the literature. Data were therefore aggregated in 10 main seagrass habitats subdivided in either pure (i.e., meadows constituted by a single seagrass) or mixed (i.e., seagrass in combination with other seagrass and/or seaweeds, coralligenous or *Ruppia*). We then reconstructed a species incidence matrix where each entry corresponded to the number of papers in which each fish species was reported in each habitat. We further arranged our data by characterizing the life stage at which each species was found in each seagrass habitat (adults, juveniles and both stages). The FishMed database (Albouy et al. 2015) was used to extract species-specific traits associated with the potential use of seagrass by fish: 1) maximum length; 2) benthic domain (i.e., vertical distribution); 3) diet type and iv) trophic level.

A distance-based redundancy analysis (dbRDA; Legendre and Anderson 1999) was used to evaluate the association between a dependent matrix consisting of the presence of each species reported in different seagrass habitats at a given life stage and the independent matrix of functional traits. dbRDA

is a constrained ordination method allowing the use of non-Euclidean dissimilarity matrices, reducing the 'double-zero problem' and, therefore, the uncertainty of absences in species compositional datasets. The dissimilarity matrix representing the dependent variable was constructed with the Jaccard distance, while quantitative traits in the independent matrix were scaled and centred before analysis. A pseudo-F statistic was used as an overall test of the dbRDA and to measure the significance of explanatory variables. All analyses were performed in R using the function *capscale* in the 'vegan' package of R (Oksanen et al. 2022).

Results

Workflow and literature overview

At the first search performed, we obtained 62,881 results from the six bibliographic databases, including articles, book chapters, technical reports and conference papers. The resolution power of this research was low, since we reduced this number to 35,955 papers by just eliminating duplicates and publications showing incomplete information (Fig. 1).

The further filtering actions sorted out papers that did contain information on the presence of fish species on Mediterranean native seagrass by using a combination of keyword-based filters. The application of filter 1 reduced the total number of papers by 77%, excluding papers that did not meet the requirements about the minimum number of keyterms in title and abstract (27,574). Another 1,706 poorly relevant papers (filter 2, Relevance Score < 0.667) were further discarded resulting in 6,675 remaining papers. By using filter 3, we focused on the 1,073 papers possibly containing extractable data by eliminating those either containing Negative Keywords or not fitting Most Frequent Keywords thresholds (5,602). Abstracts were read to identify papers likely containing data of interest; 183 were retained and used as the base for *a posteriori* backward snowballing to further search possible papers not indexed in the databases or escaped to research strings. Only fifteen papers were added after this final check, indicating that the searching pipeline implemented in this work was efficient in recalling the scientific literature containing data usable for our research aims. Finally, 33 papers were discarded since reporting data already published elsewhere (for example for meta-analytic purposes) and then data were extracted from 165 papers reporting original, unduplicated data. The complete list of reference papers is available in the provided dataset (see Data Availability Statement).

An overall summary of the literature recovered is reported in Fig. 2, showing that most papers were published between 1982 and 2023, with an overall increasing trend over this time (Fig. 2a). Nearly

96% of papers were peer reviewed articles, and only a minor fraction was composed by technical reports, book chapters and master's theses (Fig. 2b). Nearly half of the papers (94) reported data collected using visual census methods, while 73 were based on capture data and 16 used other methods (Table 1, Fig. 2c). Some studies (12) used both capture and visual census approaches. A large part of studies reporting the sampling season gathered their data across two to all four seasons (65%), while over a quarter focused on summer (27%) and a minority collected information during either the autumn, spring, or winter (4%, 3% and 1%, respectively) (Fig. 2d). Concerning the geographic coverage, a large majority of studies were from the Western Mediterranean Sea (116 over 165), while other ecoregions were characterized by a far lower number of studies, from 30 in the Adriatic Sea to 15 and 12 in the Eastern and Central Mediterranean, respectively (Table 1, Fig. 3).

Within the Mediterranean Sea, five native species of seagrasses occur (Ruiz et al. 2009; do Amaral Camara Lima et al. 2023). The endemic *Posidonia oceanica* (L.) Delile has a paramount importance in terms of ecosystem services and biodiversity along with *Cymodocea nodosa* (Ucria) Ascherson, *Zostera marina* L. and *Z. noltei* Hornemann 1832 that have a broader temperate distribution, and *Ruppia cirrhosa* (Petagna) Grande, 1918, typical of brackish lagoons and salt marshes (Duarte 2009). Two more species, *Halophila stipulacea* (Forsskål) Ascherson, 1867, and *H. decipiens* Ostenfeld, 1902 are Lessepsian and ballast introduced (Gerakaris et al. 2020) and were not considered in this review. *Posidonia oceanica* meadows were the most studied habitat, with 127 papers, while 28 works reported data collected from *C. nodosa* and three regarded *Z. marina*, with another three studying mixed meadows of Zosteraceae. Mixed seagrass meadows studies were reported in 21 papers and 29 works analysed habitats characterized by a mix of seagrass with seaweeds, coralligenous or *Ruppia cirrhosa* complex (Table 1). The database regarding each study site was also visualized and disclosed on an interactive map based on Fig. 3, produced using the *qgis2web* plugin (https://plugins.qgis.org/plugins/qgis2web/) of QGis (QGIS Development Team 2023) and rendered via Leaflet (https://leafletjs.com/), available at https://brunobellisario.github.io/SeagrassFishMed (hosted by GitHub, Inc.© 2022).

Fish records

A total of 248 fish species belonging to 75 families recorded from 101 localities and 10 different habitats were signalled for a total of 9,487 records. At the family level, the highest number of records concerned Labridae (1,939 records) and Sparidae (2,316), followed by Serranidae (666), Gobiidae (611), Blenniidae (442), Syngnathidae (362), Scorpaenidae (356), Mullidae (297), Mugilidae (198) and Pomacentridae (191). Nearly all observed species were recorded by both capture (225) and visual

census (218) studies, while a low number of studies carried out using other sampling methods recovered 76 species only (Table 1). The greater number of species was signalled from the Western Mediterranean (231), the wider geographic area also providing the higher number of studies. A comparable number of species was recorded within the other, less investigated, ecoregions ranging between 132 (Central Mediterranean) and 162 (Adriatic Sea) (Table 1).

The data extracted from literature witness that virtually all species recorded were spotted in *P. oceanica* meadows (240 over 248) while the species pool observed in any other habitat was much more restricted, with *C. nodosa* beds hosting about 60% of the recorded species (146) and *Z. marina* only 15% (38 species) (Table 1). Habitats of mixed seagrasses were characterized by an intermediate number of recorded species; 88 in mixed meadows of *C. nodosa* with Zosteraceae and 81 in *P. oceanica*/*C. nodosa*. A low number of species was observed on mixed Zosteraceae either associated or not with *P. oceanica*. The small number of studies reported for this habitat is unlikely to be the cause of the few species recorded, since a comparable number of sources documented a higher number of species from mixed habitats of seagrass with seaweeds (Table 1).

We extracted the number of species that have been recorded as exclusive for each sampling method, ecoregion, and habitat (Table 1). Within the sampling methods, captures were able to spot 29 species unrecorded by any other method, against 21 exclusives of visual census, suggesting a certain degree of complementarity of the two methods. The number of species found exclusively in single ecoregions was high in the western Mediterranean (45) but very low in the Adriatic Sea (4). The pattern of fish species shared among different seagrass habitats was represented by a bipartite network, linking each fish species to the seagrass(es) where it was recorded, evidencing the remarkable difference in the number of exclusive species observed in *P. oceanica* with respect to other seagrass habitats (Fig. 4). We found that about one third of exclusive species has been spotted on *P. oceanica* (82 species), while other combinations of seagrass showed a remarkably lower number of unique species; two in *C. nodosa* (*Apricaphanius iberus* and *Hemirhamphus far*), and three in *C. nodosa* mixed with Zosteraceae (*Hyphorhamphus picanti*, *Merlangius merlangus*, *Sygnatus taenionotus*).

Fish distribution patterns in Mediterranean seagrasses

Fish species were subdivided in three main frequency classes through a piecewise regression between the number of records of listed species and the number of localities that by identified two main breakpoints (Supplementary Figure S2): 1) frequent and widespread species recorded many times from a high number of localities; 2) species with an intermediate frequency of records; 3) uncommon species spotted quite rarely and from a low number of localities.

We identified 23 frequent species showing between 106 and 284 records each from 55 to 85 localities. Among them, the most frequently observed were all the species belonging to the genera *Diplodus* (except *D. cervinus*) and *Symphodus* (except *S. doderleini* and *S. melops*) followed by *Mullus surmuletus* and *Coris julis*. Other species were: *Serranus scriba* and *S. cabrilla*, *Sarpa salpa*, *Chromis chromis*, *Boops boops*, *Oblada melanurus*, *Scorpaena porcus*, *Spondyliosoma cantharus*, *Labrus merula* and *L. viridis* and *Dentex dentex.* Another 55 species were recorded at intermediate frequencies, showing 25 to 124 records from 18 to 52 localities. Here are included for example the zebra seabream *Diplodus cervinus* and the two *Symphodus* species *S. doderleini* and *S. melops*, both sand smelts *Atherina boyeri* and *A. hepsetus*, and all the blennies belonging to the genus *Parablennius*, except the uncommon *P. zvonimiri*. The larger number of species (170) was recorded at low frequencies, being signalled 1 to 46 times from 1 to 17 localities. This long list includes species typical from coastal habitats different from seagrass, or the many pelagic species occasionally occurring on coastal seagrass meadows mainly while foraging. The 15 Lessepsian species recorded so far in seagrass habitats are also uncommon, some of them being reported by single studies (Supplementary Table S6).

One of the objectives of this review was to analyse the distribution of fish life stages across various seagrass habitats. Information on the life stage was available for 175 species in at least one study, while 73 species lacked these data and were thus excluded from further analyses. A heat-map was used to visualize at which life stage (adult, juvenile, both stages and undefined) each species was recorded in each seagrass habitat (Fig. 5a). Our findings showed that nearly all 175 species have been recorded in several studies without assessing their life stage: only 7 species were always classified from this point of view (Fig. 5a). The heat-map evidenced that a high number of species observed in *P. oceanica* meadows were reported mainly as adults, either exclusively or associated with juvenile stages. It is worth noting that nearly all species reported as adults in *P. oceanica* have been also recorded in further studies that miss the life stage. A high number of species was also recorded on *C. nodosa* but in this case the larger part of the data concerned juveniles in pure meadows and both adults and juveniles in mixed meadows of *C. nodosa* with *P. oceanica* (Fig. 5a). In the case of *C. nodosa* too, many studies did not report the life stage of the recorded specimens, leaving a knowledge gap open.

A goal of this review was to test if species-specific traits usually associated with the use of seagrass habitats in fish were somehow related to their presence on different seagrasses at a given life stage. The first two axes of dbRDA accounted for 83% of the total variability, with maximum length and trophic level significantly contributing to the observed pattern of ordination ($F > 2.073$ and $p < 0.01$ in both cases), while the main benthic domain of fish was only slightly significant ($F = 1.771$, $df = 2$,

p = 0.05). Trophic level and, to a lesser extent, fish length mostly contributed to the ordering of species along the first axis of dbRDA, while length and benthic domain to the ordering along the second axis, with species having mainly pelagic distributions separated from benthic and demersal ones (Fig. 5b). Overall, our results showed a gradient of increasing length and trophic level for fish species recorded in seagrass meadows during their adult stage, from mixed layers of *C. nodosa* and Zosteracee, to *C. nodosa* and *P. oceanica* (either pure or in combination). Therefore, large piscivorous (often pelagic) species at the top of the food web are spotted on seagrasses, and in particular on *P. oceanica*, mainly as adults. Although the global model was significant (F = 2.421, df = 7, $p < 0.001$), the real variance explained by functional traits (i.e., the constrained part of ordination) was only ca. 10% of total variance, possibly suggesting the effect of latent and unexplored traits in determining the observed pattern of ordination.

Discussion

This review represents a first effort to synthesize the present knowledge on fish species occurring in native seagrass habitats across the whole Mediterranean Sea, taking advantage of the high number of studies carried out so far. The database built up from the 165 papers recovered following a PRISMA modified approach provided support to several assumptions repeatedly stated in literature, but so far sustained by data from local to sub-basin scale and allowed evidencing some unexpected knowledge gaps on the highly studied fish/seagrass system.

Fish species in Mediterranean seagrass

The high value of Mediterranean seagrasses as marine hotspot of biodiversity has been evidenced for many macrofaunal groups, from polychaetes to amphipods (Buia et al. 2000; Borg et al. 2006; Como et al. 2008; Bellisario et al. 2019). This tenet is considered holding for fish fauna too, but there are only few papers supporting this idea by providing geographically broad data (see for example Francour 1997; Guidetti 2000; Koutsidi et al. 2020).

Our dataset provides for the first time a comprehensive overview of fish species from native seagrass habitats across the whole Mediterranean basin and confirms that seagrass habitats are biodiversity hotspots. We found 248 fish species belonging to 75 families, recorded at list twice by independent samplings (except Lessepsian species, considered even if signalled once). This result supports the widespread postulate that seagrasses host a relevant number of fish and have therefore high importance for Mediterranean biodiversity. Indeed, considering that a total of about 650 fish

species has been reported for the whole Mediterranean Sea (Coll et al. 2010), our data show that 38% of them are linked at various degrees to seagrass beds.

When considering the data at the whole basin scale, the observed pattern of species distribution is consistent with that evidenced by single local studies. The families Labridae and Sparidae showed the highest number of records in *P. oceanica* and were the most frequent across both western and eastern Mediterranean in any sampling season, as witnessed by many studies (Deudero et al. 2008; Kalogirou et al. 2010). Labridae was also the most frequent family recorded in *C. nodosa* and *Z. noltei*, although the composition of fish fauna in these habitats is highly variable across seasons, with necto-benthic fish prevailing in summer (Guidetti and Bussotti 2000). Highly recorded families were also Serranidae, Gobiidae, Syngnathidae and Scorpaenidae, consistently signalled as abundant in all Mediterranean seagrass communities by several studies, although their relative abundance may vary according to local conditions and human impacts (Deudero et al. 2008; Ourgaud et al. 2015). The overall data confirmed significant seasonal variations, with Serranidae as the third most recorded family after Labridae and Sparidae in summer, winter, and autumn, while Gobiidae become more frequently spotted in spring.

Matching the ecological and biological features with the reported observations of fish species suggests that their frequency in literature reflects their real occurrence in seagrass habitats, confirming the high species richness of fish characterizing seagrass habitats, but also showing that only few very common species occurred, while the majority are rare and/or occasional visitors. Indeed, despite the high number of observed fish species, our data show that only 23 were frequently recorded. Among them *Boops boops* and *Chromis chromis* were the most observed, both known as gregarious planktivorous species forming large aggregations on seagrass, during either reproductive season (*B. boops*) or all year long (*C. chromis*) (Guidetti and Bussotti 1998; Deudero et al. 2008). Other frequent species are known to be strictly linked to *P. oceanica* beds, as *Mullus surmuletus* and *Symphodus cinereus*, besides *Sarpa salpa* that feeds directly on *P. oceanica*, being its main herbivore consumer along with the sea urchin *Paracentrotus lividus* (Guidetti and Bussotti 2000; Prado et al. 2007; Máñez-Crespo et al. 2022). Many other species are known to be frequent and abundant in both seagrass habitats and other substrates, as *Symphodus ocellatus, S. rostratus, Serranus cabrilla, Coris julis*, and several *Diplodus* species, these latter recruiting either in seagrass or rocky substrates (Garcìa-Rubies and Macpherson 1995; Diaz-Gil et al. 2017; Cheminée et al. 2021). Some of these species are of commercial interest across the whole Mediterranean Sea (e.g., *B. boops* and *M. barbatus*) or in the Central sub-basin (e.g., *D. annularis*), further underlining the relevance of seagrass habitats in sustaining Mediterranean fisheries (Jackson et al. 2015; Unsworth et al. 2018; FAO 2022).

Our results show very low recording frequencies for most of species, whose ecology supports the idea that the low number of records really reflects either their rarity or occasional presence in seagrass fish communities, more than representing a lack of information. Indeed, the large majority is considered rare, because of their restricted geographic range and/or low population density. For instance, the range of black-headed benny *Microlipophrys nigriceps* is limited to the western and central Mediterranean Sea and the Belotti's goby *Gobius ater* is known from a few localities (Kovačić et al. 2022). Many uncommonly recorded species occur occasionally on seagrasses being typical of other habitats, as the killifish *Apricaphanius fasciatus*, usually living in brackish water lagoons (Mosesso et al. 2012). Habitat differences may also be associated with species' bathymetric range, as in the case of deep-sea scaldback *Arnoglossus rueppelii* or the mesopelagic garrick *Cyclothone braueri*, one of the most abundant and frequent species of the twilight zone (Mytilineou et al. 2005; Olivar et al. 2012). Other species are pelagic and seldom occur in coastal habitats, as in the case of mackerels and tunas: as an example, the Atlantic horse mackerel (*Trachurus trachurus*) is usually reported as occasional visitor in *P. oceanica* and using this habitat exclusively for active prey foraging (Kalogirou et al. 2010). Differences may also regard the substrate; this is the case of the many flatfish recorded in seagrasses although being typical of sandy bottoms as the solenette *Buglossidium luteum* or the Senegalese sole *Solea senegalensis*, that is also restricted to the western Mediterranean Sea being a Herculean migrant entered through the Gibraltar Strait (Golani et al. 2002). Some rarely recorded species are also declining throughout their whole range due to human impacts, as for the endangered elasmobranchs rough ray (*Raja radula*), sandbar shark (*Carcharinus plumbeus*) and common smoothound (*Mustelus mustelus*) (Mancusi et al. 2016; Jabado et al. 2021; Rigby et al. 2021).

According to our dataset, Mediterranean seagrass meadows host 15 Lessepsian species, all signalled in the ORMEF Geoportal listing the 221 exotic fish species inhabiting the Mediterranean Sea (Azzurro et al. 2022; last access April the 10th, 2024). All these species are well established and quite common, although they entered the Mediterranean Sea at different times, with their first sight ranging from 1927 (*Hemiramphus far*) to 2003 (*Lagocephalus sceleratus*). All Lessepsian species have been recorded on *P. oceanica* meadows except *Sargocentron rubrum*, *Siganus luridus*, *S. rivulatus* and *Stephanolepis diaspros* that were recorded on *C. nodosa* too, and *H. far* that has been seen only a single time on *C. nodosa* (Selfati et al. 2019). The Lessepsian species spotted on seagrass in the invaded Mediterranean are mainly associated with either soft bottoms or rocky and coral reefs in their native range, with the only exception of *Sphyraena flavicauda* (Gell and Whittington 2002; Nakamura et al. 2003). This pattern is coincident with the relatively low number of records reported in seagrass according to our data, with respect to the high number of observations across the Mediterranean Sea

reported in the ORMEF database (Azzurro et al. 2022). Nevertheless, some studies have shown a high abundance of Lessepsian species in the eastern Mediterranean seagrass meadows (Kalogirou et al. 2010; Koutsidi et al. 2020). This can be attributed to the Lessepsians' ability to expand their original niche to invade relatively empty niches, as they are often opportunistic species. Two such examples are both *Siganus* species, which are herbivorous and likely found relatively unexploited resources in the Mediterranean Sea, due to the low diversity and abundance of herbivorous fish species compared to their native ranges (Bariche et al. 2004). This allowed these species to attain high population densities, making them economically significant in terms of both landings and economic value for the eastern Mediterranean (Koutsidi et al. 2020; FAO, 2022).

Patterns of fish diversity

Our analyses show that the high species richness of fish found on seagrass beds is far from being evenly distributed among different seagrasses at the Mediterranean scale, a heterogeneity missed when looking at single studies that frequently concern the comparison of seagrass habitats against bare substrates, as either rocks, gravel, or sand (e.g., Biagi et al. 1998; Franco et al. 2006; Bussotti and Guidetti 2011; La Mesa et al. 2011). At the Mediterranean scale, *P. oceanica* habitats host the highest fish diversity, with 240 species over the 248 recorded, while 146 were observed in *C. nodosa* and 38 in *Z. marina*. Only few studies compared simultaneously and consistently fish communities associated with different seagrasses, sometimes providing contrasting results. For instance, Manent and Abella (2005) studied the fish fauna of *P. oceanica* and *C. nodosa* beds from Menorca, finding a slightly higher number of species in *C. nodosa* (16) than in *P. oceanica* (13). A similar result was found by Bonaca and Lipej (2005) within the Venice Lagoon, where the lower number of species recorded in *P. oceanica* was attributed to the very small extension of the remnant patch of this seagrass (about 1 km^2) with respect to the area occupied by *C. nodosa*. Conversely, a comparison of juveniles' distribution across 14 different vegetated and unvegetated habitats highlighted a higher fish species richness and abundance in *P. oceanica* with respect to *C. nodosa*, although comparable to soft and rocky substrates (Chemineé et al. 2021). A recent pioneering study investigating metazoan communities in *P. oceanica*, *C. nodosa* and the invasive *Halophila stipulacea* across the last century by using eDNA showed a higher diversity in *P. oceanica* for all examined phyla, including fish (Wesselmann et al. 2022). The Authors linked such diversity to the structural complexity of seagrass beds, known to be higher for the large *P. oceanica* than for the smaller *C. nodosa* and *H. stipulacea* (Buia et al. 2000; Hemminga and Duarte 2000).

It is worth mentioning that our dataset defined the habitats according to the main seagrass types and combinations. Detailed information on the differences among habitat patches over small scales are frequently unreported in study cases, so missing relevant information. Indeed, recent works highlighted the link between fish richness and habitat heterogeneity, especially for *P. oceanica* beds. For instance, the seascape context was found to be the main driver of Adriatic fish communities, with higher diversity associated with habitat mosaics of *P. oceanica* patches either intermingled with rocky/algal reefs and boulders or bordering sands (Zubak Čižmek et al. 2021). Accordingly, the interfaces between *P. oceanica* and other unvegetated habitats showed high species richness and abundance when looking at juvenile fish assemblages in 14 different habitats from northern Tyrrhenian Sea (Chemineé et al. 2021). Therefore, part of the high fish richness assigned to *P. oceanica* meadows could be ascribed to not reported intermix of different habitats at the local- to micro-scale, deserving specific studies so far lacking. Moreover, some occasional pelagic or demersal highly vagile species may have been recorded because either moving across habitats or following their prey.

Patterns of functional diversity

A main goal of this review was to investigate if species-specific traits associated with the potential use of seagrasses (i.e., diet, trophic level, vertical distribution and size) could be linked to the presence of fish on different seagrass habitats at a given life stage. Large carnivorous or piscivorous predators resulted to be more frequently observed and almost exclusively in their adult stage in *P. oceanica* and, to a lesser extent, in *C. nodosa* beds. Smaller species, with benthic to demersal distribution, and herbivorous to omnivorous diet are present in all their life stages, from juvenile to adult, in both monospecific and mixed seagrass habitats. Such pattern seems to be associated with the species' ability to use seagrasses during specific life stages, with highly mobile predators only seldom observed during their juvenile stages being mainly, although uncommonly, recorded as adults on *P. oceanica*.

