

Depth structure and habitat associations of flatfish assemblages in a productive semi-enclosed sea

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ABSTRACT

Flatfish are key components of demersal ecosystems and valuable targets of fisheries, yet their community structure and habitat associations remain poorly resolved in the Mediterranean. Using 20 years of data from a standardized bottom-trawl survey in the western part of the North–Central Adriatic Sea, we aimed to describe flatfish assemblage composition along habitat gradients and identify spatially specific indicator taxa. Using haul-level data from 2021, 2023, and 2024, we further related flatfish assemblages to benthic invertebrate biomass, bottom water temperature, and seafloor substrate type to examine habitat associations. Assemblages differed significantly among the bathymetric strata investigated (North: 10–50 and 51–100 m; Central: 10–50, 51–100, 101–200 and 201–500 m; PERMANOVA, $R^2 = 0.73$). The shallow-shelf communities (10–50 m) were characterised by soleids, pleuronectids, bothids and scophthalmids, while in central deep-shelf (101–200 m) and upper-slope assemblages (201–500 m), scophthalmids and cynoglossids became progressively more prominent. Bathymetric strata were characterised by different indicator taxa, with the highest number found in the northern shallow shelf. Despite sharing the same depth range, the northern and central shallow-shelf assemblages remained markedly different, indicating that depth alone does not explain community organisation. Variation partitioning confirmed significant independent contributions of bottom temperature and substrate type. Together, these results provide the first spatially resolved baseline for flatfish assemblage organisation and habitat associations for the North–Central Adriatic Sea and highlight the value of long-term standardized surveys for monitoring future reorganisation of demersal communities under climate change.

1. Introduction

The spatial structure of demersal communities in marine shelf ecosystems is affected by climate and fishing disturbances (Jennings and Kaiser, 1998; Perry et al., 2005; Pecl et al., 2017). In particular, climate change may drive shifts in the suitable depth ranges of demersal species, thereby altering community composition along shelf–slope gradients (Perry et al., 2005; Pinsky et al., 2013). Understanding how marine

assemblages are structured across environmental gradients is therefore becoming increasingly important in ecosystem monitoring and ecosystem-based fisheries management (Perry et al., 2005; Hollowed et al., 2013; Pinsky et al., 2013).

Species distributions and co-occurrence in marine ecosystems emerge from the interaction among environmental filtering, habitat heterogeneity, trophic processes, and disturbance regimes, which together shape community organisation across spatial gradients (Wis-

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et al., 2013). Because these drivers operate simultaneously and interactively, species may exhibit shared or contrasting responses, generating assemblage-level patterns that are not always detectable through single-species analyses alone (Gilman et al., 2010; Ovaskainen et al., 2017). Community-level analyses can therefore provide broader insight into how demersal assemblages are structured across heterogeneous marine habitats and help establish baselines for evaluating future community reorganisation under environmental change (Pech et al., 2017; Pinsky et al., 2020).

In marine shelf systems, depth often emerges as a major organising axis of demersal communities because it integrates multiple gradients, including bottom temperature and substrate type (Mueter and Norcross, 1999; Demestre et al., 2000). In addition, trophic interactions and fishing disturbance may further shape this spatial structure, which is typically expressed as turnover in community composition along these interconnected habitat gradients (Jennings and Kaiser, 1998; Bianchi et al., 2000; Demestre et al., 2000).

Within demersal assemblages, flatfish (order *Pleuronectiformes*) represent a functionally important component across continental shelves, deep-ocean margins and semi-enclosed seas. Through their benthic feeding habits and their role as prey for higher trophic levels, flatfish assemblages contribute substantially to transferring benthic production to upper trophic levels, thereby mediating benthic–pelagic coupling and supporting demersal fisheries yields (Sartor et al., 2002; Link et al., 2014). Because flatfish assemblages are closely associated with bottom habitats and benthic communities, they are highly susceptible to perturbations of the seabed (Jennings and Kaiser, 1998; Mueter and Norcross, 1999; Gibson, 2005). Consequently, they may provide useful indicators of bottom alteration, environmental change and fishing disturbance in shelf ecosystems (Link et al., 2014).

Despite their functional importance, Mediterranean flatfish have been studied mainly through single-species, trophic, or species-specific distributional approaches, whereas assemblage-level analyses remain scarce (Darnaude et al., 2001; Cicala et al., 2019; Ugrin et al., 2025). Although flatfish contribute substantially to Mediterranean commercial landings (Sartor et al., 2002), basin-scale understanding of how their assemblages are organised along habitat gradients remains limited, constraining broader understanding of demersal community organisation in Mediterranean shelf ecosystems.