This finding could match the Seagrass Superiority Hypothesis, postulating that the dense, three-dimensional structure of seagrass may offer protection to prey with respect to bare substrates, so warranting a lower risk of predation in these habitats (Heck and Orth, 1980; Bell and Pollard 1989; Zubak et al. 2017). However, predators too may benefit from such habitats due to either the high prey density, if they are transient species, or the many hideaways if they are ambushing residents. Therefore, predation risk is not fixed for each habitat but depends largely on both the relative abundance of predators and their mode of searching and catching (Kruschel and Schultz 2020). The

differential predation risk associated with different predation modes will in the end select or train prey to choose the habitat that better balances their foraging needs with the protection against the most frequent kind of predators. This is the so-called Predation Mode Hypothesis, that accounts for the role of predators in shaping fish communities and is supported by an increasing number of studies (Gilliam and Fraser 1987; Schultz et al. 2009; Fouzai et al. 2019). The results of a meta-analysis suggested that fish communities in *P. oceanic*a meadows are structured in response to the presence and abundance of piscivorous species, so indicating seagrass as a partial refuge for preys (Zubak et al. 2017). Research carried out on fish communities from vegetated and unvegetated habitats in eastern Adriatic Sea showed that prey and predators resulted negatively associated in various habitats and this negative correlation was as much stronger as predators were more aggressive. In this geographic area prey showed a positive association with *C. nodosa* and *P. oceanica*, besides unconsolidated sediments, in agreement with our analysis (Kruschel and Schultz 2020). Also, the local environment may play a main role in producing different patterns of prey/predator association through habitat patchiness, interspecific interactions, fishing activities and many other variables (Kruschel and Schultz 2020).

Our results are drawn from a high number of heterogeneous studies applying different sampling methods in different seasons, taking into consideration only seagrass habitats without bare substrates, and skipping details on predation mode. This lack of detailed information may explain the relatively low percentage of constrained variance captured by the dbRDA analysis and suggest the need for further in-depth studies mainly including functional traits regarding both foraging behaviour and life history.

Literature review and research gaps

Although the 165 papers included in the dataset covered the entire Mediterranean Sea, a geographic imbalance has been observed in the distribution of localities from which data were extracted (Fig. 3). The western Mediterranean Sea received greater attention, with 67 sampled localities, while the Adriatic Sea had 17, and central and eastern Mediterranean had eight and nine localities, respectively. This existing gap in research has been recognized in the past and continues to persist in current literature and could be partly attributed to the less continuous distribution or even the absence of seagrasses in southern and eastern regions of the basin (Ruíz et al. 2009). However, a significant contribution to this gap comes from the disparity in study efforts between EU *vs*. non-EU countries (Ruíz et al. 2009; Chefaoui et al. 2018). Indeed, in the western Mediterranean Sea most sampling localities are located along the coasts of European countries, where *P. oceanica* beds is under

protection by the European Union's Habitats Directive (92/43/CEE) as a priority Habitat Type (*1120). Furthermore, seagrasses have all been appointed as relevant coastal bioindicators within the EU Water Framework Directive (WFD 2000/60/CE). Consequently, EU countries promoted a comprehensive knowledge of these habitats to effectively implement these Directives (Ruíz et al. 2009).

A significant portion of the studies focused on *P. oceanica*, either in pure meadows or in combination with other seagrass and seaweeds (Table 1). This is partly due to the mentioned EU legislation but the wide distribution, endemicity to Mediterranean Sea and acknowledged role in providing ecosystem services have also driven studies on various biological and ecological aspects of this seagrass (Chefaoui et al. 2018). Moreover, other studies investigated pure and mixed beds of *Cymodocea nodosa* that, although not endemic to the Mediterranean, is protected under both the Bern and OSPAR conventions being considered relevant for coastal biodiversity (Chefaoui et al. 2016). According to this sampling bias, a significant difference was observed in the number of fish species recorded, both overall and exclusive, between the species-rich *P. oceanica* and any other seagrass habitat (Table 1).

The two most frequently used sampling methods, capture and visual census, were equally applied and both effectively identified nearly all the species recorded. Investigating fish presence in seagrass meadows is challenging due to their dense multilevel canopy, so that there is not a single universally acknowledged method to efficiently survey all seagrass sub-habitats (French et al. 2021). Nevertheless, visual and capture methods complement each other, with capture being more efficient in sampling crypto-benthic species living into the canopy, while visual approaches better perform in recording planktivorous and good swimmer species (Harmelin-Vivien and Francour 1992; French et al. 2021). Accordingly, large pelagic fish likely transient on seagrass meadows as *Coryphaena hippurus*, *Euthynnys alletteratus*, *Thunnus thynnus* and *T. alalunga* were exclusively recorded through visual methods, along with other schooling and good swimmers like the blue runner *Caranx caranx* and the Mediterranean flyingfish *Cheilopogon heterurus*. On the other hand, most fish exclusively sampled through capture methods were either benthic species (e.g., *Callionymus filamentosus,* and *C. maculatus*, *Merlangius merlangus* juveniles and *U. pori*), flatfish (e.g., *Arnoglossus kessleri, Buglossidium luteum, Citharus linguatula*, *Microchirus variegatus, Platichthys flesus)* or elusive species that seek shelter under rocks and seagrass (es. *Gobius couchi*). As expected, the two methods are not totally alternative and there is no strict division among the species they efficiently sample. For instance, the marine planktivorous mesopelagic silvery lightfish *Maurolicus muelleri* was exclusively recorded by netting, while the blennid *Scartella cristata*, known to hide in empty shells or under rocks, was spotted only through visual approaches.

The retrieved data confirmed seagrass habitats as key biodiversity hotspots, characterized by a high fish species richness, but they present a remarkable gap in terms of direct comparison among different seagrasses, since a relevant percentage of studies are centred on the confrontation of highly different substrates as seagrasses *vs*. sediments, rocks, coralligenous, seaweeds. Recent works have been able to provide a direct confrontation of fish communities associated with different seagrasses taking advantage of the emerging eDNA techniques, so paving the way for the use of a quick and reliable approach allowing to overcome this scarcity of relevant data (He et al. 2022; Wesselmann et al. 2022).

Another key topic largely understudied is the role of habitat heterogeneity in determining fish diversity. Seagrass meadows are frequently intermingled with sandy or rocky substrates and a few recent works started to point out the relevance of habitat patchiness at the local scale in influencing fish richness. The lack of detailed studies considering habitat heterogeneity is also a limitation to understand the role of seagrasses in mediating prey/predator coexistence and in providing an effective protection as nursery, which is increasingly signalled as relevant in determining habitat choice by prey. Aggressive piscivorous predators have been observed to preferentially patrol the edges among different habitats, including seagrasses, so that prey species along with less aggressive predators tend to avoid heterogeneous habitats. These observations have generated the hypothesis that aggressive predation may be a primary constraint to fish community diversity. Although our overall data support this view at the whole basin scale, this hypothesis deserves to be tested through a higher number of diversified approaches, stated its relevance for both the management of coastal resources and the implications for seagrass habitat restoration planning and implementation.

An unexpected lack of data concerned the life stage of recorded fish, which has never been reported for about one third of the species and was recorded from a minority of studies for many other species. This gap clashes with the overall acknowledged idea that seagrass beds are the habitat of choice as nursery for many fish species (Lilley and Unsworth 2014). Most studies were frequently oriented either at examining seasonal juveniles and adult's occurrence in a single habitat, or at comparing highly differentiated substrates within a single geographic region, or at examining single species. This gap is even more surprising if we consider that the degree of association between fish species and seagrasses is frequently assigned looking at the co-presence of different life stages on the same substrate (Kalogirou et al. 2012). Recently, an alternative view on the role of seagrass as nursery has been proposed, based on observations from 14 different habitats along the Mediterranean French coasts (Cheminée et al. 2021). The results showed that rocky substrates were as species rich as *P. oceanica* interfaces, and that the most abundant fish species used several different habitats as nursery at various times. This agrees with global data suggesting that research is needed to fully understand the links between different nursery habitats and to provide a more complete picture of the use of

seagrass by fish settlers and juveniles to better understand their relevance in warranting fish diversity and addressing their sustainable management (McDevitt-Irwin et al. 2016; Unsworth et al. 2018).

Conclusions

Although Mediterranean seagrasses are acknowledged as biodiversity hotspots, comparative studies on fish assemblages are still fragmented and only seldom covering scales larger than sub-basins. This results in a partial view of fish distribution patterns within different seagrasses inhabiting the Mediterranean Sea, hiding important mechanisms associated with habitat use. To this end, our dataset could enable to verify and extrapolate specific hypotheses at basin-wide scale, which might otherwise remain unverified due the complex nature of scale-dependent mechanisms structuring ecological communities (Weiher et al. 2011), with the hope to provide a sound basis for scientists and managers across many fields, from fisheries to biodiversity assessment and conservation. For instance, understanding the extent to which seagrasses are able to host the same fish fauna, both from a taxonomic and functional point of view, would help identifying peculiar functional strategies more at risk in the face of anthropogenic pressures, or to provide important information about how global change will reshape seagrass biodiversity. Overall, our findings confirm the ability of seagrasses in sustaining a high percentage of fish biodiversity and seem to highlight the emergence of a general pattern in the use of habitat by fish, mostly based on the life history of species and driven by specific functional traits. While large piscivorous species are reported almost exclusively during their adult phase, smaller species with a more diversified diet are usually reported during all life stages, a pattern so far observed at smaller geographic scales in fragmented studies. Such ‘segregation’ seems to be associated in some way with the species' ability to use seagrasses during specific life stages, ultimately suggesting how different functional strategies may coexist within Mediterranean seagrasses. However, further insights are necessary for a generalization of the observed pattern and to better understand the mechanisms behind the structuring of fish communities, fundamental for the maintenance of marine biodiversity.

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Author contributions

AL: Methodology, investigation, formal analysis, drafted the manuscript methodology, final review; **BB**: Conceptualization, methodology, investigation, formal analysis, drafted the manuscript, final review; **RC**: Conceptualization, critical revision, drafted the manuscript, final review, investigation and supervision, resources. All authors read and approved the manuscript and agree to the submission.

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Data availability

The dataset generated and analysed during the current study is available at Figshare, https://doi.org/10.6084/m9.figshare.24100077

Conflict of interest

The authors have no conflict of interest to declare.

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List of Tables

Table 1 – Summary table showing the total number of: i) papers, *n*; ii) fish species, s_{tot} and iii) exclusive fish species, $s_{exclusive}$ with respect to different sampling methods, ecoregions, and seagrass habitats.

		n	s_{tot}	$s_{exclusive}$
Sampling methods	Net	73	225	29
	Visual census	95	218	21
	Other	17	76	1
Ecoregions	Western Mediterranean	116	231	45
	Central Mediterranean	12	132	0
	Adriatic Sea	30	162	4
	Eastern Mediterranean	15	140	9
Seagrass Habitats	*Posidonia oceanica*	127	240	82
	Cymodocea nodosa	28	146	2
	Zostera marina	3	38	0
	Posidonia oceanica / *Cymodocea nodosa*	7	81	0
	Posidonia oceanica / Zosteraceae	1	1	0
	Cymodocea nodosa / Zosteraceae	14	88	3
	Zosteraceae	3	6	0
	Seagrass / seaweeds	23	173	2
	Seagrass / Coralligenous / seaweeds	4	62	0
	Seagrass / *Ruppia* sp. / seaweeds	2	26	0

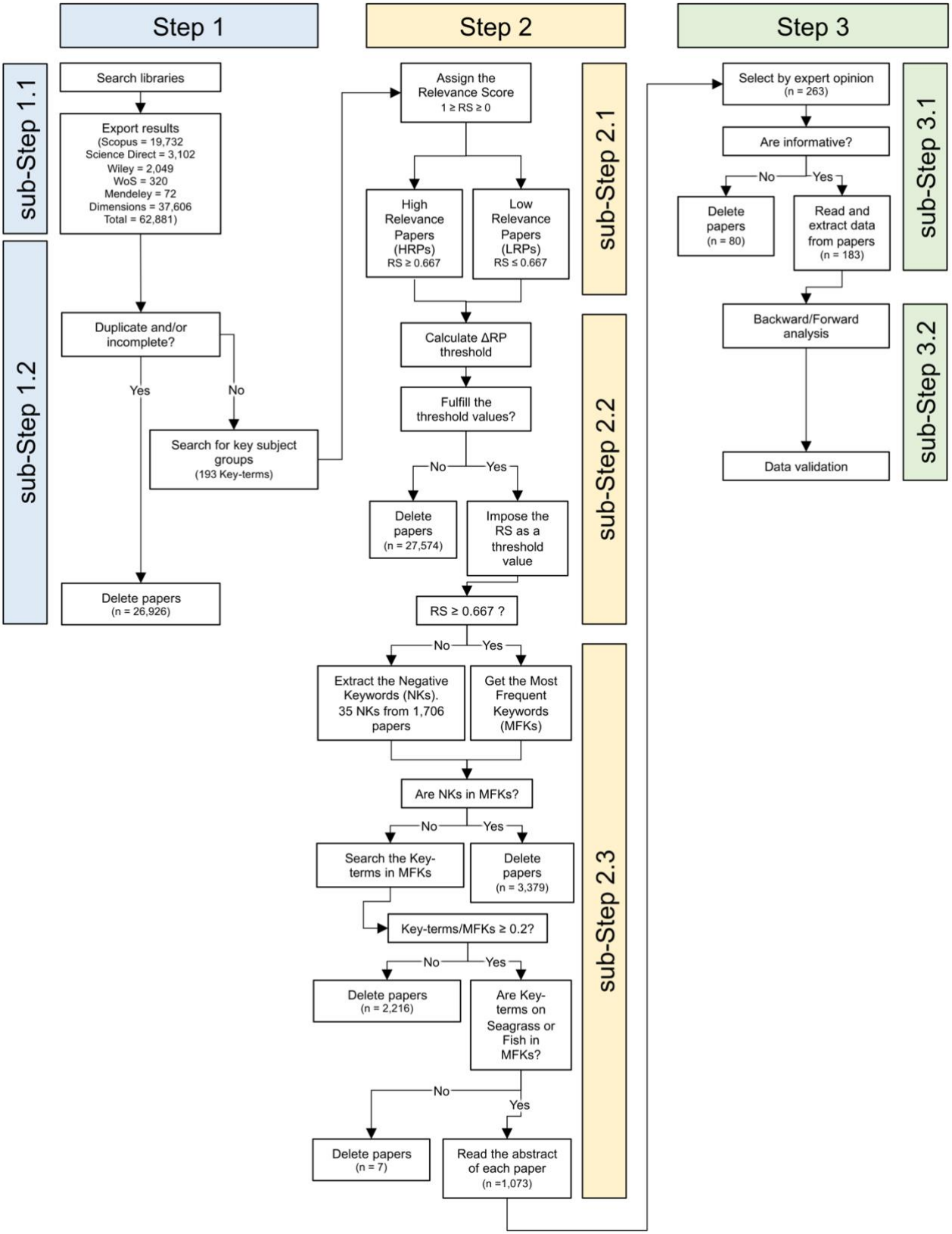


Figure 1 –Flowchart showing each Step and sub-Step implemented in the filtering pipeline.

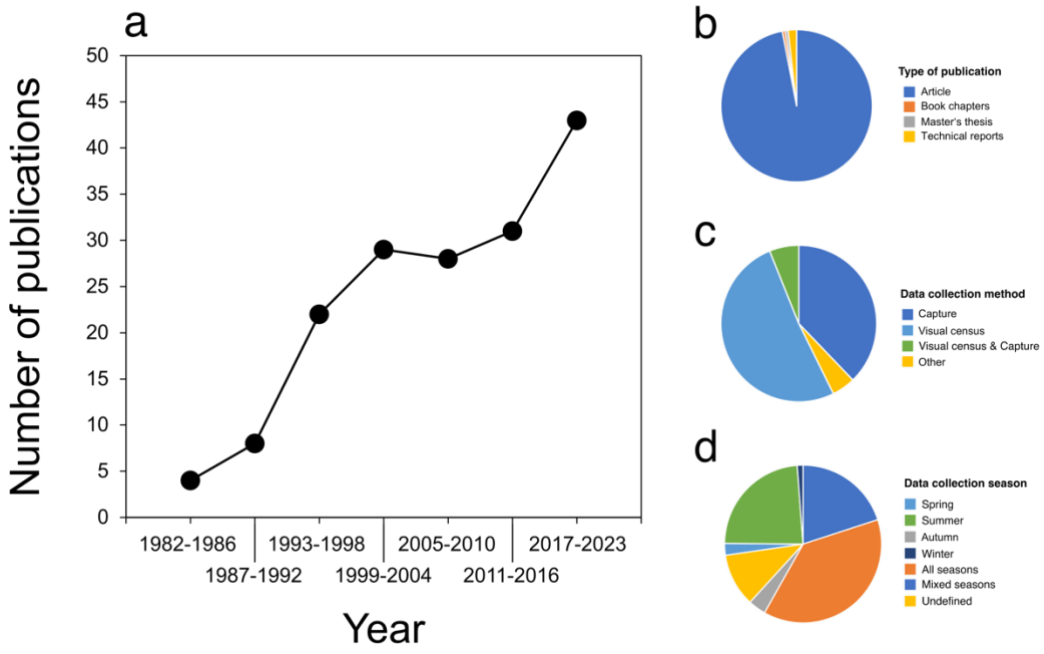


Figure 2 – Summary of the literature overview showing a) the number of publications, aggregated for the five-year period; b) type of publication; c) data collection methods and d) data collection seasons.

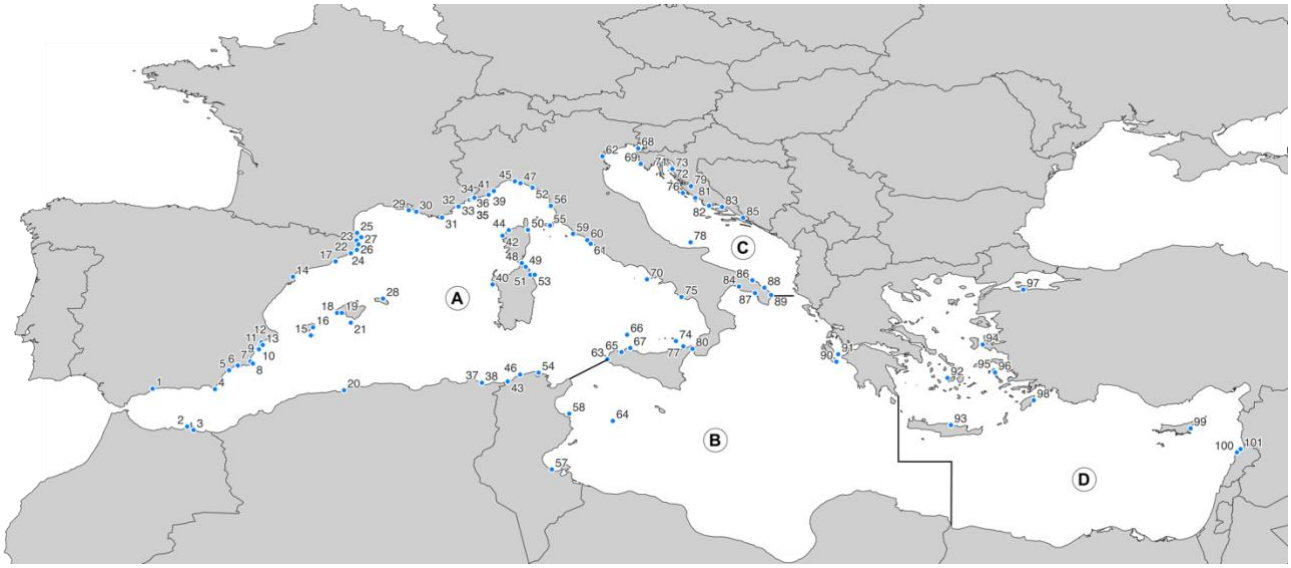


Figure 3 – Geographic distribution of the 101 localities providing data on fish assemblages on seagrasses. A, Western Mediterranean Sea; B, Central Mediterranean Sea; C, Adriatic Sea; D, Eastern Mediterranean Sea. A detailed and interactive map showing all available information from our dataset can be consulted at https://brunobellisario.github.io/SeagrassFishMed.

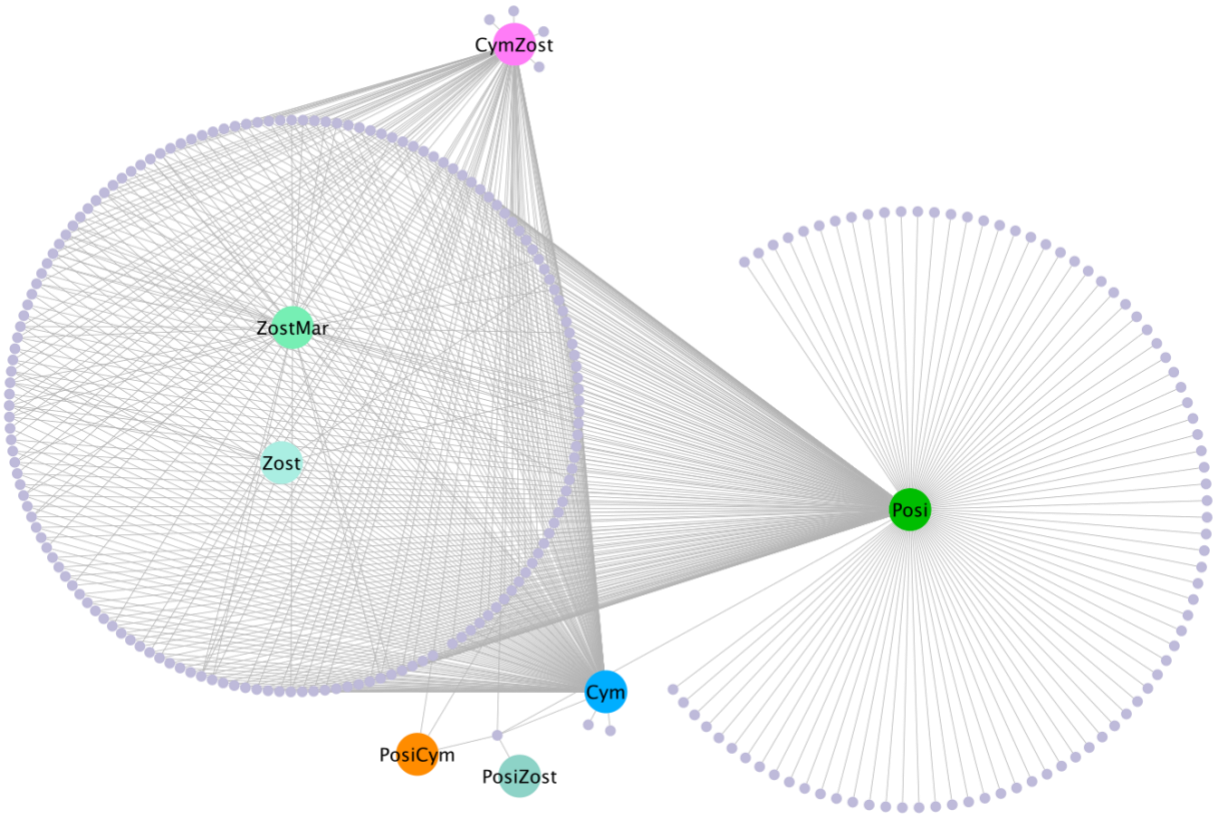


Figure 4 – Network representing the association between fish species and native seagrasses in the Mediterranean Sea: Posi, *Posidonia oceanica*; Cym, *Cymodocea nodosa*; ZostMar, *Zostera marina*; Zost, Zosteracee; CymZost, *C. nodosa* mixed with Zosteracee; PosiCym, *P. oceanica* and *C. nodosa*; PosiZost, *P. oceanica* mixed with Zosteracee.