Among Mediterranean sub-basins, the Adriatic Sea provides an ideal system for addressing this knowledge gap because of its pronounced bathymetric and hydrographic gradients and its high socio-economic importance as one of the major fishing grounds in southern Europe (Lipej and Dulčić 2010; Fouzai et al., 2012). The Adriatic Sea is a distinct biogeographical and ecological area of the Mediterranean whose bathymetric, hydrographic, and climatic characteristics have strongly shaped its ichthyofauna (Lipej and Dulčić 2010). The North–Central Adriatic Sea is among the most productive areas of the Mediterranean Sea, supporting numerous commercially exploited demersal and small pelagic stocks (Fouzai et al., 2012). This makes the study of demersal assemblage structure particularly relevant for understanding ecological change and spatial community organisation. However, studies in this area have focused mainly on individual species, particularly *Solea solea* in the western sector (Grati et al., 2013; Scarcella et al., 2013) and, more recently, *Lepidorhombus* spp. in the eastern sector (Ugrin et al., 2021, 2025), whereas a basin-scale assessment of flatfish assemblage organisation across habitat gradients is still lacking.

The Mediterranean Bottom Trawl Surveys (MEDITS) program provides a suitable platform to address these gaps. Although MEDITS was originally developed for fisheries assessment and has been widely used to investigate Mediterranean demersal communities, its potential for assemblage-level analyses of flatfish communities has remained comparatively underexploited. Nevertheless, the survey represents one of the longest-running standardized ecosystem monitoring programmes for Mediterranean demersal communities, providing spatially extensive information on species distributions, assemblage composition, and

habitat associations across continental shelves and upper slopes (Bertrand et al., 2002; Piccinetti et al., 2012; Spedicato et al., 2019). Such long-term standardized surveys are increasingly recognised as valuable tools for detecting ecosystem change and evaluating spatial redistribution of marine communities under ongoing environmental change (Shin et al., 2010).

In this study, we used standardized flatfish data collected during MEDITS in the North–Central Adriatic Sea to examine assemblage structure across habitat gradients. Specifically, we (i) describe flatfish assemblage composition across areas and depth ranges, (ii) identify indicator species for distinct depth–area combinations, and (iii) assess whether potential differences in flatfish assemblages along the spatial gradient are coupled to habitat conditions (benthic invertebrate biomass, temperature and substrate type). Together, these analyses provide an ecosystem-level spatial baseline for understanding how flatfish assemblages are organised across this productive Mediterranean shelf system and for evaluating future reorganisation of demersal communities under environmental and anthropogenic change.

2. Materials and methods

2.1. Study area

The study area is the North–Central Adriatic Sea, a semi-enclosed basin in the Central Mediterranean corresponding to FAO Geographical Sub–Area 17 (GSA17; Fig. 1), located between the Italian peninsula and the Balkans.

Across the Adriatic basin, depth, seafloor morphology, and hydrography vary markedly along both longitudinal and latitudinal axes. The North–Central area includes the shallow, mainly eutrophic northern Adriatic and extends southward across the central basin. It encompasses the meso-Adriatic depressions (Pomo/Jabuka Pit; Fig. 1), where depths reach approximately 270 m, and continue offshore toward the upper slope, where depths in the central portion of the study area reach approximately 500 m.

The general circulation is cyclonic, with inflow of water masses from the Eastern Mediterranean along the eastern side of the basin and outflow along the western side.

The eastern coast is predominantly rocky and indented, with numerous islands, whereas the western coast is flat, alluvial, and strongly influenced by river runoff. The western seafloor is mostly covered by recent muddy and coastal sandy sediments of fluvial origin that are transported predominantly southward by the prevailing cyclonic circulation, although part of this material is recirculated northward, whereas offshore areas of the northern Adriatic preserve relict sedimentary features and limited modern sedimentation (Russo and Artegiani, 1996). The Po and other northern Italian rivers contribute a substantial fraction of the total Mediterranean river runoff and deliver large nutrient loads to the basin (Hopkins et al., 1992; Cozzi and Giani, 2011). These riverine inputs and associated nutrient enrichment jointly affect salinity and temperature and generate pronounced seasonal variability in coastal waters, where bottom temperatures range from about 7 °C in winter to 27 °C in summer. In deeper shelf areas, thermal variability is less pronounced, with values ranging from ~10 °C in winter to 18 °C in summer at 50 m depth (Russo and Artegiani, 1996; Artegiani et al., 1997).