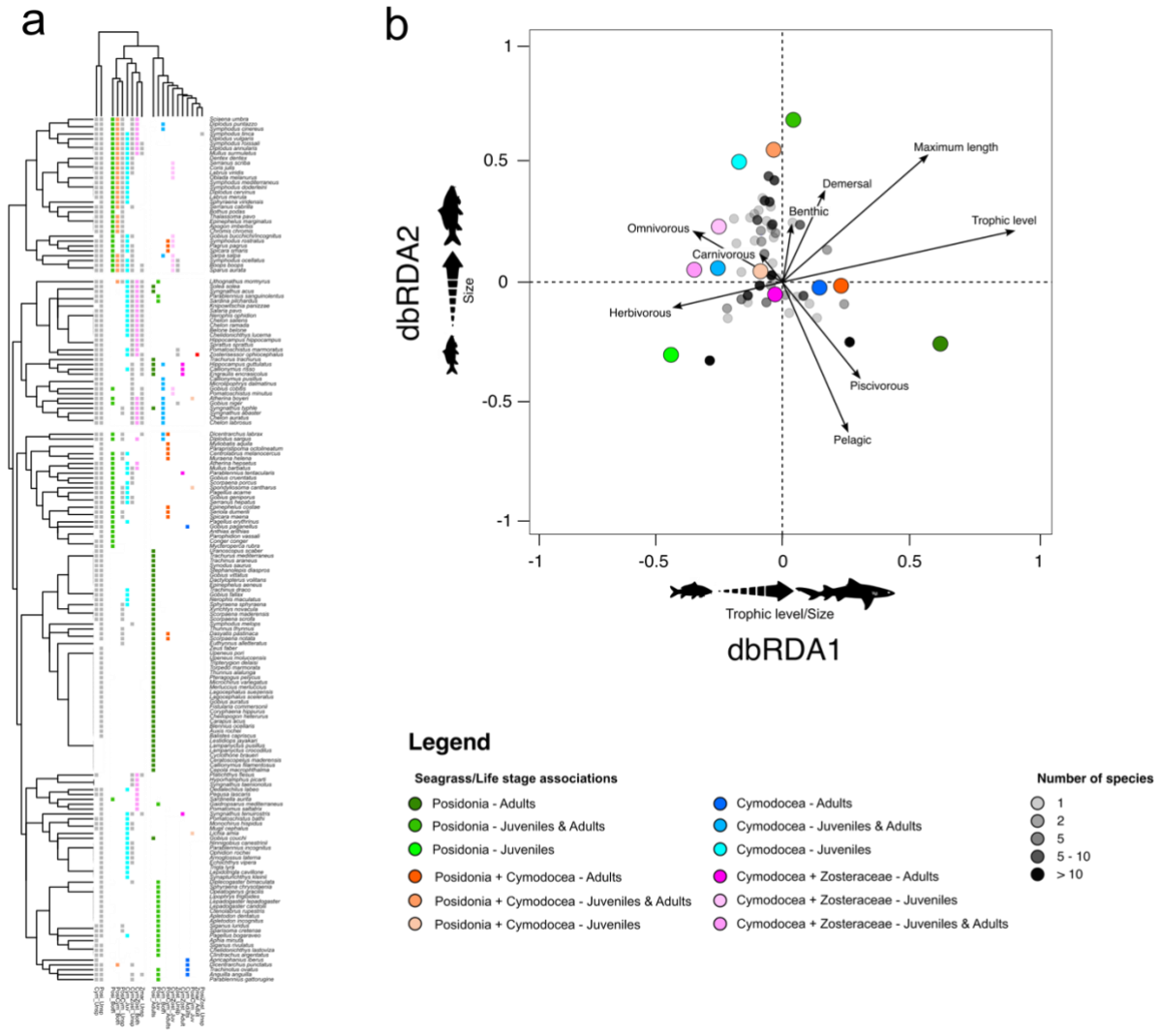


Figure 5 – Overall picture of fish distribution, alongside their life stages and traits on different seagrass habitats. a) Heatmap showing the association between each life stage of fish reported in literature and seagrasses. Dendrograms above and alongside the heatmap represent the cluster subdivision of fish and seagrasses based on their pattern of association, using the complete linkage (also known as the farthest neighbour) method to calculate distance between the furthest points of the two clusters being merged; b) distance-based redundancy analysis (dbRDA) showing the association between the presence of fish species reported in different seagrass habitats at a given life stage and functional traits. Colours in the figures match the ones in the legend, with the only exception of grey-coloured squares in a), which correspond to unknown life stages of fish.

SUPPLEMENTARY INFORMATION

Step 1 - Searching the libraries

Sub-step 1.1

The keyword-based search was addressed to six databases: Dimension, Mendeley, ScienceDirect, Scopus, Web of Science and Wiley.

The query string included the name of the Mediterranean countries, the scientific name of the Mediterranean autochthonous seagrass species belonging to the genera *Cymodocea*, *Zostera* and *Posidonia* together with the common names 'seagrass', 'sea grass', 'eelgrass', and the terms 'fish', 'fishes' and 'ichthyofauna'. Through a preliminary analysis based on the method proposed by Foo and co-workers (2021) in the framework of the PRISMA approach, we added further words identifying the life history stage of fish, i.e., eggs, larvae, juveniles and adults, besides words defining the target of the observations (e.g., 'community' and 'assemblage)' and the sampling methods. This produced 69 keywords identifying the three main fields of the research objective (Mediterranean Sea, seagrass and fish fauna), linked by 68 *OR"* and three *AND"* Boolean operators.

Advanced searches were therefore carried out in each of the possible research fields (Title, Abstract, Author Keywords, Text and References) of the six analysed bibliographic databases using a different query for each library due to both their different query limits and years of coverage (Supplementary Table S1). Results have been exported as an Excel file containing the abstract, the Authors' keywords and the title of each paper, which represents the basis of subsequent searches.

Supplementary Figure S1 - Graphical representation of the 69 keywords used for each field of our research objective during the implementation of the filtering pipeline. Keywords are divided into six-word categories: “Mediterranean Sea”, “Fish”, “Seagrass”, “Sampling”, “Community”, “Life Stages”.

Supplementary Table S1 - Query strings submitted to each library database.

Database	Field tags	Character or word limits	Boolean operator limits	Query strings
Dimensions	All Fields	None	None	(“Mediterranean Sea” OR “ Mediterranean” OR “ Alboran” OR “ Balearic” OR “ Ligurian” OR “ Tyrrhenian” OR “ Adriatic” OR “ Ionian” OR “ Aegean” OR “ Levantine” OR “ Spain” OR “ France” OR “ Monaco” OR “ Italy” OR “ Malta” OR “ Slovenia” OR “ Croatia” OR “ Bosnia-Herzegovina” OR “ Montenegro” OR “ Albania” OR “ Greece” OR “ Turkey” OR “ Cyprus” OR “ Syria” OR “ Lebanon” OR “ Israel” OR “ Palestine” OR “ Libya” OR “ Egypt” OR “ Tunisia” OR “ Algeria” OR “ Morocco”) AND (“seagrass” OR “ sea grass” OR “ eelgrass” OR “ *Posidonia oceanica*” OR “ *Cymodocea nodosa*” OR “ *Zostera marina*” OR “ *Zostera noltii*” OR “*Zostera noltei*“ OR “ phanerogam” OR “ cymodoceaceae” OR “ posidoniaceae” OR “ zosteraceae”) AND (“fish” OR “ fishes” OR “ ichthyofauna” OR “ nekton” OR “ teleostei” OR “chondrichthyes”) AND (“associated” OR “ community” OR “ assemblage” OR “ assemblages” OR “ association” OR “ communities” OR “ adult” OR “ adults” OR “ larva” OR “ larvae” OR “ egg” OR “ eggs” OR “ larval” OR “ juvenile” OR “ juveniles” OR “ nursery” OR “ visual census” OR “ sampling” OR “ capture”)
Mendeley	All Fields	None	None	“Mediterranean” AND “seagrass” AND “fish” AND “assemblage”
ScienceDirect	All Fields	500 characters	max 8 per field	“Mediterranean” AND (“seagrass” OR “sea grass” OR “phanerogam”) AND (“fish” OR “ichthyofauna”) AND (“assemblage” OR “juvenile” OR “sampling”)
Scopus	All Fields	None	None	(“Mediterranean sea” OR “Mediterranean” OR “Alboran” OR “Balearic” OR “ Ligurian” OR “Tyrrhenian” OR “Adriatic” OR “Ionian” OR Aegean” OR “Levantine” OR “ Spain” OR “France” OR “Monaco” OR “Italy” OR “Malta” OR “ Slovenia” OR “Croatia” OR “Bosnia-Herzegovina” OR “ Montenegro” OR “Albania “ OR “Greece” OR “Turkey” OR “Cyprus” OR “Syria” OR “Lebanon” OR “Israel” OR “Palestine” OR “Libya” OR “Egypt” OR “ Tunisia” OR “Algeria” OR “Morocco”) AND (“seagrass” OR “sea grass” OR “eelgrass” OR “*Posidonia oceanica*” OR “*Cymodocea nodosa*” OR “*Zostera marina*” OR “*Zostera noltii*” OR “*Zostera noltei*” OR “phanerogam” OR “cymodoceaceae” OR “posidoniaceae” OR “zosteraceae”) AND (“fish” OR “fishes” OR “ichthyofauna” OR “nekton” OR “teleostei” OR “chondrichthyes”) AND (“associated” OR “community” OR “assemblage” OR “assemblages” OR “association” OR “communities” OR “adult” OR “adults” OR “larva” OR “larvae” OR “egg” OR “eggs” OR “larval” OR “juvenile” OR “juveniles” OR “nursery” OR “visual census” OR “sampling” OR “capture”)
WebOfScience	All Fields	50 terms for “All Fields”	None	(“Mediterranean” OR “Alboran” OR “Balearic” OR “Ligurian” OR “Tyrrhenian” OR “Adriatic” OR “Ionian” OR “Aegean” OR “Levantine”) AND (“seagrass” OR “sea grass” OR “eelgrass” OR “*Posidonia oceanica*” OR “*Cymodocea nodosa*” OR “*Zostera marina*” OR “*Zostera noltii*” OR “*Zostera noltei*” OR “phanerogam” OR “cymodoceaceae” OR “posidoniaceae” OR “zosteraceae”) AND (“fish” OR “fishes” OR “ichthyofauna” OR

				“nekton” OR “teleostei” OR “chondrichthyes”) AND (“associated” OR “community” OR “assemblage” OR “assemblages” OR “association” OR communities” OR “visual census” OR “nursery” OR “sampling” OR “capture”)
Wiley Online Library	All fields	None	None	(“Mediterranean sea” OR “Mediterranean” OR “Alboran” OR “Balearic” OR “ Ligurian” OR “Tyrrhenian” OR “Adriatic” OR “Ionian” OR Aegean” OR “Levantine” OR “ Spain” OR “France” OR “Monaco” OR “Italy” OR “Malta” OR “ Slovenia” OR “Croatia” OR “Bosnia-Herzegovina” OR “ Montenegro” OR “Albania “ OR “Greece” OR “Turkey” OR “Cyprus” OR “Syria” OR “Lebanon” OR “Israel” OR “Palestine” OR “Libya” OR “Egypt” OR “ Tunisia” OR “Algeria” OR “Morocco”) AND (“seagrass” OR “sea grass” OR “eelgrass” OR “*Posidonia oceanica*” OR “*Cymodocea nodosa*” OR “*Zostera marina*” OR “*Zostera noltii*” OR “*Zostera noltei*” OR “phanerogam” OR “cymodoceaceae” OR “posidoniaceae” OR “zosteraceae”) AND (“fish” OR “fishes” OR “ichthyofauna” OR “nekton” OR “teleostei” OR “chondrichthyes”) AND (“associated” OR “community” OR “assemblage” OR “assemblages” OR “association” OR “communities” OR “adult” OR “adults” OR “larva” OR “larvae” OR “egg” OR “eggs” OR “larval” OR “juvenile” OR “juveniles” OR “nursery” OR “visual census” OR “sampling” OR “capture”)

Sub-step 1.2 - Removing duplicates and selecting key-terms

After collecting the search results, we removed from the paper list records having partial searchable information (i.e., literature without abstract) and duplicate papers, by using both Microsoft Excel and the function 'removes.duplicates' in the package *litsearchr* of R (Grames et al. 2019; R Core Team 2022).

We subsequently performed a new search for a higher, more specific and exhaustive number of key-terms (193) related to the four key-subjects (hereafter groups) of the research: Group S - Seagrass, 47 key-terms related to the seagrasses and habitat targets; "Group F - Fish, 52 key-terms related to fish biology; "Group A - Assemblage, 42 general key-terms related to either the sampling methods or fish assemblages; "Group G – Geographic locality, 53 key-terms related to the Mediterranean basin and geographic localities (Supplementary Table S2).

Supplementary Table S2 - Key-terms subdivided in the four subject groups.

Key-subjects	Key-terms
S - SEAGRASS	"Angiosperm"; " Bed"; " Bedform"; " Bedforms"; " Beds"; " Canopies"; " Canopy"; " Cover"; " Cymodocea"; " Cymodoceaceae"; " Eelgrass"; " Grass"; " Grasses"; " Intertidal"; " Leaves"; " Macrophyte"; " Marina"; " Matte"; " Meadow"; " Meadows"; " Monocots"; " Monocotyledons"; " MPAS"; " Nanozostera"; " Neptune"; " Nodosa"; " Noltei"; " Noltii"; " Oceanica"; " Phanerogam"; " Phanerogams"; " Plant"; " Plants"; " Posidonia"; " Posidoniaceae"; " Protected"; " Rhizome"; " Seagrass"; " Seagrasses"; " Substratum"; " Subtidal"; " Tapeweed"; " Tidal"; " Vegetated"; " Vegetation"; " Zostera"; " Zosteraceae"
F - FISH	"Adult"; " Adults"; " Assemblage"; " Assemblages"; " Benthic"; " Benthos"; " Breeding"; "Chondrichthyes"; " Communities"; " Community"; " Demersal"; " Egg"; " Eggs"; " Fauna"; " Feeding"; " Fish"; " Fishes"; " Grazer"; " Grazers"; " Ichthyofauna"; " Ichthyofaunal"; " Juvenile"; " Juveniles"; " Larva"; " Larvae"; " Larval"; " Lifespan"; " Necton"; " Nectonic"; " Nekton"; " Nektonic"; " Nurseries"; " Nursery"; " Pisces"; " Piscivore"; " Piscivorous"; " Piscivory"; " Recruit"; " Recruitment"; " Recruits"; " Settlement"; " Settler"; " Settlers"; " Spawn"; " Spawner" ; " Spawners"; " Spawning"; " Stock"; " Teleost"; " Teleostei"; " Teleosts"
A - ASSEMBLAGE	"Capture"; " Captures"; " Catch"; " Catches"; " Census"; " Censused"; " Censuses"; " Coast"; " Coastal"; " Count"; " Counts"; " Discarded"; " Discards"; " Fished"; " Fisheries"; " Fishery"; " Fishing"; " Littoral"; " Net"; " Nets"; " Occurrence"; " Occurrences"; " Recapture"; " Recaptured"; " Residence"; " Residency"; " Sample"; " Sampled"; " Samples"; " Sampling"; " Samplings"; " Seine"; " Seiners"; " Telemetry"; " Tracking"; " Transect"; " Transects"; " Trawl"; " Trawling"; " Trawls"; " Video"; " Visual"
G - GEOGRAPHY	"Adriatic"; " Aegean"; " Albania"; " Albanian"; " Alboran"; " Algeria"; " Algerian"; " Balearic"; " Bosnia"; " Bosnian"; " Croatia"; " Croatian"; " Cypriot"; " Cyprus"; " Egypt"; " Egyptian"; " France"; " French"; " Greece"; " Greek"; " Ionian"; " Israel"; " Israeli"; " Italian"; " Italy"; " Lebanese"; " Lebanon"; " Levantine"; " Libya"; " Libyan"; " Ligurian"; " Malta"; " Maltese"; " Mediterranean"; " Monacan"; " Monaco"; " Montenegrin"; " Montenegro"; " Moroccan"; " Morocco"; " Palestine"; " Palestinian"; " Slovenia"; " Slovenian"; " Spain"; " Spanish"; " Syria"; " Syrian"; " Tunisia"; " Tunisian"; " Turkey"; " Turkish"; " Tyrrhenian"

Step 2 – Scoring and filtering papers

Sub-step 2.1

In the second step, we detected the presence/absence of the key-terms above mentioned in Title, Abstract and Authors' keywords of each search result using the 'str_detect' function in the package stringr of R (Wickham 2019).

To quickly identify papers containing relevant information, we defined a "Relevance Score (RS) built by assigning a relative weight to each of the four key-subject groups. We assigned a maximum value of one (100%) to those papers dealing with (hence containing key-terms related to) all the four key-subject groups, and modulated the score attributed to each group according to the level of relevance for our research objective, as follows:

1) 1/3 of the score was assigned if the paper contained at least one key-term belonging to Group S- Seagrass, i.e., Group S = 0.333;
2) 1/3 of the score was assigned if the paper contained at least one key-term belonging to Group F- Fish, i.e., Group F = 0.333;
3) 2/9 of the score were assigned if the paper contained at least one key-term belonging to Group A - Assemblage, i.e., Group A = 0.222;
4) 1/9 of the score was assigned if the paper contained at least one key-term belonging to Group G - Geographic locality, i.e., Group G = 0.111.

The Relevance Score (RS) was therefore based on presence/absence of the key-terms and summed up the values attributed to all key-terms found in each paper, ranging from 0 to 1. Papers with a RS $\geq$ 0.667 contain either both key-terms from high relevant key-subject groups (i. e., groups S or F) or one of them in combination with both key-terms from the other groups (A, G). Based on this, papers were subdivided in "High Relevance Papers" (HRP, RS $\geq$ 0.667) and "Low Relevance Papers" (LRP, RS <0.667) (Supplementary Table S3).

Supplementary Table S3 - Relevance Score values obtained from the various possible combinations of key-terms *per* key-subject group found in the abstract and title of the papers. High Relevance Score combinations are evidenced in bold.

Group S	Group F	Group A	Group G	Relevance Score Values
0.333	**0.333**	**0.222**	**0.111**	**1**
0.333	**0.333**	**0.222**	**0**	**0.889**
0.333	**0.333**	**0**	**0.111**	**0.778**
0.333	**0.333**	**0**	**0**	**0.667**
0	**0.333**	**0.222**	**0.111**	**0.667**
0.333	**0**	**0.222**	**0.111**	**0.667**
0.333	0	0.222	0	0.556
0	0.333	0.222	0	0.556
0.333	0	0	0.111	0.444
0	0.333	0	0.111	0.444
0	0	0.222	0.111	0.333
0.333	0	0	0	0.333
0	0.333	0	0	0.333
0	0	0.222	0	0.222
0	0	0	0.111	0.111

Sub-step 2.2-– Filter #1

We performed a sequential filtering to keep only those papers containing available information to build up the final dataset. In this first filtering step, we analysed the overall number of key-terms belonging to each of the four key-subject groups (i.e., not only their presence/absence as in the previous step) to set a threshold value based on the representativeness of each of the four key-subject groups in each paper.

To this end, we counted for each paper the overall number of key-terms belonging to each key-subject group and summed them up in four combinations: i) SFAG = all four groups (i.e., all the key-terms retrieved); ii) SFG = the sum of the key-terms belonging to the subject groups related to fish, seagrass and the Mediterranean Sea; iii) SFA = the sum of the key-terms belonging to subjects groups related to fish, seagrass and assemblages; iv) SF = the sum of the key-terms belonging to subject groups related to fish and seagrass. This allowed associating four different values to each paper, one for every combination (*n*). For each *n* we then counted the corresponding number of HRPs and LRPs (as reported in Supplementary Table S4). This allowed us to: 1) calculate the difference among HRPs and LRPs for each *n* (ΔRP); 2) find the

highest ΔRP for each *n*, corresponding to the higher key-terms presence in HRPs with respect to LRP; 3) set the number of key-terms corresponding to the highest ΔRP for each *n* as a threshold (Supplementary Table S5); 4) filter out the papers having a number of key-terms lower than the threshold values for even a single combination.

Supplementary Table S4 - Filter 1. Summary of ΔRP values obtained for the combination of the four key--subject groups SFAG, SFG, SFA and SF. n: the total number of Key-terms retrieved; LRP and HRP: total number of papers containing n key-terms; ΔRP: difference between LRP and HRP papers for each n recorded. The maximum difference observed is evidenced in red bold characters.

SFAG				**SFG**				**SFA**				**SF**			
n	**LRP**	**HRP**	**ΔRP**	**n**	**LRP**	**HRP**	**ΔRP**	**n**	**LRP**	**HRP**	**ΔRP**	**n**	**LRP**	**HRP**	**ΔRP**
0	1737	0	-1737	0	4143	0	-4143	0	1935	0	-1935	0	5016	0	-5016
1	1845	0	-1845	1	3392	0	-3392	1	2090	0	-2090	1	3323	581	-2742
2	2132	174	-1958	2	2476	795	-1681	2	2248	325	-1923	2	2284	1250	-1034
3	1863	448	-1415	3	1720	1239	-481	3	1843	676	-1167	3	1545	1521	-24
4	1798	632	-1166	4	1441	1349	-92	4	1725	868	-857	4	1308	1442	134
5	1444	845	-599	5	999	1392	393	5	1379	1042	-337	5	918	1438	520
6	1290	981	-309	6	800	1285	485	6	1198	1137	-61	6	740	1289	549
7	1029	1007	-22	**7**	**583**	**1271**	**688**	7	971	1141	170	**7**	**543**	**1107**	**564**
8	915	1015	100	8	514	1161	647	8	856	1097	241	8	480	1041	561
9	715	1090	375	9	375	1024	649	9	684	1028	344	9	378	873	495
10	617	1036	419	10	332	927	595	10	583	1002	419	10	312	799	487
11	502	971	469	11	242	802	560	**11**	**472**	**967**	**495**	11	224	692	468
12	417	902	485	12	218	680	462	12	407	832	425	12	211	633	422
13	**306**	**862**	**556**	13	179	625	446	13	282	776	494	13	167	528	361
14	280	757	477	14	145	538	393	14	261	677	416	14	140	457	317
15	208	714	506	15	104	500	396	15	201	608	407	15	103	426	323
16	191	616	425	16	105	402	297	16	182	572	390	16	100	340	240
17	189	532	343	17	71	360	289	17	183	473	290	17	67	333	266
18	121	507	386	18	70	314	244	18	117	440	323	18	66	274	208
19	111	459	348	19	47	268	221	19	105	398	293	19	41	244	203
20	83	386	303	20	35	256	221	20	83	324	241	20	35	208	173
21	66	343	277	21	30	214	184	21	67	337	270	21	32	173	141
22	52	315	263	22	23	180	157	22	50	271	221	22	22	149	127
23	61	273	212	23	18	155	137	23	56	249	193	23	13	129	116
24	34	249	215	24	14	133	119	24	31	194	163	24	11	106	95
25	28	214	186	25	8	106	98	25	30	181	151	25	10	73	63
26	20	196	176	26	9	77	68	26	19	161	142	26	8	67	59

27	6	160	154	27	1	94	93	27	6	122	116	27	1	63	62
28	7	147	140	28	3	71	68	28	7	107	100	28	3	48	45
29	8	119	111	29	6	49	43	29	6	92	86	29	4	47	43
30	10	94	84	30	2	32	30	30	9	65	56	30	1	19	18
31	8	75	67	31	2	36	34	31	8	56	48	31	2	23	21
32	7	58	51	32	2	19	17	32	6	47	41	32	1	17	16
33	4	55	51	33	0	21	21	33	4	26	22	33	0	16	16
34	2	36	34	34	1	12	11	34	2	35	33	34	1	6	5
35	0	23	23	35	0	10	10	35	0	25	25	35	0	5	5
36	3	31	28	36	0	10	10	36	3	14	11	36	0	7	7
37	0	20	20	37	0	7	7	37	0	10	10	37	0	2	2
38	0	15	15	38	0	8	8	38	0	15	15	38	0	2	2
39	0	20	20	39	0	6	6	39	0	14	14	39	0	3	3
40	0	15	15	40	0	2	2	40	0	11	11	40	0	3	3
41	0	12	12	41	0	3	3	41	0	5	5	41	0	2	2
42	0	7	7	42	0	2	2	42	0	2	2	43	0	1	1
43	0	5	5	43	0	1	1	43	0	5	5	45	0	2	2
44	0	7	7	45	0	2	2	44	0	2	2	46	0	2	2
45	0	3	3	46	0	2	2	45	0	1	1				
46	0	3	3	51	0	1	1	46	0	2	2				
47	1	1	0					47	1	1	0				
49	0	4	4					48	0	2	2				
50	0	1	1					49	0	2	2				
51	0	2	2					50	0	1	1				
52	0	1	1					51	0	2	2				
55	0	2	2					54	0	1	1				
60	0	1	1												

According to the results rereported in Table S4, we retained the papers containing at least 13, 7, 11 and 7 key-terms (Supplementary Table S5).

Supplementary Table S5 - Key-terms combinations listed with the threshold values (n), the total number of LRPs and HRPs characterised by that n, and the corresponding ΔRP.

	n	LRP	HRP	ΔRP
ALL	13	306	862	556
FSG	7	583	1271	688
FSA	11	472	967	495
FS	7	543	1107	564

Sub-step 2.2 -– Filter 2

After their use in filter 1, we discarded LRPs papers as they contain scanty information for our research objective (i.e., RS < 0.667).

Sub-step 2.3 – Filter 3

A further filtering was implemented to exclude the papers that, although containing most of the 193 key-terms, may be empty of relevant information. To this end, we selected 35 "Negative Keywords" (NK) from LRPs, by means of a Document-Term Matrix (DTM). Formally, a DTM is a word frequency table where columns are words and rows are documents, with entries representing the frequency of retrieval of any specific word in each document. We used the function 'TermDocumentMatrix' from the *tm* package of R (Feinerer and Hornik 2023), and the total number of NK was obtained from the average number of Authors' keywords. We vectorized the Authors' keywords of each paper removing any punctuation and special character and converted the text to lower case using the package *tm* of R before DTM. The selected NK therefore identified keywords frequently present in research providing irrelevant information, because carried out outside the Mediterranean basin or not focusing on seagrass and/or fish communities although mentioning them, for instance for comparison purposes. (Supplementary List 1)

Supplementary List S1 - List of the 35 Negative Keywords NK. We used these keywords to filter out the papers that contain even just one of these words in their Most Frequent Keywords (see M&M): “America”; “Anthozoa”; “Aquaculture”; “Australia”; “Bioaccumulation”; “Botany”; “Brazil”; “Carbon”; “Chemical”; “Chemistry”; “China”; “Coral”; “Crustacea”; “Estuarine”; “Estuary”; “Eutrophication”; “Gene”; “Genetic”; “Isotope”; “Isotopes”; “Mercury”; “Metal”; “Metals”; “Mexico”; “Nitrogen”; “Photosynthesis”; “Physiological”; “Physiology”; “Pollutant”; “Pollutants”; “Pollution”; “Portugal”; “River”; “Sediment”; “Sediments”

We obtained the “Most Frequent Keywords” (MFK) of HRPs identifying the recurring and relevant keywords of each paper. To this end, in papers featuring the Authors’ keywords we retained them as MFK. In papers where keywords were absent, we extracted the 40 terms most frequently reported in the title and abstract of each paper using a value of frequency calculated again through a Document-Term Matrix (DTM) and obtaining the number of most frequent words equal to the average number of the MFK present in the papers featuring the Authors’ keywords.

We filtered the list of papers by removing: i) all papers containing one or more NK within their MFK; ii) all papers with a Key-Terms/MFK ratio lower than 0.2, i.e. all papers that contain a Key-Terms/MFK ratio lower than MFK/(n key-subject groups + 1) ratio ; iii) all papers that do not have any keyword related to Group S (seagrass) or F (fish) in their MFK.

Results

Fish records

In our dataset, after manual data extraction from the papers and data validation, a total of 248 fish species were detected within the 10 habitat combinations, belonging to 75 families. For each species, scientific name was checked in World Register of Marine Species (WoRMS, Ahyong et al. 2024) using the “match taxa” tool provided in the WoRMS website, last accessed on April 10, 2024.

Supplementary Table S6. - List of the 248 species recovered from literature subdivided by family, with their frequency of observation. Colour codes correspond to Fig. S1 (see below): white (rare), grey (intermediate), black (frequent). Lessepsian species are highlighted in red.

Family	Scientific Name	Frequency
Alosidae	*Alosa fallax*	
Alosidae	*Sardina pilchardus*	
Ammodytidae	*Gymnammodytes cicerelus*	
Anguillidae	*Anguilla anguilla*	
Apogonidae	*Apogon imberbis*	
Atherinidae	*Atherina boyeri*	
Atherinidae	*Atherina hepsetus*	
Atherinidae	*Atherina presbyter*	
Balistidae	*Balistes capriscus*	
Belonidae	*Belone belone*	
Blenniidae	*Aidablennius sphynx*	
Blenniidae	*Blennius ocellaris*	
Blenniidae	*Coryphoblennius galerita*	
Blenniidae	*Lipophrys trigloides*	
Blenniidae	*Microlipophrys canevae*	
Blenniidae	*Microlipophrys dalmatinus*	
Blenniidae	*Microlipophrys nigriceps*	
Blenniidae	*Parablennius gattorugine*	
Blenniidae	*Parablennius incognitus*	
Blenniidae	*Parablennius pilicornis*	
Blenniidae	*Parablennius rouxi*	
Blenniidae	*Parablennius sanguinolentus*	
Blenniidae	*Parablennius tentacularis*	
Blenniidae	*Parablennius zvonimiri*	
Blenniidae	*Salaria pavo*	
Blenniidae	*Scartella cristata*	
Bothidae	*Arnoglossus kessleri*	
Bothidae	*Arnoglossus laterna*	
Bothidae	*Arnoglossus rueppelii*	
Bothidae	*Arnoglossus thori*	
Bothidae	*Bothus podas*	
Callionymidae	*Callionymus filamentosus*	
Callionymidae	*Callionymus maculatus*	
Callionymidae	*Callionymus pusillus*	
Callionymidae	*Callionymus risso*	
Carangidae	*Caranx crysos*	

Carangidae	*Lichia amia*		
Carangidae	*Pseudocaranx dentex*		
Carangidae	*Seriola dumerili*		
Carangidae	*Trachinotus ovatus*		
Carangidae	*Trachurus mediterraneus*		
Carangidae	*Trachurus trachurus*		
Carapidae	*Carapus acus*		
Carcharhinidae	*Carcharhinus plumbeus*		
Cepolidae	*Cepola macrophthalma*		
Citharidae	*Citharus linguatula*		
Clinidae	*Clinitrachus argentatus*		
Clupeidae	*Sprattus sprattus*		
Congridae	*Ariosoma balearicum*		
Congridae	*Conger conger*		
Coryphaenidae	*Coryphaena hippurus*		
Cyprinodontidae	*Aphanius fasciatus*		
Cyprinodontidae	*Apricaphanius iberus*		
Dactylopteridae	*Dactylopterus volitans*		
Dasyatidae	*Dasyatis pastinaca*		
Dorosomatidae	*Sardinella aurita*		
Engraulidae	*Engraulis encrasicolus*		
Exocoetidae	*Cheilopogon heterurus*		
Fistulariidae	*Fistularia commersonii*		
Gadidae	*Merlangius merlangus*		
Gobiesocidae	*Apletodon dentatus*		
Gobiesocidae	*Apletodon incognitus*		
Gobiesocidae	*Diplecogaster bimaculata*		
Gobiesocidae	*Lepadogaster candolii*		
Gobiesocidae	*Lepadogaster lepadogaster*		
Gobiesocidae	*Opeatogenys gracilis*		
Gobiidae	*Aphia minuta*		
Gobiidae	*Buenia affinis*		
Gobiidae	*Deltentosteus collonianus*		
Gobiidae	*Deltentosteus quadrimaculatus*		
Gobiidae	*Gobius ater*		
Gobiidae	*Gobius auratus*		
Gobiidae	*Gobius bucchichi/incognitus*		
Gobiidae	*Gobius cobitis*		
Gobiidae	*Gobius couchi*		
Gobiidae	*Gobius cruentatus*		
Gobiidae	*Gobius fallax*		
Gobiidae	*Gobius geniporus*		
Gobiidae	*Gobius niger*		

Gobiidae	*Gobius paganellus*		
Gobiidae	*Gobius vittatus*		
Gobiidae	*Gobius xanthocephalus*		
Gobiidae	*Knipowitschia panizzae*		
Gobiidae	*Ninnigobius canestrinii*		
Gobiidae	*Odondebuenia balearica*		
Gobiidae	*Pomatoschistus bathi*		
Gobiidae	*Pomatoschistus marmoratus*		
Gobiidae	*Pomatoschistus minutus*		
Gobiidae	*Pomatoschistus quagga*		
Gobiidae	*Pseudaphya ferreri*		
Gobiidae	*Thorogobius ephippiatus*		
Gobiidae	*Thorogobius macrolepis*		
Gobiidae	*Zebrus zebrus*		
Gobiidae	*Zosterisessor ophiocephalus*		
Gonostomatidae	*Cyclothone braueri*		
Haemulidae	*Parapristipoma octolineatum*		
Haemulidae	*Pomadasys incisus*		
Hemiramphidae	*Hemiramphus far*		
Hemiramphidae	*Hyporhamphus picarti*		
Holocentridae	*Sargocentron rubrum*		
Labridae	*Centrolabrus melanocercus*		
Labridae	*Coris julis*		
Labridae	*Ctenolabrus rupestris*		
Labridae	*Labrus merula*		
Labridae	*Labrus mixtus*		
Labridae	*Labrus viridis*		
Labridae	*Pteragogus pelycus*		
Labridae	*Symphodus cinereus*		
Labridae	*Symphodus doderleini*		
Labridae	*Symphodus mediterraneus*		
Labridae	*Symphodus melops*		
Labridae	*Symphodus ocellatus*		
Labridae	*Symphodus roissali*		
Labridae	*Symphodus rostratus*		
Labridae	*Symphodus tinca*		
Labridae	*Thalassoma pavo*		
Labridae	*Xyrichtys novacula*		
Lophiidae	*Lophius piscatorius*		
Lotidae	*Gaidropsarus mediterraneus*		
Lotidae	*Gaidropsarus vulgaris*		
Merlucciidae	*Merluccius merluccius*		
Monacanthidae	*Stephanolepis diaspros*		

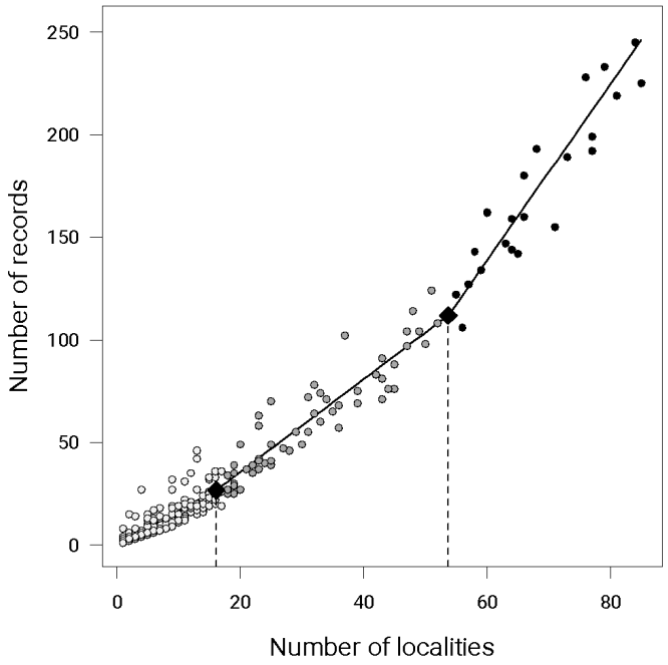
Moronidae	*Dicentrarchus labrax*		
Moronidae	*Dicentrarchus punctatus*		
Mugilidae	*Chelon auratus*		
Mugilidae	*Chelon labrosus*		
Mugilidae	*Chelon ramada*		
Mugilidae	*Chelon saliens*		
Mugilidae	*Mugil cephalus*		
Mugilidae	*Oedalechilus labeo*		
Mullidae	*Mullus barbatus*		
Mullidae	*Mullus surmuletus*		
Mullidae	*Upeneus moluccensis*		
Mullidae	*Upeneus pori*		
Muraenidae	*Muraena helena*		
Myctophidae	*Ceratoscopelus maderensis*		
Myctophidae	*Lampanyctus crocodilus*		
Myctophidae	*Lampanyctus pusillus*		
Myctophidae	*Myctophum punctatum*		
Myliobatidae	*Myliobatis aquila*		
Ophichthidae	*Echelus myrus*		
Ophichthidae	*Ophisurus serpens*		
Ophidiidae	*Ophidion barbatum*		
Ophidiidae	*Ophidion rochei*		
Ophidiidae	*Parophidion vassali*		
Paralepididae	*Lestidiops jayakari*		
Phycidae	*Phycis phycis*		
Pleuronectidae	*Platichthys flesus*		
Pomacentridae	*Chromis chromis*		
Pomatomidae	*Pomatomus saltatrix*		
Rajidae	*Raja asterias*		
Rajidae	*Raja clavata*		
Rajidae	*Raja radula*		
Scaridae	*Sparisoma cretense*		
Sciaenidae	*Sciaena umbra*		
Sciaenidae	*Umbrina cirrosa*		
Scomberesocidae	*Scomberesox saurus*		
Scombridae	*Auxis rochei*		
Scombridae	*Euthynnus alletteratus*		
Scombridae	*Sarda sarda*		
Scombridae	*Scomber colias*		
Scombridae	*Thunnus alalunga*		
Scombridae	*Thunnus thynnus*		
Scophthalmidae	*Scophthalmus maximus*		
Scophthalmidae	*Scophthalmus rhombus*		

Scorpaenidae	*Pterois miles*	
Scorpaenidae	*Scorpaena maderensis*	
Scorpaenidae	*Scorpaena notata*	
Scorpaenidae	*Scorpaena porcus*	
Scorpaenidae	*Scorpaena scrofa*	
Scyliorhinidae	*Scyliorhinus canicula*	
Scyliorhinidae	*Scyliorhinus stellaris*	
Serranidae	*Anthias anthias*	
Serranidae	*Epinephelus aeneus*	
Serranidae	*Epinephelus caninus*	
Serranidae	*Epinephelus costae*	
Serranidae	*Epinephelus marginatus*	
Serranidae	*Mycteroperca rubra*	
Serranidae	*Serranus atricauda*	
Serranidae	*Serranus cabrilla*	
Serranidae	*Serranus hepatus*	
Serranidae	*Serranus scriba*	
Siganidae	*Siganus luridus*	
Siganidae	*Siganus rivulatus*	
Soleidae	*Buglossidium luteum*	
Soleidae	*Microchirus ocellatus*	
Soleidae	*Microchirus variegatus*	
Soleidae	*Monochirus hispidus*	
Soleidae	*Pegusa impar*	
Soleidae	*Pegusa lascaris*	
Soleidae	*Solea senegalensis*	
Soleidae	*Solea solea*	
Soleidae	*Synapturichthys kleinii*	
Sparidae	*Boops boops*	
Sparidae	*Dentex dentex*	
Sparidae	*Dentex gibbosus*	
Sparidae	*Diplodus annularis*	
Sparidae	*Diplodus cervinus*	
Sparidae	*Diplodus puntazzo*	
Sparidae	*Diplodus sargus*	
Sparidae	*Diplodus vulgaris*	
Sparidae	*Lithognathus mormyrus*	
Sparidae	*Oblada melanurus*	
Sparidae	*Pagellus acarne*	
Sparidae	*Pagellus bogaraveo*	
Sparidae	*Pagellus erythrinus*	
Sparidae	*Pagrus pagrus*	
Sparidae	*Sarpa salpa*	

Sparidae	*Sparus aurata*		
Sparidae	*Spicara maena*		
Sparidae	*Spicara smaris*		
Sparidae	*Spondyliosoma cantharus*		
Sphyraenidae	*Sphyraena chrysotaenia*		
Sphyraenidae	*Sphyraena flavicauda*		
Sphyraenidae	*Sphyraena sphyraena*		
Sphyraenidae	*Sphyraena viridensis*		
Sternoptychidae	*Maurolicus muelleri*		
Syngnathidae	*Hippocampus guttulatus*		
Syngnathidae	*Hippocampus hippocampus*		
Syngnathidae	*Nerophis maculatus*		
Syngnathidae	*Nerophis ophidion*		
Syngnathidae	*Syngnathus abaster*		
Syngnathidae	*Syngnathus acus*		
Syngnathidae	*Syngnathus taenionotus*		
Syngnathidae	*Syngnathus tenuirostris*		
Syngnathidae	*Syngnathus typhle*		
Synodontidae	*Synodus saurus*		
Tetraodontidae	*Lagocephalus sceleratus*		
Tetraodontidae	*Lagocephalus suezensis*		
Torpedinidae	*Torpedo marmorata*		
Torpedinidae	*Torpedo torpedo*		
Trachinidae	*Echiichthys vipera*		
Trachinidae	*Trachinus araneus*		
Trachinidae	*Trachinus draco*		
Trachinidae	*Trachinus radiatus*		
Triakidae	*Mustelus mustelus*		
Triglidae	*Chelidonichthys cuculus*		
Triglidae	*Chelidonichthys lastoviza*		
Triglidae	*Chelidonichthys lucerna*		
Triglidae	*Chelidonichthys obscurus*		
Triglidae	*Eutrigla gurnardus*		
Triglidae	*Lepidotrigla cavillone*		
Triglidae	*Trigla lyra*		
Tripterygiidae	*Tripterygion delaisi*		
Tripterygiidae	*Tripterygion melanurus*		
Tripterygiidae	*Tripterygion tripteronotum*		
Uranoscopidae	*Uranoscopus scaber*		
Zeidae	*Zeus faber*		

Slope Analysis

The Akaike Information Criterion (AIC, Burnham and Anderson 1998) identified the piecewise regression as the best model in explaining the relationship between the number of records for each of the 248 fish species reported in literature and the number of localities where they were observed, $AIC_{piecewise}$ = 1743.752, AIC_{linear} = 1933.885 and ΔAIC = 190.133. The piecewise regression improved the adjusted R-squared (from 0.951 to 0.978), identifying two main breakpoints at ca. 17 and 55 on the x-axis, corresponding to a significant change in slope (Fig. S1). Computations were performed by using the *segmented* package of R (Muggeo 2008).



Supplementary Figure S2 - The curve slope analysis identifies two main breakpoints (black diamonds) corresponding to a significant change in the slope of regression and the consequent subdivision of species in three main groups: white circles are for rarely observed species, grey for species with intermediate frequencies and black for common species (see Supplementary Table S6).

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CHAPTER 2

THE FINGERPRINT OF FUNCTIONAL STRATEGIES IN MEDITERRANEAN SEAGRASS FISH ASSEMBLAGES

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Abstract

1. In the Mediterranean Sea, fish assemblages associated with seagrasses host a relevant percentage of the total fish biodiversity. While the structural complexity, coverage and distribution of seagrasses are known to influence species richness and abundance, their effect on the functional composition of faunal assemblages is still unclear. Moreover, little is known about the relationships of specific feeding, behavioural and reproductive strategies of fish with the potential use of such habitat during different life stages.

2. We characterized the functional structure of fish assemblages in three Mediterranean seagrasses, using specific functional traits known to be associated with the potential use of meadows (e.g., as nursery, refuge and/or foraging areas). We also hypothesized that given combinations of traits could be associated with the probability of species being observed on seagrasses in well-defined life stages, thereby linking different strategies to the use of habitat.

3. Mediterranean seagrasses host a core of functionally similar fish species characterized by r-like reproductive strategies and low-to-intermediate trophic levels, although differing in the range of traits exhibited by their associated predator fauna. Functional assemblages are non-random structured, independently of the seagrass, taxonomic composition and species diversity, suggesting a certain degree of complementarity in specific functions provided by seagrasses.

4. Our findings reinforce the view that the predominant use of different seagrasses by fish may be driven by a trade-off between different life-history and feeding strategies. As different functional strategies are largely involved in the structuring of food webs and species recruitment, their characterization in seagrass-associated fish assemblages would enhance our understanding of the impact of multiple threats on marine biodiversity.

Keywords: fish assemblages; functional traits; life-stages; Mediterranean Sea; seagrass meadows

1. Introduction

Seagrasses represent a key habitat in the marine environment and play a crucial role in maintaining marine biodiversity (Duffy, 2006). Indeed, seagrasses are habitat-forming species, facilitating the occurrence and persistence of other organisms by creating favourable conditions in terms of food supply and shelter from predation, ultimately influencing the distribution and abundances of species (Bertness & Callaway, 1994; Bulleri et al., 2018). This positive feedback is often associated with the ability of seagrasses to create complex structures and to form dense meadows with respect to bare substrates, although hosting less biodiversity than mangroves or coral reefs (Jones et al., 2021; Yeager & Hovel, 2017). Moreover, seagrasses play an important role in shaping fish coastal communities in terms of spatial connection among fundamental habitats such as mangroves, coral reefs and rocks, whose connectivity enhance fish diversity (Gilby et al., 2018; Goodridge Gaines et al., 2022; Unsworth et al., 2008).

Among the five native seagrasses of the Mediterranean Sea, *Posidonia oceanica* (L.) Delile, *Cymodocea nodosa* (Ucria) Ascherson and, to a lesser extent, *Zostera marina* are the most prevalent, differing in canopy complexity, distribution, and environmental tolerance (Ruiz et al., 2009). *P. oceanica*, the only endemic Mediterranean seagrass, forms dense, structurally complex meadows up to 40 m deep, spanning from the Alboran Sea to the Levantine Basin, although its range is declining due to anthropogenic impacts (Chefaoui et al., 2018; Ruiz et al., 2009). *C. nodosa* is widely distributed across the Mediterranean and adjacent Atlantic and tolerates broader environmental ranges and disturbances. This adaptability allows it to colonize degraded areas previously dominated by *P. oceanica* (Ruiz et al., 2009). In contrast, *Z. marina* has a restricted range, primarily in cooler northern regions such as the Adriatic and western Mediterranean, where it forms sparse meadows in sheltered, shallow waters (Ruiz et al., 2009).

Besides differences in their distributional range, seagrasses in the Mediterranean Sea also differ in peculiar characteristics able to determine their structural complexity and extension (e.g., canopy height, number of leaves per shoot, length and width of the leaves). For instance, *P. oceanica* forms dense, canopy-like meadows consisting of tall shoots (with leaves reaching up to 1 – 1.2 cm wide and 1.5 meters in length) and long-lasting matte due to its robust rhizome system. Conversely, *C. nodosa* creates looser, patchy beds, offering moderate habitat complexity, whilst *Z. marina* has only sparse shoots with thin leaves, providing basic habitat support in cooler or less stable zones (Ruiz et al., 2009). Although such characteristics have found to potentially determine the abundance and diversity of fish fauna (Lürig et al., 2016; McDevitt-Irwin et al., 2016), the extent to which the functional composition of fish assemblages differs between Mediterranean native seagrasses remains largely unexplored, with research

primarily focusing on comparisons between individual seagrass species and other substrates, such as bare areas or macroalgae-covered habitats (Biagi et al.; 1998; Bussotti & Guidetti; 2011; Franco et al.; 2006; La Mesa et al.; 2011).

A recent meta-analysis (Lattanzi et al., 2024) has shown how, in the Mediterranean Sea, seagrasses host about 38% of total fish species, with most of them (240 over 248) spotted on the endemic *P. oceanica* and 82 recorded as exclusive (i.e., never observed in other seagrasses). Interestingly, such exclusive species have been reported almost totally as adults, being in most cases large-sized, highly-mobile predators (Kalogirou et al., 2010; Lattanzi et al., 2024). Large and mobile predators as, for instance, the Atlantic horse mackerel (*Trachurus trachurus*), are indeed reported as occasional visitors on seagrass meadows, using this habitat exclusively for active prey foraging (Kalogirou et al., 2010). Another meta-analysis based on Mediterranean visual-census data has suggested that large predators such as the greater amberjack (*Seriola dumerili*) or the goldbloch grouper (*Epinephelus costae*) play a relevant role in shaping *P. oceanica* prey community, although being transient species not associated with the seagrass itself (Zubak et al., 2017).