2.2. Fish data

Fish data were obtained from the MEDITS standardized bottom-trawl surveys conducted in the Mediterranean GSA17, which have been carried out annually since 1994 with the aim of providing a common bottom-trawl survey along the Mediterranean coasts in late spring–summer using a shared sampling protocol among participating countries (Bertrand et al., 2002; Anonymous, 2017; Spedicato et al., 2019). At the scale of the whole Mediterranean, MEDITS covers trawlable areas

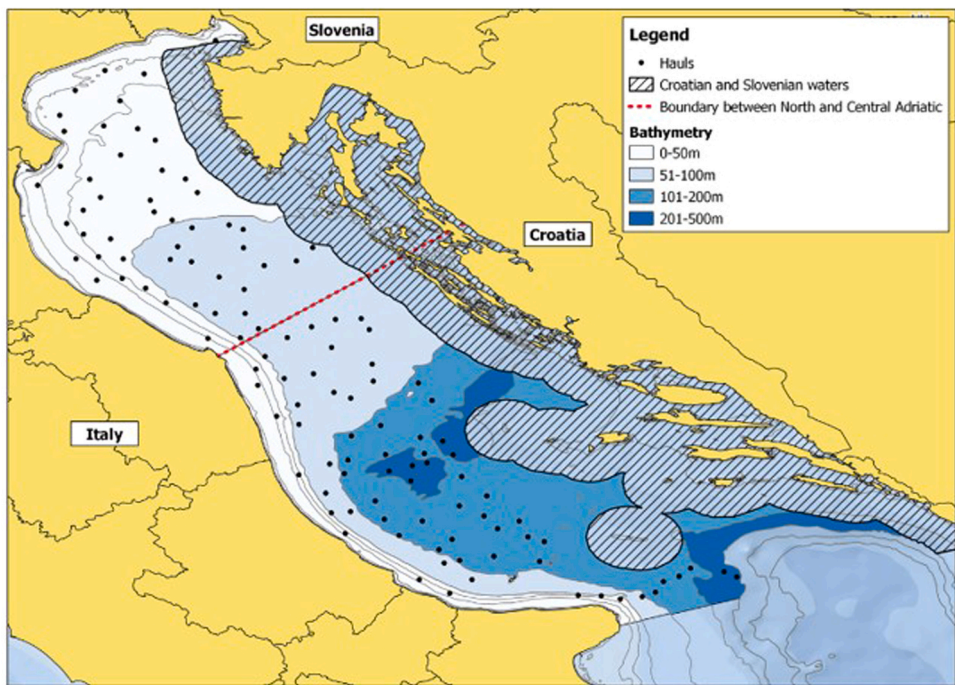


Fig. 1. Study area in the North–Central Adriatic Sea (GSA17). Black dots show an example of the spatial distribution of MEDITS bottom-trawl hauls within the study area (year 2023, 120 hauls). The dashed red line separates the North from the Central area (Table 1). Coloured areas indicate bathymetric strata (10–50 and 51–100 m in the northern Adriatic; 10–50, 51–100, 101–200 and 201–500 m in the central Adriatic). The deep areas in the middle of the central Adriatic Sea correspond to the Pomo/Jabuka Pit. Black hatched areas correspond to Croatian and Slovenian waters. Map lines delineate study area and do not necessarily depict accepted national boundaries.

of continental shelves and upper slopes from 10 to 800 m depth, thereby extending substantially deeper than most coastal bottom-trawl surveys (Anonymous, 2017). Sampling stations are allocated according to a depth-based stratified random sampling design to achieve a compromise between classical random sampling and geostatistical requirements (Green, 1979; Hilborn and Walters, 1992). Trawling is conducted during daylight using the standardized GOC73 bottom trawl (Fiorentini et al., 1999), with a stretched codend mesh size of 20 mm. Further sampling details are reported in the MEDITS handbook (Anonymous, 2017). For each haul, the total catches larger than 1 cm are sorted, identified to the lowest taxonomic level possible, counted, and weighed. Although benthic invertebrates were recorded in MEDITS surveys before 2021, the taxonomic resolution and consistency of benthic records improved in the most recent survey years (2021, 2023, 2024). Species density is therefore estimated in numbers (abundance density, $N\ km^{-2}$) and weight (biomass density, $kg\ km^{-2}$). As for other otter-trawl surveys, the GOC73 gear is less efficient at sampling flatfish and other strictly benthic organisms than specialised flatfish gears, because many flatfish species rest on or partially bury into the sediment, reducing their contact with the trawl and allowing some individuals to escape capture (Gibson, 2005; Ryer, 2008). However, MEDITS represents a unique large-scale standardized survey which can therefore serve to perform temporal and spatial comparisons of demersal and benthic species and communities (Ungaro et al., 1999; Terribile et al., 2016).