How species perceive and use habitats may relate to peculiar adaptations linking species-specific attributes (e.g., morphology, ecological requirements, trophic ecology, behaviour) to the physical complexity of habitats, suggesting non-random species assembly along gradients of increasing/decreasing complexity (Ferreira et al., 2023; Sanabria-Fernández et al., 2024). Moreover, many marine organisms, in particular fish, often undergo changes in the diet, feeding modes, or social aggregation during the development, determining an ontogenetic shift in the use of habitats (Fobert et al., 2020; Polte et al., 2017). Therefore, it is possible that specific combinations of traits may influence the use of seagrass habitat by fish, with occasional visitors observed almost exclusively as adults having reproductive and/or feeding modalities different from resident species with a stronger tendency to use such habitats during their entire lifetime. How specific functional strategies, determined by peculiar combination of both life-history and feeding traits, may be related to fish use of habitats during their life cycle is a topic that has been recently object of attention by researchers (Koutsidi et al., 2020; Pecuchet et al., 2017). Indeed, community assembly mechanisms have been typically examined based on abundance data or taxonomic diversity, possibly hindering the relative importance of deterministic processes driving the convergence/divergence of traits among co-occurring species (Ford & Roberts, 2019; Kraft et al., 2015).

In this paper, we analysed the functional diversity of fish assemblages in the three main native Mediterranean seagrasses, with the aim of identifying traits that may discriminate their communities and exploring the potential relationships between differences in the structural

complexity of seagrasses and the functional traits of associated fish fauna. We also explored whether the probability of species being observed on seagrasses at different life stages is related to the presence of unique combinations of traits that determine specific life cycle and feeding strategies. To this end, we used an up-to-date and recently published database about the presence and the life stages at which fish species have been reported on the Mediterranean seagrasses, alongside specific functional traits known to be associated with habitat use by fish (Lattanzi et al., 2024). We discuss our results in light of the different mechanisms possibly associated with the structuring of fish communities, since either the importance of seagrass structural complexity in providing refuge and resources or the presence of predators in shaping fish communities have been alternatively proposed as main shaping forces (Heck & Orth, 1980; Schultz et al., 2009; Zubak et al., 2017).

2. Materials and methods

2.1 Data extraction and functional traits selection

We used a recently compiled database (Lattanzi et al., 2024) to retrieve all available information about the presence and the life stages at which fish species have been reported from the three main native seagrasses of the Mediterranean Sea, that is, meadows dominated by *P. oceanica*, *C. nodosa* and *Z. marina*. We checked for data consistency and excluded from the list those species for which we did not have at least two papers reporting the life stage. The most recent version of FishBase (Froese & Pauly, 2024), FishMed (Albouy et al., 2015) and a survey of current literature (last update 12/12/2024) were used to extract a set of specific functional traits related to the trophic ecology, size, growth and generation time (Table 1). Indeed, specific combinations of life history and feeding-related traits might determine how species use habitats according to the peculiar characteristics of the seagrass (e.g., structural complexity, ability to form extensive meadows, distributional ranges), as either refuge, nursery and/or foraging areas. Before analysis, we controlled for multicollinearity using the eigenvalues of the predictor correlation matrix to measure the condition number (κ), which quantifies the sensitivity of the predictors (Belsley et al., 1980; Montgomery et al., 2021). Values of $\kappa < 30$ indicate a negligible or absent collinearity, while values of $\kappa > 30$ and $\kappa > 100$ indicate a moderate to severe collinearity between the selected functional traits (see Supplementary Information for further details).

2.2 Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Ecological community	Mediterranean Sea	169 (fish) + 3 (seagrasses)

2.3 Functional traits imputation

To fill missing information in the functional traits of species, we performed a trait imputation procedure using random forest algorithms as in the function 'impute' from the *funspace* package of R (Carmona et al., 2024; R Core Team, 2024). Previous works have shown how traits imputation can handle missing data effectively and can successfully quantify large-scale functional diversity even with high data missingness (Johnson et al., 2021; Stewart et al., 2023).

Although its efficacy on categorical traits still remains controversial (Akande et al., 2017; Kim et al., 2018), the use of phylogenetic information (when available) may improve the performance of trait imputation, especially when traits have high levels of correlation and are conserved in the phylogenetic tree (Johnson et al., 2021; Pigot et al., 2020; Stewart et al., 2023). Moreover, the strong relationship between form and function in fish (e.g., body shape and size often relate with the feeding behaviour and/or reproductive strategies) allows phylogenetically informed imputation methods to be particularly reliable for this group (Thorson et al., 2023).

Before analyses, we subdivided the dataset based on the main two classes of Actinopterygii (ray-finned fish, downloaded from https://fishtreeoflife.org) and Chondrichthyes (cartilaginous fish, Villalobos-Segura et al., 2022), for which complete phylogenetic information is available only separately. Then, we filled missing information by means of a phylogenetic trait imputation procedure on the two separate datasets, by adding the corresponding phylogenetic trees and finally merged the datasets. Quantitative traits were log-transformed, centred and scaled before imputation procedure. Following Penone et al. (2014) and Carmona et al. (2021), we added ten phylogenetic eigenvectors to the trait matrix, while species not included in the phylogeny were added to the root of their genus using the 'addingSpecies' argument of the above-mentioned 'impute' function.

Since a rigorous data checking for biases before and after imputation is necessary to minimize errors (Johnson et al., 2021), we controlled for the number of missing information in both each trait and combinations of traits by using the function 'aggr' in the package *VIM* of R (Kowarik & Templ, 2016). We further checked whether data were completely missing at random (MCAR), at random (MAR), and not at random (MNAR), as they might affect the reliability of imputation, especially in presence of MNAR-type data (Nakagawa & Freckleton, 2008). To this end, we used the Little's test, a multivariate test based on maximum likelihood estimates to compare the observed variable means for each pattern of missing data with the expected population means (Little, 1988). A statistically significant result provides evidence against MCAR, suggesting that data might not be missing at random (MNAR). The Little's test was computed using the function 'na.test' in the *misty* package of R (Yanagida, 2024). Post imputation diagnostic was evaluated using the function 'post_imp_diag' implemented in the package *missCompare* of R (Varga & Westergaard, 2024), a missing data imputation pipeline which gives an informative assessment of the congruence between original (with missing data) and imputed dataset via bootstrapping. See Supplementary Information for further details.

2.4 Functional structure

The multivariate space given by a set of traits determines the community functional space, and how densely species occupy different parts of this space defines the functional structure of a given community (Carmona et al., 2016). From a mathematical point of view, the functional structure can be measured with a traits' probability density function (TPD) using a kernel density estimation with unconstrained bandwidth, starting from raw traits data or any given combination following a multivariate ordination (Carmona et al., 2019; 2021). According to Carmona and co-authors (2016), the functional space analysis provides useful information on both functional richness (FRic, the amount of functional space occupied by species) and divergence (FDiv, how much the species distribution is closed to the extremes of the functional volume), as well as on the identification of areas of particularly dense species occupation in the traits' space (i.e., functional hotspots, *sensu* Díaz et al., 2016 and Carmona et al., 2021). Given the mixed nature of traits used in this work (Table 1), we used a Factor Analysis of Mixed Data (function 'FAMD' in the package *FactoMineR* of R, Lê et al., 2008), an ordination technique that uses a principal components analysis (PCA) for quantitative variables and a multiple correspondence analysis (MCA) for qualitative variables (transformed into a disjunctive data table). The first two axes of ordination were used to measure the TPD (function 'funspace' in the package *funspace* of R) of fish assemblages in *P. oceanica*, *C. nodosa* and *Z. marina*.

We also tested whether the fish functional spaces measured in different seagrasses significantly deviated from randomness by comparing the amount of functional space occupied by the species against 100 null TPDs following a uniform distribution, where all combinations of traits within the range of observed functional trait space axes were equally possible (function 'funspaceNull' in the package *funspace* of R). The observed and null trait space were compared by means of a two-tailed *t*-test using standardized effect sizes (SES, the difference between the observed value and the mean of the simulated values after standardization by their standard deviations, Diaz et al., 2016).

2.5 Fish traits combination and life stages in *P. oceanica*

We explored the hypothesis that the presence of species on seagrasses in well-defined life stages might reflect the differential use of the habitat, likely due to species-specific combinations of traits. Specifically, we hypothesized that those species commonly reported exclusively as juveniles will be more likely to use seagrass as nursery and/or refuge areas. Conversely, species reported exclusively as adults should represent occasional visitors, whose presence would be mainly linked to the use of seagrass as foraging area. Those species reported both as juveniles and adults will use the seagrass as both nursery, refuge and foraging areas,

being classified as true seagrass residents. Unfortunately, information on the fish life stages is very scarce in the literature for *C. nodosa* and *Z. marina* (even if considering mixed meadows), so preventing to test this hypothesis for these seagrasses. We instead focused this analysis on *P. oceanica*, for which a large amount of data is available.

For each species, we assigned values on a 0 - 1 scale based on the probability that a species was observed exclusively as a juvenile. Therefore, species reported as adults-only were assigned 0 (no probability), while to juvenile-only species we assigned 1 (highest probability). For those species reported both as juvenile and adult, we assigned a middle probability value (0.5). We used generalized additive models (GAMs) with a beta regression distribution (useful for modelling continuous and constrained responses within the interval 0 - 1 as, for instance, proportions, probabilities, or percentages, Douma & Weedon, 2019) to regress this measure against the bidimensional functional space provided by TPD using the function 'funspaceGAM' in the *funspace* package of R.

3. Results

3.1 Fish functional structure comparison among seagrass habitats

From the total pool of 248 species already reported on seagrasses at Mediterranean Sea scale (Lattanzi et al., 2024), the data filtering for known life stages provided a total of 169, 123 and 36 species reported on *P. oceanica*, *C. nodosa* and *Z. marina*, respectively. Fish assemblages had a nested structure with respect to seagrasses, with species associated with *Z. marina* representing a subset of those observed in *C. nodosa* and these latter being a subgroup of the numerous species found in *P. oceanica*. For all seagrasses, the fish functional space captured more than 60% of total variation, with the first axis of ordination positively associated mainly with the maximum length and generation time (ML and Gt in Fig. 1 and Table 2). To enhance the clarity and accessibility of the results, we developed an interactive figure as a web application using Shiny (Chang et al., 2024). The application is accessible via the following link https://brunobellisario.shinyapps.io/Fish4Fun/.

In *P. oceanica*, the trophic level (TL) was strongly correlated with ML ($R^2 = 0.485$, $p < 0.001$), being also an important trait determining the ordination of species along the first dimension of the FAMD (Fig. 1A and Table 2). Conversely, TL was only weakly, although significantly, correlated with ML and Gt in *C. nodosa* ($R^2 < 0.3$, $p < 0.05$ in both cases), while showing no significant correlation in *Z. marina* ($R^2 < 0.2$, $p > 0.09$ in both cases). However, the trophic level TL contributed equally to the distribution of species along both axes of ordination in *C.*

nodosa and almost equally in *Z. marina* (Fig. 1B and 1C and Table 2). Both the growth coefficient k and feeding behaviour contributed to the ordination of species along the first two axes, with the only exception of *C. nodosa*, where the feeding strategy was the main trait determining the distribution of species along the second axis (Fig. 1B and Table 2). Independently of the seagrass considered, the distribution of species within the measured functional spaces was uneven, with large species at the top of the food web and with feeding habits based on waiting and/or chasing prey always placed at the periphery of the functional space (Fig. 1). However, there were substantial differences among the seagrasses. Indeed, while in *P. oceanica* and *Z. marina* we observed a continuum in the functional space (with the only exception of three active predators in *P. oceanica*, Fig. 1A), in *C. nodosa* small-sized ambush predators represented a well-defined and separated cluster of species (Fig. 1B).

In all seagrasses, the functional hotspot (i.e., the smallest portion of functional space including 50% of the species, Diaz et al. 2016) consistently had a small extent if compared to the total area of the functional space, ranging from ca. 9% in both *P. oceanica* and *C. nodosa* to ca. 12% in *Z. marina* and included almost exclusively omnivore species, grazing on substrates mainly represented by seagrass leaves (Fig. 1). Overall, the position of large predators, far from the hotspots and peripheral in the functional spaces, indicated a low probability of occurrence of their trait's combinations, while their scattered distribution suggested low or no functional redundancy. The peripheral position of the functional hotspot in *P. oceanica* and *C. nodosa* (close to the boundaries of occupied space) indicated high values of functional divergence in these assemblages (FDiv = 0.65 and FDiv = 0.71, respectively), while in *Z. marina* the central position of the hotspot within the functional space suggested low functional divergence (FDiv = 0.482). The functional richness (i.e., the total amount of functional space occupied by the species) also differed between seagrasses and was higher in *Z. marina* and *P. oceanica* (FRich = 47.772 and 41.137, respectively) than in *C. nodosa* (FRich = 32.901).

Under the null scenario of a uniform distribution of traits among species (i.e., all trait combinations were equally possible for all species), the amount of functional space occupied was significantly smaller than the null expectation in all seagrasses, in line with the lumped distribution of species and the high functional divergence measured. This was more pronounced in both *P. oceanica* and *C. nodosa* (*SES* = - 20.47 and $p < 0.01$ in both cases). In *Z. marina* the distribution of the functional space suggested a greater uniformity in the species' traits, as indicated by the lowest, albeit significant, difference in the observed *vs*. null functional richness (*SES* = - 3.72 and $p < 0.01$).

3.2 Functional strategies and association with seagrasses

GAM models showed a significant association between the probability of species to be observed at a given life stage on *P. oceanica* meadows and specific combination of traits, as provided by the functional trait space (χ^2 = 34.29, $p < 0.001$). Species at the periphery of the functional space, that are those with extreme combinations of traits in terms of size and trophic level, had the highest probability to be observed exclusively as adults. Examples are large active and/or ambush predators as the common dolphinfish (*Coryphaena hippurus*) or the marbled electric ray (*Torpedo marmorata*) that have been reported in the literature as occasional visitors on *P. oceanica* (Kalogirou et al., 2010). Conversely, very small-sized species with fast reproductive strategies and non-active predation modes had a high probability to be observed as juveniles only (Fig. 2). Intermediate combinations of traits as, for instance, medium-sized fish with low-to-intermediate trophic level and/or relatively high k and Gt are associated with the presence of both adults and juveniles (Fig. 2). Examples are the salema porgy (*Sarpa salpa*), the main consumer of *P. oceanica* in the Mediterranean Sea, or the spinefoots (*Siganus luridus* and *S. rivulatus*) that, despite being Lessepsian migrants, over the decades have established stable populations of *P. oceanica* residents in the eastern Mediterranean (Kalogirou et al., 2012).

4. Discussion

The taxonomic richness of fish assemblages differs in Mediterranean autochthonous seagrasses, as shown by a recent review (Lattanzi et al., 2024). In this work, we show how the three main native Mediterranean seagrasses host an array of functionally similar species, regardless of species richness. Fish assemblages in different seagrasses were characterized by non-random traits assembly, with small-to-medium fish mainly grazing on substrates representing the core of functionality in seagrass habitats. Conversely, large active (top) predators characterized by slow growth rates and high generation time were always found far from the core and at the periphery of the functional space, suggesting that such functional strategies are quite uncommon. Our results also indicate that peculiar combinations of both life-history and feeding strategies are related to the life stage at which species use the seagrasses, suggesting that functional traits may shape the ontogenetic habitat use of seagrass by fish.

4.1 Functional space comparison

Seagrasses are known to host a remarkable number of fish species in all the seas where they live and many studies have shown the importance of their structural complexity and coverage in structuring fish assemblages, evidencing that different seagrasses may provide different habitat features for associated species (Jones et al., 2021; Unsworth et al., 2022). Higher canopy height, greater number of leaves per shoot and shoot density increase the structural complexity of some seagrasses, allowing for a greater range of microhabitats and faunal assemblages with greater abundance and richness (Jones et al., 2021). For instance, along the south-eastern coasts of Australia *Posidonia sinuosa* meadows form uniform and dense canopies inhabited by more fish species, with greater density and biomass with respect to the less structured meadows of either *Amphibolis griffithii* or *P. coriacea* (Hyndes et al., 2018).

In the Mediterranean Sea, the same pattern is observed, with native seagrasses hosting a significant percentage of the total fish diversity and sharing a large number of species. However, the fish species richness differs in meadows dominated by different seagrasses, with *P. oceanica* meadows hosting a unique and diversified fish fauna if compared to *C. nodosa* and, even more markedly, to *Z. marina* (Lattanzi et al., 2024). This is in line with seagrasses features (e.g., the ability to create dense and complex meadows and their range extension), since the eelgrass *Z. marina* is a species well-adapted to colder temperatures and its distribution becomes sparse in the Mediterranean Sea, where it is mostly found as small, isolated stands and only occasionally occurring as dense beds (Ruíz et al., 2009). Conversely, *C. nodosa* is a warm tolerant species widely distributed throughout the Mediterranean Sea, where it forms large meadows sometimes in association with *P. oceanica*. This latter is the only endemic seagrass of the Mediterranean Sea where it forms dense and structurally complex meadows (Ruíz et al., 2009). These structural differences are due to both the larger size of *P. oceanica* and the more marked seasonal cycle of both *Z. marina* and *C. nodosa*, whose shot density decreases during the cold season making the canopy poor or even absent (Guidetti & Bussotti, 2000; Marbà et al., 1996).

Our findings evidence that, despite the difference in species richness and meadows structure, fish assemblages in the three main Mediterranean seagrasses show a common core of functional strategies. Fast growth rates, small sizes and low trophic levels are the trademarks of fish functional traits in all studied seagrasses, shared by those species included in or closed to the functional hostpots, whose small space extent witnesses a high redundancy for these combinations of traits (Carmona et al., 2019; 2021).

In *P. oceanica*, functional core species are predominantly grazers with diverse diets resulting in low to moderate trophic levels, mainly consuming detritus, algae, and small crustaceans. This aligns with studies showing that seagrass-associated fish exhibit varied feeding modes and diets

and are capable of exploiting both benthic and planktonic resources, although being often classified as carnivores (Stergiou & Karpouzi, 2002; Vizzini, 2009). For instance, benthic feeders like *Diplodus sargu*s and *D. annularis* also consume plankton, while typically planktivorous species like *Atherina presbyter* also feed on benthic invertebrates (Pinnegar & Polunin, 2000). Many core species overlap across the studied seagrasses, highlighting a consistent pattern and including some of the most abundant usually reported in the literature (e.g., sparids as *Boops boops* and seabreams, *Syngnathus* pipefishes, *Sparisoma cretense* and *Mullus surmuletus*, Guidetti & Bussotti, 2000; Máñez-Crespo et al., 2022). Ambush predators like *Scorpaena* and *Gobius* species (e.g., *Scorpaena porcus, Gobius cruentatus, G. buchicchi/incognitus and G. cobitis*) belong to fish families frequently signalled in seagrass worldwide (Espino et al., 2015; Pollard, 1984). These species are recorded at the periphery of the functional space in all the seagrasses, particularly in *C. nodosa* and *Z. marina*. In *Z. marina*, ambushers account for a small percentage of species records (Lattanzi et al., 2024), while in *C. nodosa* ambush predators are grouped into a distinct and well-separated cluster away from the functional hotspot. This suggests that, regardless of size and life history strategies, foraging modalities based on waiting and ambush represent uncommon strategies in both seagrasses. Interestingly, the most abundant species recorded on *C. nodosa* in both Mediterranean and Atlantic areas by a recent study do not include ambushers, despite the meadows in the Canary Islands benefiting from local climatic stability and high temperatures. This indicates that the probability of observing this combination of traits is more likely determined by seagrass characteristics than by environmental drivers (Máñez-Crespo et al., 2022). Life cycle and feeding traits associated with larger body sizes, higher trophic levels, and active predation modes occupy the periphery of functional spaces, with a scattered distribution and far from the hotspot. This pattern indicates an overall low level of redundancy of this traits combination and evidence that species bearing these traits have lower probabilities of being observed on seagrasses. Examples are pelagic predators like *Euthynnus alletteratus, Auxis rochei, Trachurus mediterraneus, Sphyraena sphyraena*, and *S. viridensis*, often reported in the literature on seagrass meadows (Guidetti & Bussotti, 2000; Kalogirou et al., 2010).

Functional richness and divergence are unrelated to taxonomic richness and vary across fish assemblages in the three seagrasses. Indeed, the lumped distribution of species within the functional hotspot in *P. oceanica* and the discontinuity observed in the functional space of *C. nodosa*, both indicate a higher functional divergence compared to fish assemblages in *Z. marina*. Interestingly, this latter shows the higher functional diversity although hosting about a quarter of the species reported in other seagrasses, suggesting a high degree of complementarity in the functional strategies of associated fish fauna. Fish assemblages from *P. oceanica* are

characterized by high values of both functional richness and divergence. Three species create a discontinuity in the functional space, without however influencing the global functional richness and divergence: the European conger (*Conger conger*), the garrick (*Cyclothone braueri*) and the common dolphinfish (*Coryphaena hippurus*). These species are all characterized by peculiar combinations of traits as, for instance, very large sizes, mesopelagic/pelagic distributional ranges or different habitat preferences, being therefore classified as occasional visitors (Correia et al., 2009; Granata et al., 2023; Moltó et al., 2020; Olivar et al., 2012).

Thanks to their structural complexity, seagrass habitats have often been proposed as a refuge for mobile demersal species, which find protection against predation by reducing prey visibility and impeding predator movement, suggesting a lower risk of predation mortality than surrounding open habitats (i.e., the so called 'seagrass superiority hypothesis', Heck & Orth, 1980). However, if this hypothesis successfully explains the high diversity and abundance of generalist species placed at intermediate to low trophic levels, it fails to account for the presence of large active predators that can increase mortality risks. The so-called 'predation mode hypothesis' considers this finding and suggests the predominant role of piscivorous predators in structuring fish communities in seagrass meadows (Kruschel & Schultz, 2020; Schultz et al., 2009; Zubak et al., 2017). Indeed, active predators may face challenges when foraging in dense seagrass meadows that can obstruct their movement and reduce visibility, while ambushers may prefer vegetated bottoms offering an optimal cover (Kruschel & Schultz, 2020; Schultz & Kruschel, 2010). Studies on Mediterranean fish assemblages are still poor, but experimental data from the Adriatic Sea have evidenced that aggressive small piscivorous and their fish preys tend to separate in shallow coastal habitats including *P. oceanica* and *C. nodosa* meadows, besides rocks and macroalgae, with preys preferring more homogeneous habitats and aggressive predators preferentially patrolling habitat edges (Kruschel & Schultz, 2020).

Our results are consistent with the proposition that seagrasses may virtually serve at the same time as a critical refuge for low-sized generalist species and as foraging habitat for a lower number of large piscivore predators that are occasional visitors. Active predation requiring stalking and attack is an established strategy in all seagrasses, while ambush predation is only poorly represented in the fish assemblage of *Z. marina*. According to the predation mode hypothesis this finding could be related to the different complexity of these habitats, with active predators less affected by the complexity of seagrass canopies due to their ability to patrol from neighbouring habitats and to attack specimens moving outside the meadow. Conversely, ambush predators are more closely related to the structural characteristics of seagrasses because they require adequate hiding places to attack their preys, which are more frequent in larger

seagrass forming more complex habitats as *P. oceanica* and *C. nodosa* and almost lacking in poorly complex meadows of *Z. marina* (Horinouchi et al., 2009; Laurel & Brown, 2006; Schultz et al., 2009).

4.2 Functional strategies and life stages in *P. oceanica*

The use of seagrass habitats by fish may vary depending on species' ontogeny, with some species present exclusively during a specific life stage (i.e., larvae, juveniles and/or adults) (Kalogirou et al., 2010). The distribution of highly mobile animals such as fish reflects the balance among conflicting demands associated with foraging and predation avoidance, often bringing animals to shift habitats because foraging needs, predation risks and optimal reproductive conditions may change during ontogeny as, for instance, due to increase in body size (Dahlgren & Eggleston, 2000; Fobert et al., 2020).

Here, generalized additive models reveal that peculiar combinations of traits are significantly related to the probability of observing specific life stages in fish inhabiting *P. oceanica* meadows. Functional traits associated with fast reproductive strategies (e.g., small sizes, high growth coefficient, low generation time and trophic level) and grazer-like feeding behaviours are observed in species that are found in *P. oceanica* as both juveniles and adults, therefore suggesting the use of this habitat during their entire life cycle both as refuge/nursery and foraging area. These traits match with those characterizing the species within the functional hotspot, indicating that the most common observed combinations of traits are also those allowing fish individuals to use the seagrass during all life stages, possibly increasing the shelter/nursery value of the habitat. Indeed, most of the species within the functional hotspot are characterized by an all-life-cycle use of the seagrass and are recognised as resident species strongly associated to this habitat: *Symphodus mediterraneus*, *S. ocellatus*, *Serranus cabrilla*, *Diplodus annularis*, *Spondiliosoma cantharus* and *Sarpa salpa* among others (Guidetti & Bussotti, 2000; Kalogirou et al., 2010).

On the other hand, large predators with slow reproductive strategies (i.e., high generation time and low growth coefficient) are rarely observed in seagrass habitats during their juveniles' stages, especially if characterized by an active predation mode, for which they may therefore represent mainly a foraging habitat. This finding confirms that large pelagic species recorded in this habitat are transient species, spending their juvenile stage in other habitats and occasionally transiting on *P. oceanica* meadows. The same is observed for large ambushers, suggesting that size plays a prominent role in determining which species may utilize the meadows during the adult stage. This finding agrees with a large studied carried out in eastern

Mediterranean, showing that half of the 88 species sampled on *P. oceanica* along a whole year were occasional visitors, including some of the species here evidenced as large predators recorded only in their adult stage (e.g., the above mentioned grater amberjack *S. dumerili*, the Mediterranean morray *M. helena or* the marbled electric ray *T. marmorata*) (Kalogirou et al., 2010). These results also indicate that in *P. oceanica*, and possibly in other seagrass systems, large predators do not operate an ontogenetic shift using seagrass as nursery and leaving the meadows once reached a given size, as recorded for example in tropical seagrass (Dorenbosh et al., 2005; Nakamura et al., 2012). Although limited to *P. oceanica*, the observed similarities in the functional spaces possibly indicate the same pattern for other seagrasses, suggesting a certain degree of convergence in the functional strategies determining the seagrass use by fish.

5. Conclusions

Using a functional approach spanning decades of literature data, we identified a common 'fingerprint' in the functional strategies of seagrasses-associated fish, which however differ in their ability to support higher trophic level species, namely large active and ambush predators that use this habitat almost exclusively as foraging grounds during their adult life stage. Our findings highlight that fish assemblages in seagrass habitats are primarily shaped by a trade-off between various life cycle and feeding strategies. These strategies influence how species use habitats at different life stages, which in turn affects food web structure and species recruitment—both of which are essential for maintaining marine biodiversity. Functional diversity of seagrass fish assemblages is an important aspect in marine biodiversity conservation since studies have shown how r-K selection strategies might have a role in determining the responses of species to disturbances, with r-selected species strongly affected by climate change but less impacted by fishing pressure, while the opposite is true for K-selected fish species (Graham et al., 2011; Lynam et al., 2017). Moreover, recent studies demonstrated how seagrass meadows in the Mediterranean Sea will experience a transition from long-lived, large and slow-growing species, such as *P. oceanica*, to small and fast-growing seagrasses as, for instance, the invasive *Halophila stipulacea*, as climate change progresses (Beca-Carretero et al., 2024). Overall, the identification of a 'functional fingerprint' in seagrass-associated fish assemblages would provide a useful baseline to understand how such transition will affect fish assemblages, improving our understanding on the effects of multiple threats on marine biodiversity.

Supplementary information

The fingerprint of functional strategies in Mediterranean seagrass fish assemblages

Functional traits imputation

Data inspection

Before analysis, we controlled for multicollinearity using the eigenvalues of the predictor correlation matrix to measure the condition number (κ), quantifying the sensitivity of the predictors. Values of $\kappa < 30$ indicate a negligible or absent collinearity, while values of $\kappa > 30$ and $\kappa > 100$ indicate a moderate to severe collinearity. Here we found a value of $\kappa = 8.505$, meaning that the selected functional traits are well-conditioned (i.e., minimal or no multicollinearity), and the linear dependencies among them are not likely to distort subsequent functional analyses.

The number of observations (i.e., species) with complete functional information were about 77%, with a total fraction of missingness of about 5%. Maximum length was the only functional traits for which we have complete observations for all species and, overall, quantitative variables had low percentages of missing data (trophic level, 0.59%; k and generation time, 1,18%). As expected, the only qualitative variable, that is, the feeding behaviour, had the highest percentage of missing data (ca. 22.5%). Overall, the Little's test was not significant ($n = 169$, $\chi^2 = 20.89$, $df = 13$ and $p = 0.075$), suggesting randomness in data deficiency and, therefore, excluding biases in no-data distribution between species and functional traits.

Post imputation diagnosis

Post imputation diagnosis showed an overall agreement between original and imputed values of traits (with the only exception of maximum length for which we had no missing data), as observed by the distribution of original and imputed values (Fig. S1) and the Kolmogorov-Smirnov test statistic D values, approaching zero for each imputation.

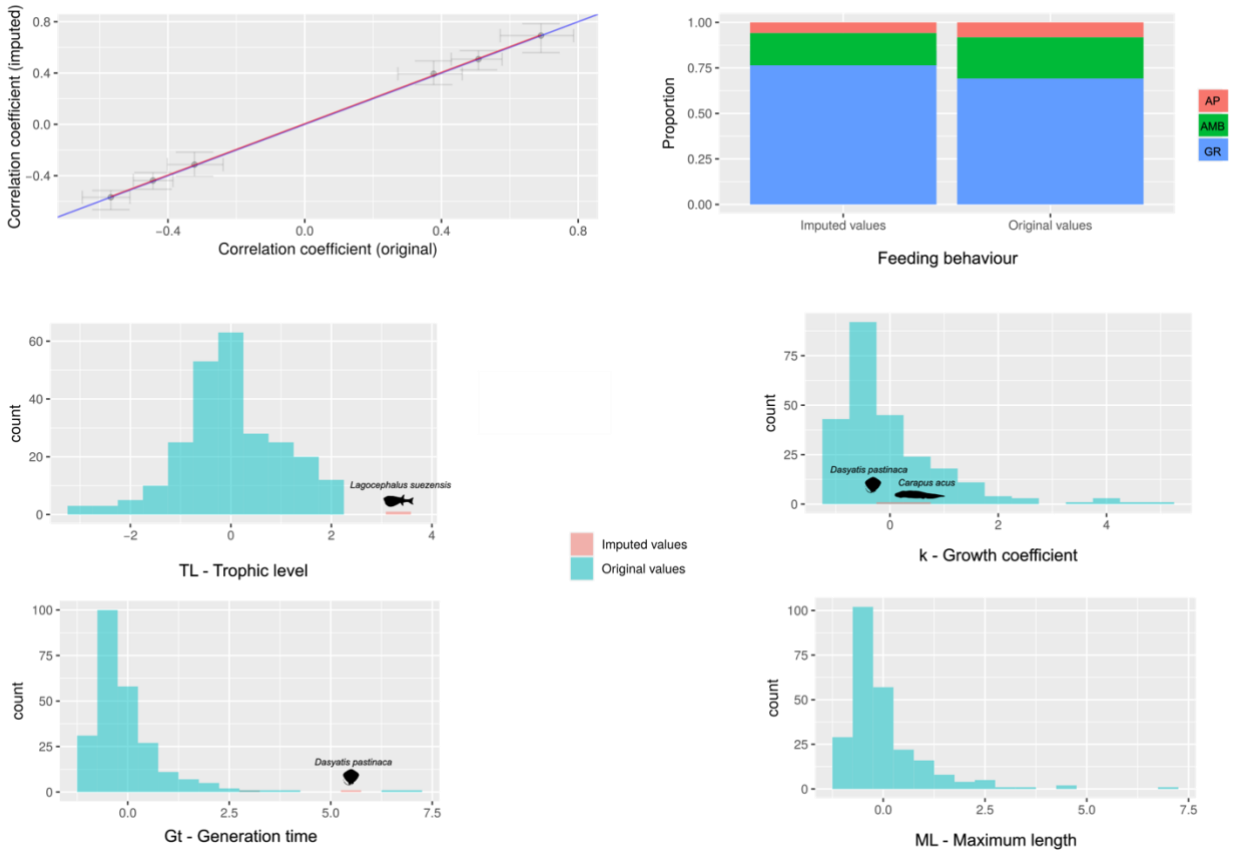

Figure S1 – The correlation plot (top-left panel) shows the bootstrapped correlation coefficients from original and imputed data after 1,000 iterations. For a good imputation procedure, bootstrapped correlation coefficients (dots with ± standard error and red line) should align as much as possible to the blue line representing a perfect correlation between data, with intercept 0 and slope 1. The top-right panel shows the goodness of imputation procedure for the qualitative variable feeding behaviour, expressed as the proportion of samples (species) falling within each category before and after imputation: AP, active predators; AMB, ambush predators and GR, grazers (see main text for more details). Other figures show the overlaid distributions of original and imputed values for quantitative variables. Silhouettes show the species (or group of species) for which the functional traits have been imputed. Note that data are scaled to a 0-1 mean and standard deviation, respectively.

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List of tables

Table 1 – List and definition of the functional traits used.

Trait	Acronym	Type	Definition
Feeding behaviour	AMB AP GR	Factor	The main feeding strategy of a species regardless of its trophic position. AMB - Ambush predators; AP - Active predators; GR - Grazers (feeding on substrates, both plants, animals and/or small crustaceans)
Maximum length	ML	Numeric	The size (in cm) of the longest individual recorded from a stock. A proxy for body size.
k	k	Numeric	The parameter of the von Bertalanffy growth function (also known as growth coefficient), expressing the rate (year $^{-1}$) at which the asymptotic length is approached. Faster growth rates are associated with higher k values.
Generation time	Gt	Numeric	The time period from birth to average age of reproduction.
Trophic level	TL	Numeric	The position of a given species in the food chain.

Table 2 – Contribution of the fish functional traits to the first two axes of the multivariate ordination in different seagrasses. Traits coded as in table 1.

	Posidonia oceanica		*Cymodocea nodosa*		*Zostera marina*	
	Dim 1	**Dim 2**	**Dim 1**	**Dim 2**	**Dim 1**	**Dim 2**
TL	0.694	0.263	0.645	0.455	0.376	0.724
ML	0.841	0.169	0.868	-0.215	0.901	-0.003
k	-0.648	0.567	-0.676	0.199	-0.686	0.494
Gt	0.839	-0.330	0.865	-0.050	0.887	-0.264
AMB	0.474	-1.027	0.477	3.150	-1.382	-2.636
AP	1.391	1.454	2.039	-0.346	2.050	0.944
GR	-0.608	-0.339	-0.646	-0.299	-0.463	-0.142
% of variance	43.205	19.064	46.498	19.093	43.477	19.430

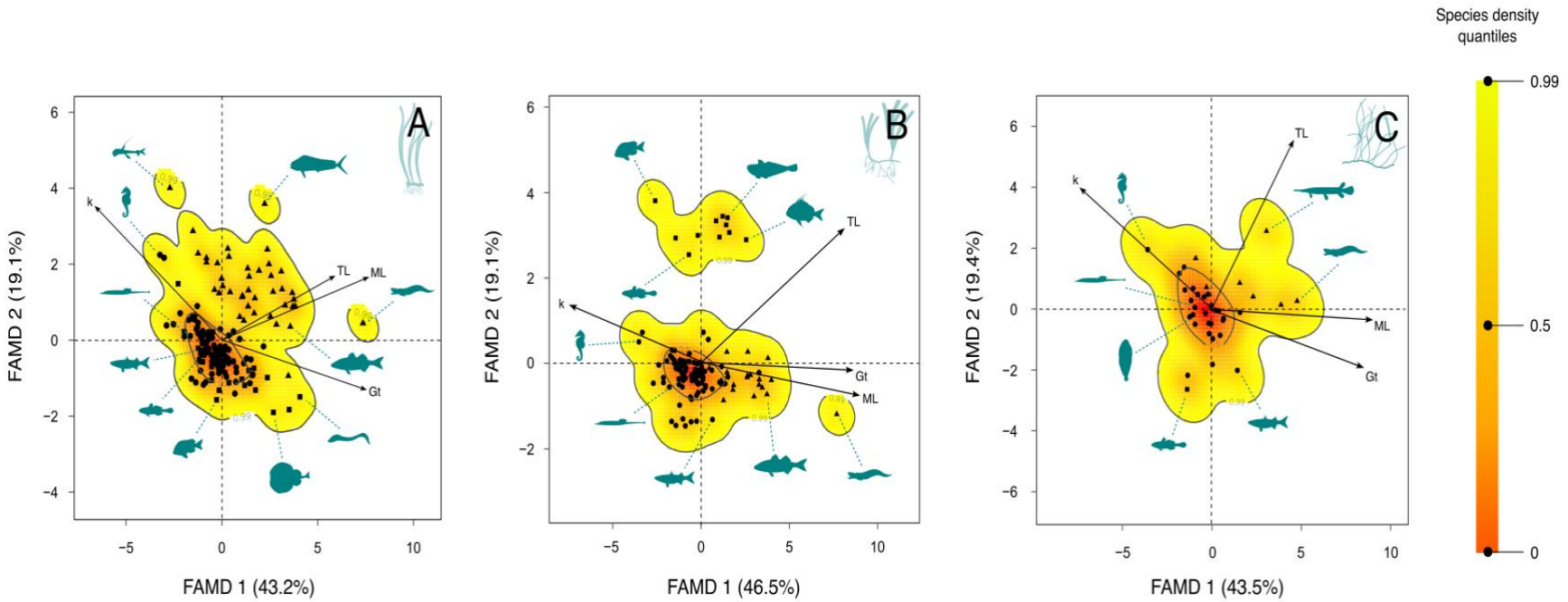

Figure 1 – Functional space of fish assemblages in *Posidonia oceanica* (A), *Cymodocea nodosa* (B) and *Zostera marina* (C), showing the probabilistic species distributions in the spaces defined by the first two dimension (FAMD 1 and FAMD 2) of the Factorial Analysis of Mixed Data (FAMD, see Materials and methods). Arrows indicate the direction and weighting of quantitative traits (TL = trophic level; ML = maximum length; Gt = generation length and k = growth coefficient) in FAMD (see Table 1). Symbols indicate the feeding behaviour of species (qualitative trait): circles = grazers; triangles = active predators; squares = ambush predators (see main text). The colour gradient indicates the density of species within the functional space (increasing density from light yellow to red), while thick contour lines indicate the 0.5 (i.e., functional hotspots, see main text) and 0.99 quantiles of distributions. Fish silhouettes were downloaded from PhyloPic (https://www.phylopic.org) under Creative Commons licenses. An interactive version of this figure can be viewed at https://brunobellisario.shinyapps.io/Fish4Fun/.

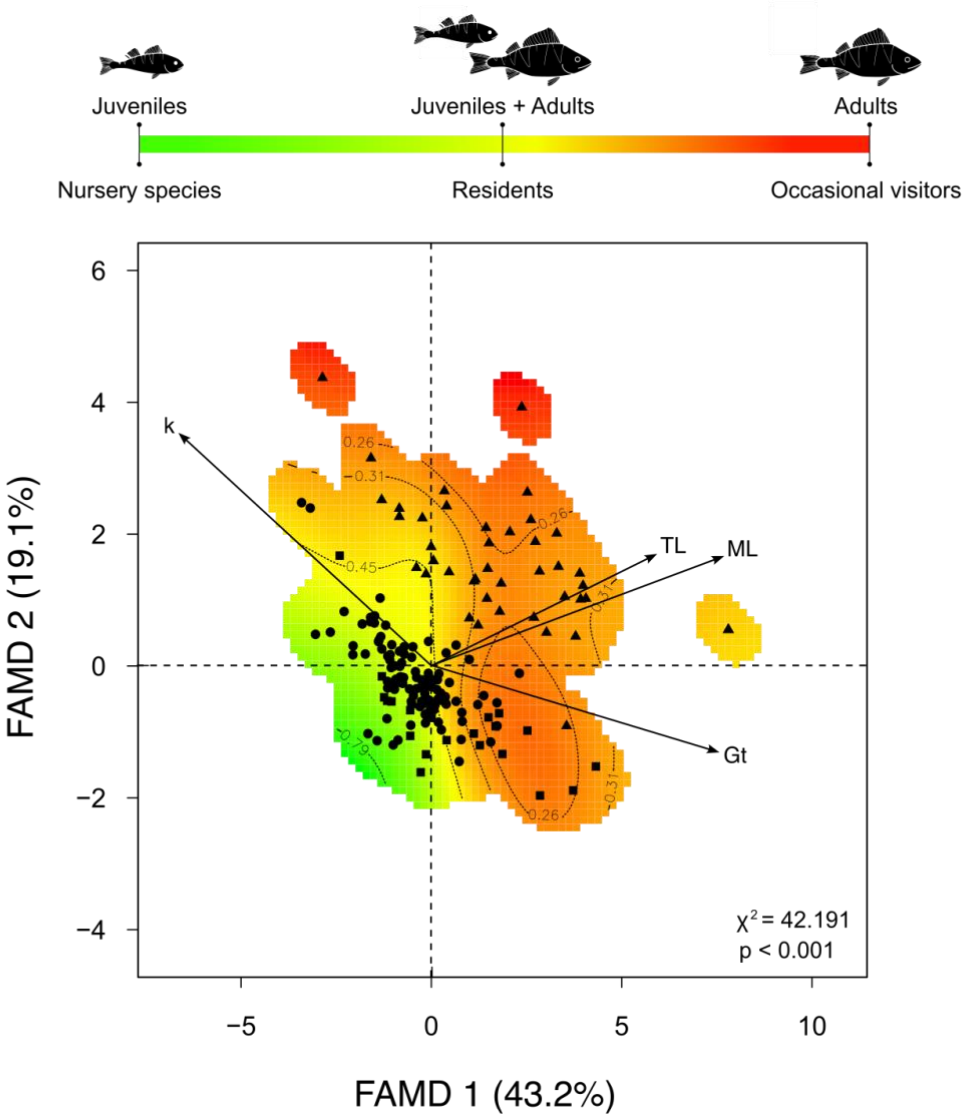

Figure 2 – Life stage distribution in the functional space of fish assemblage in *Posidonia oceanica*. The figure shows the probability of species to be found in the seagrass exclusively as juveniles and/or adults, using the position of species in the functional space as predictors according to a Generalized Additive Model (GAM) with a beta distribution (see Materials and Methods). Green tones indicate a higher probability of species to use the seagrass as juveniles (mostly nursery species), yellow as both juveniles and adults (resident species), while red tones indicate a higher probability to visit the seagrass exclusively as adults (occasional visitors). Contour lines indicate the probability values of the distribution. The legend shows χ^2 and p value of the GAM.

CHAPTER 3

LENGTH-BASED INDICATORS INCREASE AFTER TEN YEARS OF ENFORCED TRAWLING BAN IN TWO NATURA 2000 SITES FROM CENTRAL MEDITERRANEAN SEA

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Abstract

Scientific consensus supports the benefits of trawling bans for fish assemblages, particularly regarding species richness, fish size, and the overall health of food webs and seafloor habitats. Length-based indicators are commonly applied to track fish stock recovery, offering straightforward metrics for detecting shifts in population structure and providing early signs of rebuilding, even under data-limited conditions. In this study, we focused on two Mediterranean Natura 2000 sites (Special Areas of Conservation, SACs) over a ten-year period. Both areas, located along Italy's central Tyrrhenian coast, are partially protected, allowing only artisanal and recreational fishing, but the local trawling ban had been weakly enforced. In response, an Anti-trawling Artificial Reef (AAR) was installed in 2013 along the lower boundary of *Posidonia oceanica* meadows, physically restricting access to trawlers. Over the decade, three fishing campaigns were conducted to assess potential recovery of target fish species and to examine whether recovery rates differed by life-history strategy.

Our results show a significant increase in fish length over time, indicating improving stock conditions. Most species were categorized as either opportunistic or periodic, while the equilibrium strategy was less common. Length gains occurred in all functional groups, though equilibrium species exhibited a delayed response, with larger individuals appearing only in the final survey. In contrast, opportunistic and periodic species rebounded more quickly, consistent with their respective growth, reproductive, and survivorship trade-offs.

Overall, these findings suggest that the AAR approach can foster both biodiversity and small-scale fisheries recovery in the central Mediterranean, underscoring the value of combining spatial protection with effective physical barriers to deter destructive fishing practices.

Introduction

Bottom trawling has been widely recognized as one of the most impactful fishing methods on benthic ecosystems and demersal fish assemblages, causing both direct mortalities to target and non-target species and long-term alterations of benthic habitats (Collie et al, 1997; Bergman & van Santbrink, 2000; Collie et al, 2000; Steadman et al., 2021). Trawling bans or restrictions have been widely applied, aiming both at safeguarding local habitats and fish stocks and at supporting the sustainability of artisanal fisheries, due to the documented competition among these fishing activities (Whitmarsh et al., 2003; Lloret et al., 2018).

In the Mediterranean Sea artisanal coastal fisheries play a vital socio-economic role, so that fishery management tools are frequently addressed to both enhance biodiversity and safeguard small scale fishery income (Whitmarsh, 2003; Maynou et al., 2013). The enforcement of trawling bans has increasingly become a management measure through time, implementing spatial restriction strategies and generating a growing body of research on either the ecological or socio-economic effects of these prohibitions (Whitmarsh et al., 2003; Battaglia et al., 2010; Guidetti et al., 2010; Russo et al., 2019). Within the framework of Fishery Restricted Areas, both Marine Protected Areas (MPAs) and No Trawl Zones (NTZs) are widely adopted, although their scope and implementation can differ in many ways, leading to different ecological or socio-economic results (Fraschetti et al., 2018; Lloret et al., 2018; Ortega et al., 2023). NTZs focus specifically on prohibiting trawling gears while typically allowing other forms of fishing to reduce habitat destruction and facilitate the recovery of benthic and demersal communities (Pipitone et al., 2023). MPAs are designated to protect marine habitats and species through various levels and with broader objectives, encompassing habitat conservation, protection of vulnerable species, and ecosystem resilience, achieved through different management strategies including, among others, partial to complete fishing prohibitions (Boudouresque et al., 2020). A third tool for Fishery Restricted Areas is marine Natura 2000 sites. They are implemented only by European counties, since deriving from the European Union's Habitats Directive (92/43/CEE), which built up the global largest conservation network to meet the target of halting (or at least significantly reducing) biodiversity loss (Fraschetti et al., 2018). As MPAs, these sites have wider aims than specifically regulate fishing pressure but may include fishing ban or restriction to protect either marine species or habitats, a strategy frequently used for *Posidonia oceanica* meadows in the Mediterranean Sea (Guidetti et al., 2019).

Whatever the spatial strategy deployed, where compliance is low or illegal trawling persists, the positive impacts of protection can be greatly diminished, producing the so called "paper parks" (Roberts & Hawkins, 2000). For this reason, artificial reefs are frequently used in the

Mediterranean Sea to block illegal trawling, so enforcing protection and benefiting local communities that practice small scale fishing activity (Pipitone et al., 2014; Lima et al., 2019). The literature on the subject highlights the positive results of this strategy at both environmental and socio-economic level, but long-term studies are few, the bulk extending over only two years, evidencing a gap in our knowledge on the timing of the recovery (Lima et al., 2019).

There is an overall agreement on the benefits of trawling bans on fish assemblages in terms of species richness and fish size, besides food webs and sea floor health (Fraschetti et al., 2022). However, the effects can vary with local environmental conditions, enforcement efficacy, and socio-economic factors. Similarly, the timeline for ecological recovery can differ widely. Some studies note rapid improvements in fish assemblages within two to five years of a trawling ban, whereas others observe only gradual changes, especially when habitat-forming species (such as corals and seagrasses) have been extensively damaged (Steadman et al., 2012; Hiddink et al., 2017). This issue could be partly related to the metrics used to assess the recovery of the community after the ban, typically based on species richness and abundance and therefore changing at a quite slow pace (Babcock et al., 2010; Coleman et al., 2015). Conversely, functional trait-based metrics may respond more readily due to the direct link between species traits and environmental conditions, including human impacts. Therefore, functional-based approaches may be able to early signal a recovery otherwise remaining undetected if using species richness or biomass-based metrics alone (Mouillot et al., 2013; Aune et al., 2024). As data increase, evidence suggest that trait-based assessments are effective in assessing the efficacy of management actions in effectively rebuilding both the stocks and the ecological functions critical for long-term resilience, especially if they are complementing taxonomic and abundance approaches (Barnett et al., 2019; Costa et al., 2024).

This study stems from the implementation of a conservation project dedicated to two Mediterranean marine Natura 2000 sites (Special Areas of Conservation, SACs) and aimed at analyzing the state of fish assemblages across ten years. The two areas, located along the Italian coasts of the central Tyrrhenian Sea, are Partially Protected Areas, where only artisanal and recreational fishing is allowed but where the trawling ban was poorly enforced. For this reason, an artificial barrier was built in 2013, by positioning a series of submerged structures along the lower limit of the *Posidonia oceanica* meadows, closing the access to trawlers. Along the subsequent decade, three fishing campaigns were carried out in the aim of exploring if a recovery occurred for target fish species and if the recovery rates were linked to the functional features of the fish species.

2. Material and methods

2.1 Study site

This study involves two SACs (Special Conservation Areas) located along the Italian central Tyrrhenian coasts (Fig. 1). These areas are part of the European Natura 2000 network and are characterized by the presence of *Posidonia oceanica* meadows, a priority Habitat Type protected according to the European Union's Habitats Directive (92/43/CEE).

The SAC IT6000001(hereafter SAC1) has an extension of 1.761,9 ha and represents one of the most extensive meadows of *P. oceanica* in the central Tyrrhenian Sea. Its boundaries are marked by the mouths of the Chiarone River to the north and the Fiora River to the south. Mixed meadows of *P. oceanica* and *Cymodocea nodosa* are present between the coastline and the upper limit of the meadow, that is also characterized by the presence of sandy patches. The SAC IT6000002 (hereafter SAC2) has an extension of 1.761,9 ha, being characterized by an intricate bathymetry, creating a variety of microhabitats, and by a wide belt of matte along the lower bound of the meadow, at -30m of depth, witnessing a marked regression. In both areas are signaled protected species such as the critically endangered noble pen shell *Pinna nobilis* and the seahorse *Hippocampus hippocampus*.

In these areas recreational and small-scale artisanal fishery are allowed, while any other fishing activity is banned, including trawling. To fully enforce the trawling ban, in the aim to protect *P. oceanica* habitat, an anti-trawling artificial reef (AAR) has been deployed in 2013 within the frame of an EU LIFE project, by submerging 550 concrete structures along the lower limit of the meadows and so precluding trawlers from illegally entering these areas (Fig. 1). Since that moment the state of fish assemblages associated with seagrass meadows has been surveyed through experimental fishing activities involving local fishermen along with research personnel.

2.2 Experimental fishing plan and data collection

In the survey series three campaigns were carried out in 2014-15, 2019-20 and 2022-23 in both SACs, hereafter named Campaign 1, 2 and 3 (C1, C2, C3). The local artisanal fishery fleet is based in the channel harbor located at the Fiora River mouth and has been involved in sampling campaigns. The number of vessels, between 7.5 and 8 m in length, decreased through the years, passing from 8 in 2014 to 5 in 2023. A total of 5 vessels per campaign carried out the

experimental fishing activities, for a total of 32 hauls (5 hours each) per SAC per campaign, subdivided among the two SACs.

An articulated sampling plan was designed to provide an accurate representation of catches on an annual basis. The local artisanal fishing fleet employs a variety of fishing gears to maximize catches based on the species most abundant in different seasons, requiring a calibrated sampling in terms of both gear types and seasonality. Accordingly, the hauls have been taken all year long at a depth of 4–48 m, according to the seasonally used fishing gears, that are either trammel or gill nets with different mesh and structure (Table1). In particular, "incastellata" nets combine features of both trammel nets in the lower section and gillnets in the upper section, targeting species that inhabit different water column strata. "Barracuda" are specialized gillnets, tailored on the behavior and size of the target species that in this area are the shi drum (*Umbrina cirrosa*) and many sparids.

The sampling plan of the campaign 2019-2020 was affected by Covid restrictions so that 24 hauls were carried out instead of the 32 of the other two campaigns. However, to provide a representative and comparable sampling, the proportion of the hauls using the various fishing gears was kept steady in the three campaigns and across seasons (Table 1).

Since the final aim of the study was to explore the recovery patterns of different functional groups, we centered our data exclusively on target fish species, although the cuttlefish (*Sepia officinalis*) and crustaceans as lobsters and prawns (*Homarus gammarus, Palinurus elephas, Penaeus kerathurus*) were catch by the fleet. Landings were analyzed for bony and cartilaginous fish by identifying each specimen at the species level and recording the total length and the wet weight of each specimen (Table 2).

2.3 Statistical analysis

As the data did not follow a normal distribution (checked with the Shapiro-Wilk test), the non-parametric Kruskal–Wallis test and the Conover–Iman test for stochastic dominance (Conover & Iman, 1979; Conover, 1999; Kruskal & Wallis 1952) were employed to highlight statistically significant differences in fish body size among SACs and campaigns. Analyses were performed using the package 'conover.test' of R (Dinno & Dinno 2017; R Core Team, 2024). Non-taxonomic size metrics and length-based indicators (according to the European Marine Strategy Framework Directive) were calculated to describe the size structure of fish communities sampled in each SAC over the years: i) the size spectrum parameters, ii) the mean maximum length, MML and, iii) the large fish index, LFI.

2.3.1 Fish size spectra

The size spectrum analysis allows summarizing the distribution of body size classes in fish community using simple linear regressions (Kerr & Dickie 2001; Guiet et al. 2016). We performed the fish size spectra analysis (FSS) according to the methods of Arranz et al. (2021). Eleven size classes with their frequencies of occurrence were obtained by calculating the geometric series from the length-weight relationship. Since small specimens (<10 cm) caught due to the low selectivity of the fishing gears constituted a non-negligible percentage of the catch (approximately 3% of the total), they were included within the smallest size class prior to normalization (Arranz et al. 2021). Fish abundance per size class was then normalized by dividing by the size class width (Sprules & Barth, 2016).

We performed an ordinary-least-square linear regression (OLS model) between the midpoint of the size classes on the x axis and the normalized fish abundance on y axis as dependent variable at a $\log_2$-$\log_2$ scale, using Cook's Distance (Quinn & Keough, 2002). Outliers were identified and removed through the *ols_plot_cooksd_bar* function from the 'Olsrr' package of R (Hebbali A., 2024), according to the thresholds and methods proposed by Bollen & Jackman (1990) and Sprules & Barth (2016).

To avoid collinearity between spectra coefficients (Spearman rs = 0.94; $p < 0.001$), which may produce statistical artifacts of increasing intercept with decreasing slope, the y-intercept of the log-x regression was centered so that the obtained elevation reflected the "height" of the spectrum (Trenkel & Rochet, 2003; Daan et al., 2005; Sweeting et al., 2009; Guiet et al. 2016; Sprules & Barth, 2016). Both the slope and elevation were extracted from the linear regression equation.

2.3.2 Length based indicators

The mean maximum length indicator (MML) per species was calculated according to the ICES WGECO Report (2012) by assigning to each specimen an L_{max} based on its species and averaging this across all individuals in a campaign (Piet & Jennings, 2005). The large fish index (LFI) expressed the proportion of total fish biomass of a defined suite of species sampled in a particular campaign exceeding a specified threshold length (Greenstreet et al. 2010). Since the determination of a length threshold is prone to arbitrary choices, we calculated the LFI by applying a sixth-degree polynomial smoother to the LFI time-series derived using threshold body lengths of 20, 25, 30, 35 and 40 cm, and selected the threshold with the best fit (highest

r^2 value) as the "large fish" threshold length (Shephard et al., 2013; Modica et al., 2014). The measured threshold value was set at 35 cm.

2.4 Functional diversity of fish assemblages and archetypal analysis

To functionally characterize fish species, we selected 11 functional traits known to be involved in tolerance/sensitivity to overfishing and that can be grouped in three categories related to various life-history strategies in the 61 sampled species (Ladds et al., 2018; De Juan et al. 2020). (1) Life History traits influencing the potential recovery of populations: age max, trophic level, k (the growth coefficient, a parameter of the von Bertalanffy growth function), generation time (the time from birth to average age of reproduction), age at first maturity; (2) Catchability traits influencing the probability of individuals to be caught: maximum length, sociability; (3) Resilience traits, describing species' reproductive potential: fecundity, egg diameter, larval at hatching, size at first maturity. A composite index was also used, PCI (Parental Care Index, Petrik et al., 2020) considering traits linked to reproductive investment: fertilization mode, reproductive guilds (*sensu* Balon, 1990), the presence/absence of any type of parental care and the frequency of spawning. Quantitative and categorical data were weighted following Petrik and co-authors (2020).

Functional traits were derived from FishBase (Froese & Pauly, 2024) using the R package "rfishbase" (Boettiger et al., 2012) and additional trait data were obtained from searching both papers and reports, producing a dataset characterized by mixed variables, i.e. categorical and continuous. Continuous traits were log-transformed to approximate normality and reduce the impact of extreme values. We used the variance inflation factors (VIF; Dormann et al., 2013) to check for multicollinearity among explanatory variables and excluded size-at-maturity, larval size at hatching and generation time from the multivariate analysis due to their strong collinearity with age-at-maturity, k and egg diameter. The correlation coefficients between the remaining nine functional traits were below 0.7 (Pearson coefficient).

Based on these traits we performed an Archetypal Analysis (AA), an unsupervised learning method useful for characterizing life-history strategies based on traits, resulting in a continuous grouping of species according to their functional strategies (Cutler & Breiman, 1994; Hart et al., 2015; Pecuchet et al., 2016). Continuous trait data were normalized before analysis input to AA and the analysis was performed using the package 'archetypes' in R (Eugster & Leisch, 2009). We used the 'elbow criterion' to select the optimal number of strategies allowing to minimize the residual sum of squares (RSS) while minimizing the number of strategies by assessing the number corresponding to a visually significant drop in the RSS (Pecuchet et al.,

2016). The result of the AA, and notably the position in the traits space of the archetypes, was visualized using a principal component analysis (PCA) biplot. A two-way analysis of variance (ANOVA) was used to test for a significant effect of SACs and Campaigns, as well as their interaction, on the average and range of total length within different functional strategy groups.

Results

The dataset obtained is composed of 8,504 fish belonging to 61 different species distributed into 31 families (Table 2). Sparidae is the most represented family with 15 species followed by Carangidae (five species), Mugilidae (four species), Clupeidae and Serranidae represented by three species each.

The number of sampled fish was quite similar in C1 (n = 2,906) and C3 (n = 3,796), while differing in C2, where we sampled a relatively low numbers of fish (n= 1,802 records) because of the reduced sampling effort given by the Covid-19 pandemic. The minimum and maximum length observed per species were reported in Table 2.

Length-based indicators showed concordant trends in both SACs, even if the total length of sampled fish was significantly different in all the comparisons among SACs besides Campaigns except for SAC2 C2 vs. C3 (Kruskal - Wallis H = - 0.498, p = 0.309).

The obtained size-spectra provided a strong fit to the size distributions, according to R^2 adjusted values (Table 3). As shown in Fig. 2, a very similar trend can be identified in the two SACs: negative slopes and positive elevations increased through time, resulting in steeper spectra and lower elevations in C1 than in the following C2 and C3 in both areas. These findings suggest both a shift in the size abundance from relatively small fish to larger specimens and an environment that harbors more fish (Table 3).

MML values increased over the years in both SACs, ranging from 24.68 to 46.43 in SAC1 and from 21.97 to 35.97 in SAC 2 (Table 3). Accordingly, the Large Fish Index (LFI) grew in C1 vs. C3 from 0.01 to 0.30 in SAC1 and similarly from 0.02 to 0.11 in SAC2 (Table 3), suggesting an increasing presence of larger individuals/species over the years.

3.1 Functional characterization of assemblages

All 61 recorded species had complete information for all traits and were used in the Archetypal Analysis (AA). The optimal number of archetypes (k) needed to encompass the spatial volume of trait-space was found to be three since the largest drop in the RSS occurred between two to three archetypes, while adding a fourth one did not significantly reduce the

RSS. The three strategies identified by the AA were superimposed on a Principal Component Analysis (PCA) biplot, whose first two axes explained most of the trait variability (60.7%; Figure 3). The first axis (PC1) explained 40.1 % of the total variability and was driven by egg diameter, age at first maturity and PCI (Parental Care Index), while the second axis (PC2) explained 20.6%, mostly driven by fecundity and maximum age. The three functional groups showed trait combinations closely corresponding to the life-history strategies of the theoretical model of Winemiller and Rose (1992) and are henceforth referred to as Opportunistic (O), Periodic (P) and Equilibrium (E) strategies, respectively, and represented with different colors in the PCA (Table 2, Figure 3). Both the O and P strategies were prominent in the species pool, while three species only showed an E strategy: the smooth-hound *Mustelus mustelus*, the thornback ray *Raja clavata*, and the common torpedo *Torpedo torpedo*.

Both the range size and average length of species within different functional groups (O, P, E) did not differ between SACs (two-way ANOVA $F < 1.79$, $p > 0.1$ in all cases). The range size of total length increased significantly over the years (two-way ANOVA $F > 9.1$, $p < 0.05$ in all cases), according to the overall trend previously emerged (Fig. 4). The average length followed the same pattern, with the only exception for the probabilistic species (two-way ANOVA $F = 7.5$, $p = 0.071$). The post-hoc Tukey test confirmed that most of this difference was attributable to a significant increase in fish size between C1 and C3 (adjusted p-value < 0.05).

The violin plots evidence a larger bandwidth and a flattened shape for the first campaign for all the groups. The violin bandwidth become narrower, and the maximum size recorded increased through the time for all the functional groups, but the violin shapes changed in different ways. The Opportunistic species passed from a unimodal distribution of the total length to a skewed one. Periodic species showed a change in the kernel probability density, reaching a bimodal distribution of sizes in C3 with large outlier specimens (>50 cm) becoming more frequent. Equilibrium species showed a delayed change in the violin shape, passing from a nearly unimodal distribution of the length in both C1 and C2 to a more skewed one in C3, due to the presence of large outlier specimens never recorded before (>80 cm).

Discussion

It is commonly agreed that small-scale artisanal fishery would benefit of towing bans, due to the recovery of both stocks and habitats increasing the abundance and size of target species (Halpern et al., 2008; Amoroso et al., 2018). Paradoxically, in the Mediterranean Sea this principle is largely supported by experimental trawling data, providing information from which

the potential benefits for coastal fisheries are inferred despite these fisheries partially target different species (Battaglia et al., 2017; Pipitone et al., 2023). Many trade-offs contribute to this mismatch: in studies following a before-after approach the data collected before the ban largely concern trawling, so keeping trawling allows straightforward comparisons and in the case of an impact-control design, data can be compared with areas still subjected to trawling (Pipitone et al., 2023). Trawling hauls are more easily standardized due to both specifically developed statistical models and the relatively limited number of factors (Thorson & Ward, 2014; Bagley et al., 2015). Nevertheless, where data from both trawling and artisanal fishery are available, the indications obtained agree in terms of either richness/biomass of commercial fishes or economic revenue (Whitmarsh et al., 2002; 2003; Dimarchopoulou et al., 2018).

The studies that have implemented a sampling design based on small-scale fishery gears are a few, especially in the Mediterranean Sea, although increasing in recent years. This interest has been fostered by either the long-dating crisis of mediterranean artisanal fishery or the implementation of spatial based fishery management strategies requiring before-after studies to verify their efficacy (Battaglia et al., 2017; Bosquet et al., 2022; Di Cintio et al., 2023; Pipitone et al., 2023). Our data add a further case study analyzing how a trawling ban reflects on small-scale fishery catches across a decade and how the functional strategies that characterize the fish targeted by this fishery may be linked to the response provided. To evidence the effects of the trawling ban over time we used length-based indicators to skip a caveat of this study due to Covid-19 restrictions that affected C2 sampling, occurred in 2019-2020: the lower fishing effort of this campaign would make abundance-based indices poorly comparable, while the increase in fish length could be evidenced even in presence of a lower number of hauls, in any case representative of both seasons and gears.

Length-based indicators are widely employed to assess the recovery of fish stocks providing a relatively straightforward metric for evaluating changes in population structure and being able to detect early signs of population recovery. Their reliability roots in a solid knowledge base showing that in heavily exploited fish populations smaller size classes typically dominate catches but once trawling pressure relieves, fish may grow to larger sizes. For this reason, length-based indicators are widely used in data poor cases (ICES, 2015; Kell et al., 2024). The results obtained indicated that the fish reached a significantly greater length through time, suggesting a generalized improvement of stock conditions. Both Large Fish Index and Mean Maximum Length significantly increased from C1 to C2 to C3 and their post-ban growth may be explained by both the fact that larger, slower-growing fish are becoming more abundant, and that age structure is shifting toward older, hence larger, individuals previously removed by fishing. Both indices responded quite readily, showing significant increase between C1and C2,

besides between C2 and C3, so confirming that a time span of 5-10 years is appropriate for their effective use (Shin et al., 2005). Length-based indicators applied on data from C2 resulted aligned within this trend, so confirming that the sampling plan of C2 was qualitatively consistent with those of the other campaigns.

The Size Spectra Analysis showed that regression lines in both SACs flattened and lowered their elevation across the ten years of observation. The elevation of the spectra is considered a proxy of the community abundance across the entire size range (Trenkel & Rochet, 2003; Daan et al., 2005) and has been inversely correlated with the fishing pressure in many cases across the world (Gislason & Rice, 1998; Shin et al., 2005; Gristina et al., 2006). The slope of Size Spectra is related to the frequency of small-bodied specimens, so that if large fish are allowed to survive and grow, their abundance in higher size classes can increase, causing the slope to flatten. Flattening then suggests a more balanced or restored community size structure, with relatively more large individuals than before (Jennings & Blanchard, 2005). Our findings agree with the bulk of data showing that size spectra modifications of both slope and height are related to fishing pressure either while increasing or decreasing. As an historical example, in the North Sea the increasing fishing pressure recorded in the 1973-93 period was related to the increasingly steeper slope of the size spectra (Rice & Gislason, 1996).

Recent papers have evidenced the relevance of functional traits in characterizing the fish community inhabiting Mediterranean seagrasses, particularly *P. oceanica*, providing information unevidenced by taxonomic diversity (Lattanzi et al., 2024; Bellisario et al., 2025). Fish functional assemblages have been proved non-randomly structured, showing a core of functionally similar fish species characterized by *r-like* reproductive strategies and low-to-intermediate trophic levels (Bellisario et al., 2025). However, fish species poorly fit along a linear *r-like* to *K-like* continuum, since frequently showing a mix of traits belonging to both strategies and due to the fact that while functional groups definition relies on selected traits, life-history strategies rather emerge from the combined influence of several key traits that interact with and place constraints on each other (Winemiller et al., 2015). Therefore, fish life-history strategies are more frequently represented as a triangle in trait space, with each endpoint representing a unique life-history strategy characterized by a combination of key traits: Opportunistic, Periodic and Equilibrium (Winemiller & Rose, 1992; Pecuchet et al., 2017). Trademarks of the opportunistic strategy are early maturation, small adult size, short generation time, high reproductive output over short intervals, while periodic strategy is characterized by delayed maturation, large adult size, high fecundity, and low offspring survival. Finally, equilibrium strategy features moderate to late maturation, low fecundity, greater parental investment and comparatively stable juvenile survival. Furthermore, ongoing comparative

studies show that these life-history patterns are useful for predicting responses to fishing pressure, besides habitat disturbance and climate change (Hidalgo et al., 2011).

Our results showed that the bulk of species are classified as opportunistic, representing 59% of the total, followed by the periodic at 36% while the equilibrium strategy is poorly represented, 5%. This was an expected finding since a relevant part of the Mediterranean fish species are classified as opportunistic (Pecuchet et al., 2017). Also, *P. oceanica* fish assemblages have been shown as characterized by small-sized, rapidly growing and low tropic level species, so exhibiting traits typical of opportunistic strategy (Bellisario et al., 2025). Accordingly, our species belonging to this group are from families both highly associated to seagrass meadows and targeted by coastal fishery as Sparid (11 species) or Mugilid (4 species) (Lattanzi et al., 2024). Among the periodic species we found highly targeted species as the shi drum (*Umbrina cirrosa*), the brown meagre (*Sciaena umbra*) and another three sparid. Sharks and skates, representing equilibrium species, are quite rarely recorded in Mediterranean seagrasses, in accordance with our results (Lattanzi et al., 2024).

Life-history strategies explain how, and how much, fish species may face environmental fluctuations, including those of anthropogenic origin such as climate change and fishing pressure (Hidalgo et al., 2011). Data are increasingly demonstrating that reduced fishing impacts may differentially benefit fish community components, because of the interplay between life-history strategies, disturbance nature and environmental conditions (Otero & Hidalgo, 2023). Our data showed that along the 10 years of the survey, the fish length significantly increased for all the functional groups, but with different patterns. Equilibrium species showed a delayed recovery, with outlier long specimens appearing only in the last survey, while opportunistic and periodic species responded more quickly.

This is somewhat expected since it is known that when looking at length indicators a transition from rapid but short-statured recovery to a delayed but steady increase in length measures is predicted passing from opportunistic to equilibrium species. These differences stem from trade-offs in each strategy's growth, reproduction, and survivorship patterns. Opportunistic species may proliferate quickly, thanks to their high fecundity and short generation times. However, since these fish do not typically attain large body sizes, increases in length-based metrics may be less dramatic. Periodic species have quite longer generation times and delayed maturity, sometime showing pulses in recruitments success due to environmental conditions fluctuations (e.g., suitable temperature or abundant food). After these pulses, an uptick in the proportion of bigger individuals can drive shifts in size-based metrics. The recording of a bimodal distribution in the violin plot for periodic species in C3 may suggest a role for environmental factors in producing the observed pattern of recovery. Equilibrium

strategists' life-history attributes (e.g., parental care, stable juvenile survival) lead to a methodical rebound but their low growing rate takes more time to redistribute a significant rate of the biomass in the higher size classes. Accordingly, nearly all the outliers recorded in C3 are smooth-hounds, characterized by a greater body length and a lower growth rate with respect to the two ray species belonging to the equilibrium group.

Our results align with those of one of the most studied cases in the Mediterranean Sea, the trawling ban in the Castellammare Gulf where a year-round trawl ban was imposed in 1990, allowing a long-time series of data to be collected according to a BACI (Before-After-Control-Impact) design (Pipitone et al., 2000; 2023, and references herein; Withmarsh et al., 2002). Here, demersal species showed a significant increase in biomass compared to before the ban and to other trawled areas, particularly notable for highly commercial species, which saw the largest biomass increase, especially at depths used by artisanal fishermen (Pipitone et al., 2023). The size structure recovery was only partial, with some species showing larger median sizes and an increased proportion of larger individuals compared to trawled areas. The Authors noticed that sharks and rays still had a low biomass while mesopredators boosted, hypothesizing that the recovery was still taking place (Pipitone et al., 2023).

Conclusions

Our data show that the study of increase in length base indicators in the fish assemblages targeted by small-scale fishery over a decade, following the deployment of AAR along two Natura 2000 sites, and distinctive life-history strategies may explain the different recovery patterns observed for the species groups. These findings add to the increasing bulk of data showing that, besides the generalized pattern of recovery due to trawling ban, the factors influencing both the extent and the time of the recovery are multiple and interrelated. Although environmental parameters were not included in the analysis, the pattern of length increase shown by periodic species suggests a role for environmental fluctuations in boosting waves of recruitment. In our case the AAR effects could not be split form that of the enforced illegal trawling ban, since it has been shown that artificial reefs themselves may increase fish abundance, so benefiting fishery even in absence of fishing pressure mitigation (Vivier et al., 2021). On the other hand, the patterns observed in the light of the life-history strategies are largely those expected according to species traits, so suggesting that in any case AAR may be a good strategy to enhance both biodiversity and small-scale fishery recovery in the context of central Mediterranean coasts (Iannibelli & Musmarra, 2008; Vivier et al., 2021).

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List of Tables

Table 1 - Fishing gears listed according to mesh size, with fishing seasons and mean number of hauls per SAC per campaign.

Net	Mesh	Season	Hauls/SAC/Campaign
Trammel net + gillnet	22	Spring/Summer/Autumn	12 - 9- 12
Trammel net + gillnet	32-35	All year long	8 - 6 -8
Incastellata + Barracuda gillnet	40-45	All year long	8 - 6 -8
Barracuda gillnet	50	Spring/Summer/Autumn	4 - 3- 4

Table 2 - Fish species sampled with their family, life-history strategy, minimum and maximum values of total length and weight. Species marked with an asterisk represent the most frequent ones. Life-history strategies: E, equilibrium; P, periodic, O, opportunistic.

			Total Length		**Weight**	
Species	**Family**	**Life-history strategy**	**min**	**max**	**min**	**max**
Alosa alosa	Clupeidae	O	17	27	63	195
Alosa fallax	Clupeidae	P	15	46	41	789
Arnoglossus laterna	Bothidae	O	9	22	7	129
Balistes capriscus	Balistidae	P	12	22	34	138
Belone belone	Belonidae	O	34.5	48.5	40	150
Boops boops	Sparidae	O	19.9	23	109	149
Chelidonichthys lucerna	Triglidae	P	11	28	13	246
Chelon auratus	Mugilidae	O	21.5	50	131	1343
Chelon labrosus	Mugilidae	O	31.9	43.5	457	1065
*Chelon ramada**	Mugilidae	O	23	56	104	1800
Conger conger	Congridae	P	16.3	85	43	1281
Dactylopterus volitans	Dactylopteridae	O	19	19	72	72
Dentex dentex	Sparidae	P	13.4	64	52	3860
Dicentrarchus labrax	Moronidae	P	23	36.5	123	559
*Diplodus annularis**	Sparidae	O	8.1	20	11	170
Diplodus puntazzo	Sparidae	O	14.7	29	105	372
*Diplodus sargus**	Sparidae	P	12.8	32	47	636
*Diplodus vulgaris**	Sparidae	O	10	31	48	516
Engraulis encrasicolus	Engraulidae	O	8	11	5	10
Epinephelus aeneus	Serranidae	P	37	45	1000	1445
Euthynnus alletteratus	Scombridae	O	45	45	1243	1243
Lichia amia	Carangidae	P	28	41	263	840
*Lithognathus mormyrus**	Sparidae	O	12	36	27	475
Merluccius merluccius	Merlucciidae	P	16.5	45	29	626
Mugil cephalus	Mugilidae	O	30	65	326	2905
*Mullus barbatus**	Mullidae	O	9	23	17	243

Mullus surmuletus	Mullidae	O	10.5	30	34	433
Muraena helena	Muraenidae	P	68	90	684	1680
Mustelus mustelus	Triakidae	E	36	110	157	3740
Oblada melanurus	Sparidae	O	14.1	26.4	58	375
*Pagellus acarne**	Sparidae	O	8	25.8	10	270
Pagellus bogaraveo	Sparidae	P	19	20	100	132
*Pagellus erythrinus**	Sparidae	O	11	42	31	1090
Pagrus pagrus	Sparidae	P	9.3	32	14	706
Phycis phycis	Phycidae	P	16.4	31	48	487
Pomadasys incisus	Haemulidae	O	7	23	6	171
Pomatomus saltatrix	Pomatomidae	O	19	40	48	559
Pseudocaranx dentex	Carangidae	P	17	17	58	58
Raja clavata	Rajidae	E	30	77.5	150	3960
Sarda sarda	Scombridae	O	40.3	40.5	900	1005
Sardina pilchardus	Clupeidae	O	10	17	9	32
Sarpa salpa	Sparidae	O	12.2	36	38	432
Sciaena umbra	Sciaenidae	P	18.9	47	146	1583
Scophthalmus rhombus	Scophthalmidae	O	14	42	46	1380
Scorpaena porcus	Scorpaenidae	P	9.4	22.5	34	250
Scorpaena scrofa	Scorpaenidae	P	8.3	44	18	1830
Seriola dumerili	Carangidae	P	21	21	122	122
Serranus cabrilla	Serranidae	O	13.4	16.3	43	80
Serranus scriba	Serranidae	O	12.9	23	50	224
Solea solea	Soleidae	P	18	43	43	1081
Sparus aurata	Sparidae	O	14	52	77	2420
Sphyraena sphyraena	Sphyraenidae	P	22	43	60	312
Spicara maena	Centracanthidae	O	12.2	15	34	56
Spondyliosoma cantharus	Sparidae	O	11.3	27	35	392
Symphodus tinca	Labridae	O	11.1	28.5	33	334
Torpedo torpedo	Torpedinidae	E	26.5	43	330	1258
Trachinotus ovatus	Carangidae	O	19.4	28.5	120	151
*Trachurus mediterraneus**	Carangidae	O	12.8	36.7	26	333
*Umbrina cirrosa**	Sciaenidae	P	12.4	55	22	1930
Uranoscopus scaber	Uranoscopidae	O	12.6	33	58	730
Xyrichtys novacula	Labridae	O	14.8	14.8	71	71

Table 3 - Length-based indicators per SAC and Campaign: Size Spectra adjusted R-squared, slope and elevation; mean maximum length (MML); and Large Fish Index (LFI).

SAC	Campaign	Adjusted R-squared	Slope	Elevation	MML	LFI
SAC1	C1	0.94	-2.75	2.65	24.68	0.01
	C2	0.74	-1.01	4.49	36.38	0.23
	C3	0.64	-0.32	5.53	46.43	0.3
SAC2	C1	0.83	-2.71	3.39	21.97	0.02
	C2	0.57	-1.52	4.85	32.61	0.09
	C3	0.79	-0.56	7.02	35.97	0.11

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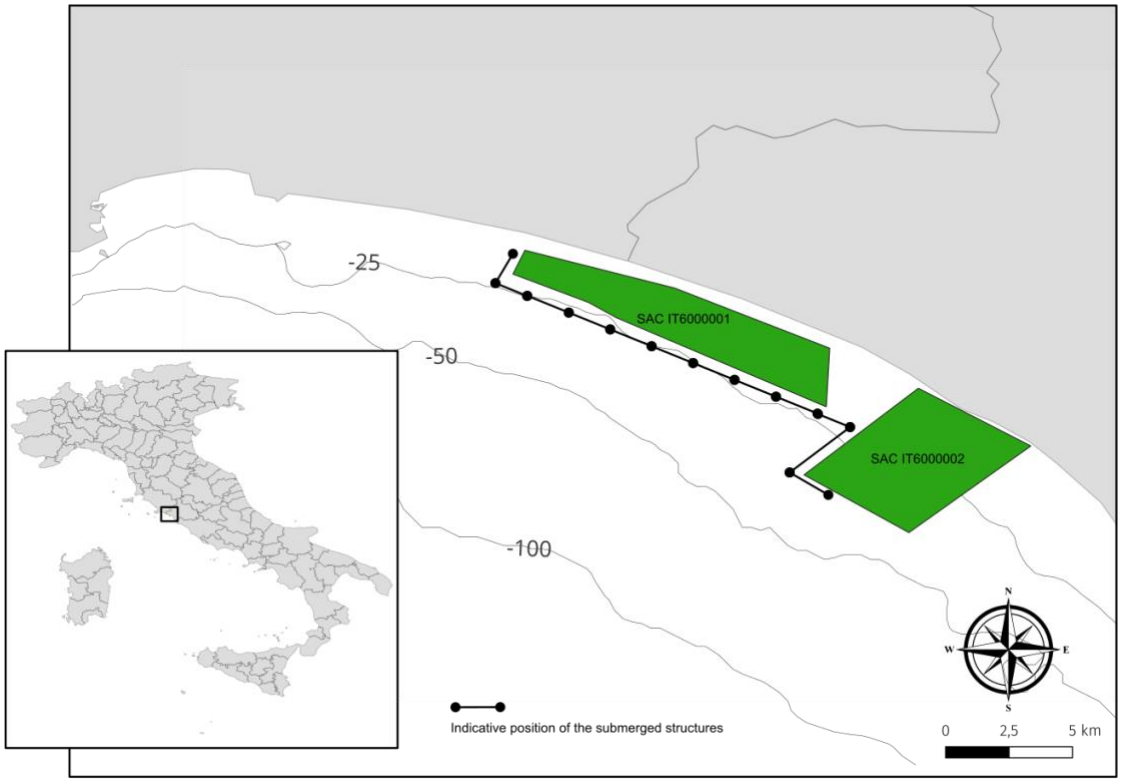

Figure 1 - Geographic position of the two studied SACs (inlet) with the approximate distribution of the Anti-trawling Artificial Reef.

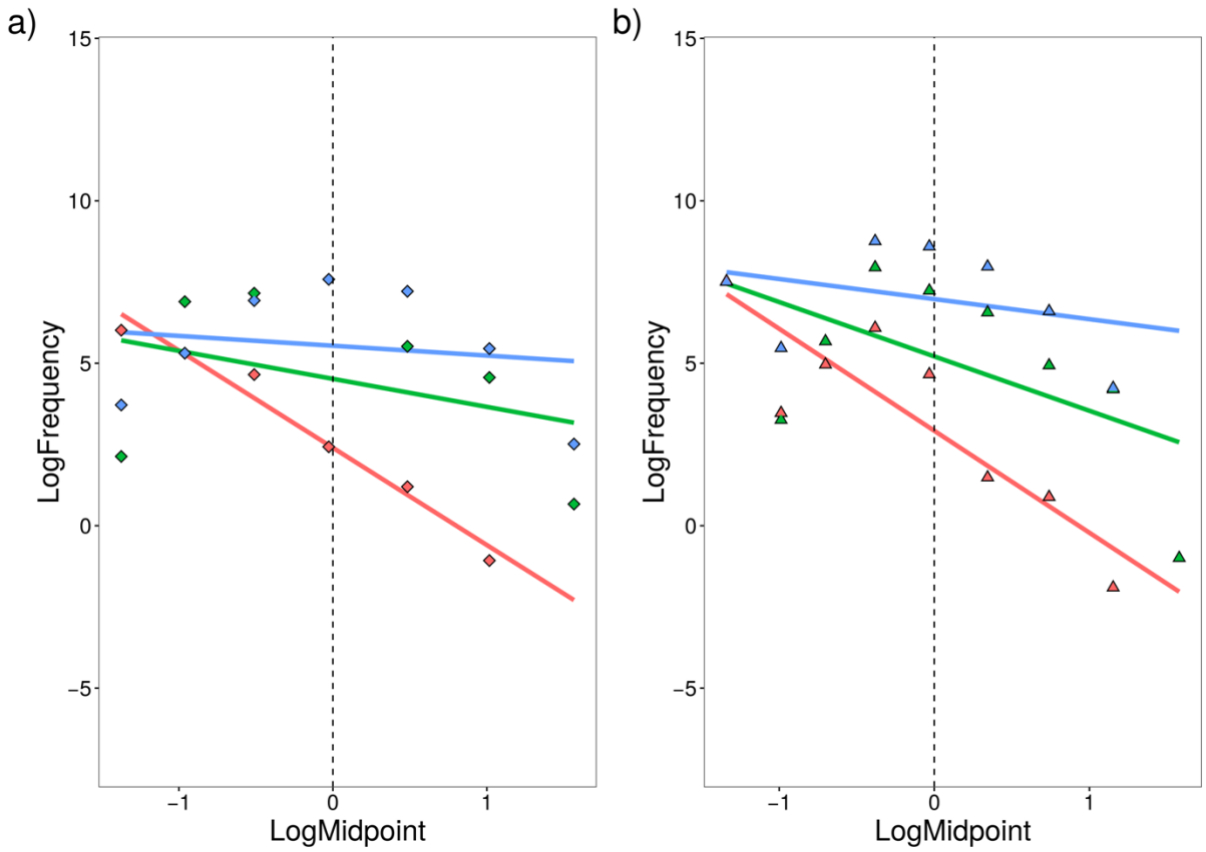

Figure 2 - Size-spectra per SAC and Campaign. The lines represent the linear fitting of the size spectrum related to C1 (light red), C2 (green) and C3 (blue).

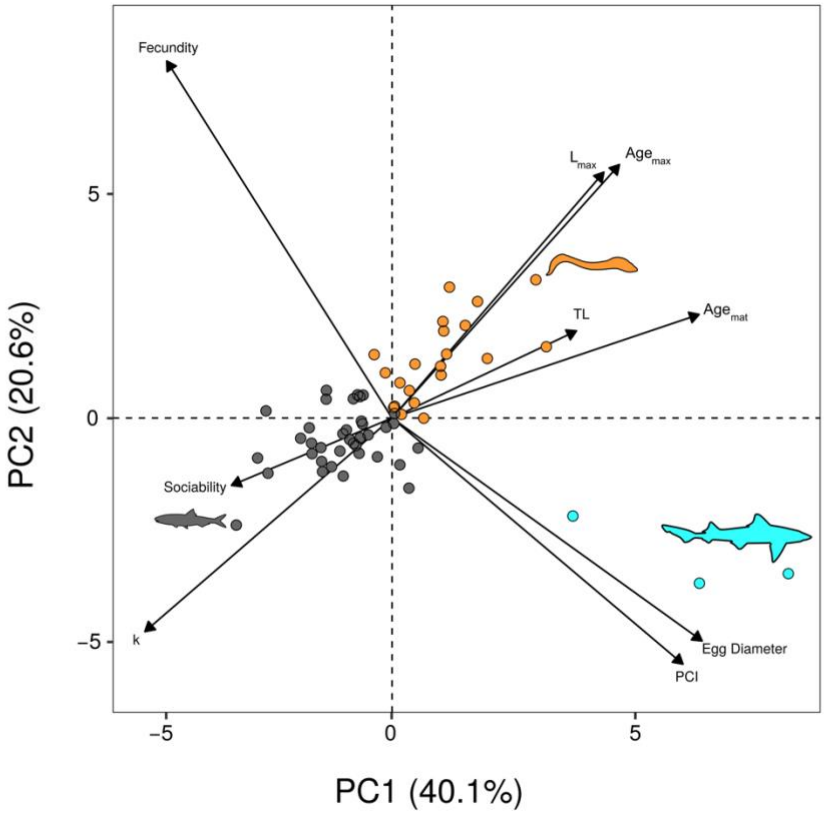

Figure 3 – Biplot of the Principal Component Analysis based on the 9 selected traits. Colors correspond to species life-history strategy (see main text). Silhouettes show the three extreme archetypes of the trait-space: *Mustelus mustelus*, equilibrium strategy (blue); *Engraulis encrasicolus*, opportunistic strategy (gray); *Conger conger*, periodic strategy (orange). Traits' abbreviations: L_{max} = Maximum Length; Age_{max} = Maximum Age; TL = Trophic Level; Age_{mat} = Age at first maturity.

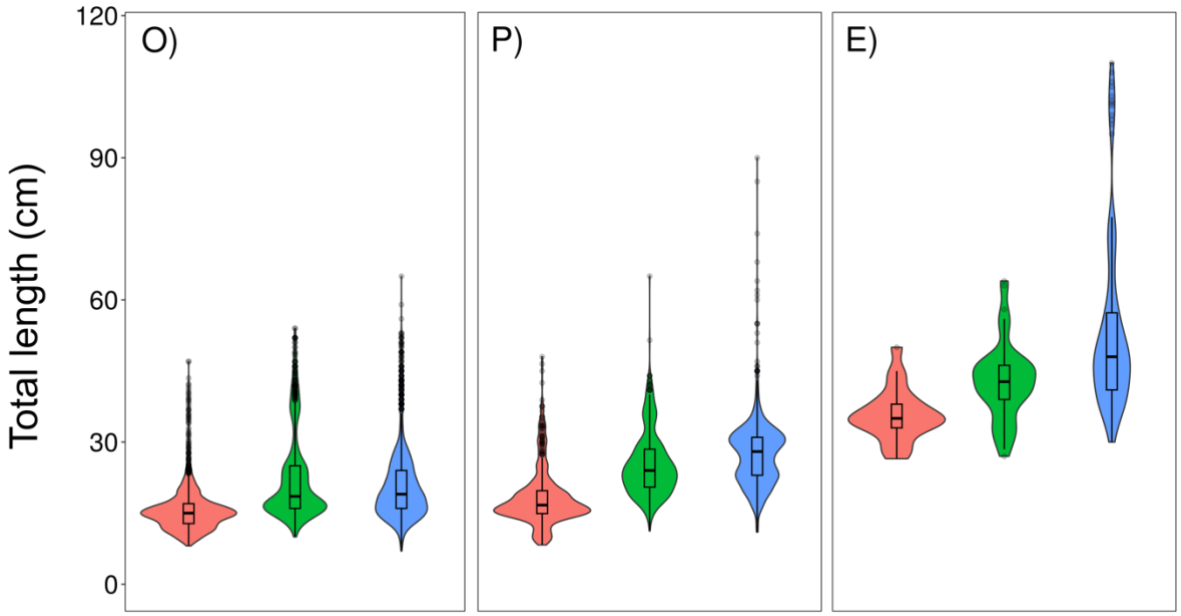

Figure 4 - Violin plots showing the distribution of the total length (in cm) in the three groups corresponding to different life-history strategies (E = equilibrium; O = opportunistic; P = periodic) in different campaigns (light red, C1; green, C2; blue, C3). The violin contours represent the kernel probability density, with thicker areas indicating a higher density of observations. Horizontal lines represent the median while dots indicate outliers.

CONCLUSIONS

Mediterranean seagrasses are widely acknowledged as biodiversity hotspots and play a crucial role as reproduction, foraging and/or refuge areas for a relevant number of species, including fish of commercial interest. Despite its importance, comparative studies on fish assemblages remain fragmented and often confined to sub-basin and local scales. This results in an incomplete understanding of fish distribution patterns across different seagrass habitats, possibly obscuring key mechanisms associated with their habitat use.

With the aim of addressing this gap, the research carried out has produced a dataset providing a complete synthesis of fish species reported in native Mediterranean seagrass habitats, alongside specific functional traits known to be involved with the potential use of seagrasses by fish. The research showed that the high species richness of fish found on seagrass beds is far from being evenly distributed among different seagrasses at the Mediterranean scale, a heterogeneity missed when looking at single studies. *P. oceanica* meadows host a unique and diversified fish fauna if compared to *C. nodosa* and, even more markedly, to *Z. marina* with a nested pattern of taxonomic richness decreasing along with seagrass complexity.

Taxonomic and functional diversity are known to evidence different patterns and mechanisms in community assemblage, so that the importance of considering both aspects is largely acknowledged. Specific combinations of life history and feeding-related traits might determine how species use habitats according to the peculiar characteristics of the seagrass (e.g., structural complexity, ability to form extensive meadows, distributional ranges), as either refuge, nursery and/or foraging areas. To explore this relationship, the dataset produced has been implemented with functional traits related to life-history strategy of the fish species observed in seagrass habitats: trophic ecology, size, growth and generation time. Fish functional assemblages show a core of functionally similar fish species characterized by *r-like* reproductive strategies and low-to-intermediate trophic levels that provide a common 'fingerprint' in the different seagrasses, irrespective of meadows' complexity. However, seagrasses vary in their ability to support ambusher predators, that decrease in their probability of occurrence while complexity decrease, suggesting a role for functional traits in determining the use of different seagrass habitats. Seagrass structure is also related to the ontogenetic use that species make of these habitats: high trophic level species, such as large predators, primarily use these habitats as foraging grounds exclusively during their adult phase, whereas the functional core of smaller species with more varied diets is present across all life stages. This pattern is related to the three-dimensional structure of seagrasses which may offer greater

protection from predators and at the same time a high density of prey compared to bare substrates.

Further research is needed to generalize these patterns and elucidate the mechanisms shaping fish communities, which are essential for preserving marine biodiversity especially in the light of ongoing climate change. Recent studies show how Mediterranean seagrass meadows undergoing a transition from long-lived, slow-growing species like *Posidonia oceanica* to smaller, fast-growing species such as the invasive *Halophila stipulacea*, a pattern likely driven by global change (Beca-Carretero et al., 2024). Since the different ecological and structural characteristics of seagrass species influence the taxonomic and functional composition of associated fish communities, this replacement may result in a significant reduction in fish biodiversity and a loss of critical ecosystem services. Indeed, *Posidonia oceanica* forms a complex three-dimensional habitat that supports a higher diversity of functionally diverse fish species. Conversely, although *Halophila stipulacea* as other seagrasses is a habitat forming that significantly increases the structural complexity of the bare habitats, it forms sparser and lower beds resulting in less structured meadows than *P. oceanica* so providing limited refuge for prey. Accordingly fish fauna associated is characterized by generalist, opportunistic or small-sized species with a low occurrence of high trophic levels species (Di Genio et al., 2021; Beca-Carretero et al., 2024 ; Di Martino et al., 2007).

The relevance of including traits-based approaches when analysing coastal fish communities has been evidenced also from a ten-year local case study studying the fish assemblages sampled in two Special Areas of Conservation (SACs) located along the Italian central Tyrrhenian coasts. Both areas are partially protected, allowing only artisanal and recreational fishing, but the local trawling ban had been weakly enforced. In response, an Anti-trawling Artificial Reef (AAR) was installed in 2013 along the lower boundary of *Posidonia oceanica* meadows, physically restricting access to trawlers. Over a decade (2014-2024), three fishing campaigns were conducted to assess the potential recovery of target fish species and to examine whether recovery rates differed by life-history strategy. The significant increase in fish length over time indicates improving stock conditions, but when fish species were subdivided according to their functional strategies, different patterns emerged. Length gains occurred in all functional groups, though equilibrium species exhibited a delayed response, with larger individuals appearing only in the final survey. In contrast, opportunistic and periodic species rebounded more quickly, consistent with their respective growth, reproductive, and survivorship trade-offs.

Overall, the data produced allowed to test specific hypotheses at a whole basin-scale, offering insights into the complex mechanisms structuring ecological communities (Weiher et al., 2011). The identification of a ‘functional fingerprint’ in seagrass-associated fish fauna

provides a crucial baseline for predicting how such environmental transitions will affect fish assemblages. Indeed, understanding the extent to which seagrasses are able to host the same fish fauna, both from a taxonomic and functional point of view, is essential for identifying peculiar functional strategies more at risk in the face of anthropogenic pressures, or addressing the combined impacts of climate change, invasive species, and anthropogenic pressures, ultimately enhancing strategies for marine biodiversity conservation.

Several studies have shown how r-K selection strategies might have a role in determining the responses of species to disturbances, with r-selected species strongly affected by climate change but less impacted by fishing pressure, while the opposite is true for K-selected fish species (Graham et al., 2011; Lynam et al., 2017). Our findings add to the aim of providing a robust foundation for scientists and managers in many fields, from fisheries to biodiversity assessment and conservation.

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