In this study, the analyses were restricted to the western (Italian) area of GSA17, where the survey is typically conducted between May and August and covers the bathymetric strata 10–50, 51–100, 101–200, 201–500 m (Table 1; Fig. 1). The number of hauls has not always been constant since the beginning of the survey, although from 2002 approximately 120 hauls per year have usually been carried out (Fig. 1). We excluded from the analyses years with low sampling effort (< 100 hauls per year; 1994–2001), as well as years when the survey was performed outside the period May–August (2014 and 2017). In 2022 the survey was not carried out in this area. The final dataset therefore

Table 1
Bathymetric strata covered during the Mediterranean Bottom Trawl Survey in the North–Central Adriatic Sea (GSA17). The table reports depth stratum codes, depth ranges (m), areas (square kilometres), geographic sectors, and the position of each stratum along the shelf–upper-slope gradient (Anonymous, 2017).

Stratum	Depth (m)	Area (km ²)	Sector
21101	10–50	17300	North Adriatic shallow shelf
21102	51–100	8200	North Adriatic intermediate shelf
21106	10–50	4700	Central Adriatic shallow shelf
21107	51–100	10350	Central Adriatic intermediate shelf
21108	101–200	14950	Central Adriatic deep shelf
21109	201–500	3900	Central Adriatic upper slope

covered 20 survey years (i.e. excluding 1994–2001, 2014, 2017 and 2022). The taxonomic scope of the study was restricted to flatfish (order Pleuronectiformes), using the standardized abundance ($N\ km^{-2}$) for each species per haul. In total, 20 flatfish species were recorded over the filtered time series (Table S1). Out of these, we retained only flatfish species occurring in at least 60% of the years (16 species in total; Table 2), so that the analysed assemblage reflects species contributing consistently to long-term community patterns rather than species appearing only in a few isolated years. This filtering step was intended to focus the analysis on the persistent core of the assemblage, reducing the influence of sporadic occurrences and improving the comparability of multiyear spatial patterns among strata.

2.3. Environmental data

We complemented flatfish data with three environmental descriptors: benthic invertebrate biomass, bottom temperature and sea-floor substrate type. Benthic invertebrate data were obtained from benthic organisms recorded in the same MEDITS hauls and survey years as the flatfish data. Organisms were assigned to standard MEDITS benthic taxonomic groups (Anonymous, 2017; Table S2). Biomass

Table 2

Flatfish species retained for analyses. For each species, the table reports family, scientific name (genus and species), common name, author and year of description, MEDITS species code, and occurrence (%). Occurrence indicates the proportion of survey years (2002–2024; excluding 2014, 2017 and 2022) in which a species occurred at least in 1 haul.

Family	Scientific name	Common name	Author, Year	Code	Occurrence
Bothidae	<i>Arnoglossus laterna</i>	Mediterranean scaldfish	(Walbaum, 1792)	ARNO LAT	100%
	<i>Arnoglossus rupepelli</i>	Rüppell's scaldback	(Cocco, 1844)	ARNO RUP	95%
	<i>Arnoglossus thori</i>	Thor's scaldfish	Kyle, 1913	ARNO THO	100%
Citharidae	<i>Citharus linguatula</i>	Spotted flounder	(Linnaeus, 1758)	CITH MAC	100%
Cynoglossidae	<i>Symphurus nigrescens</i>	Blackish tonguesole	Rafinesque, 1810	SYMP NIG	100%
Pleuronectidae	<i>Platichthys flesus</i>	European flounder	(Linnaeus, 1758)	PLAT FLE	65%
Scophthalmidae	<i>Lepidorhombus boscii</i>	Four-spot megrim	(Risso, 1810)	LEPM BOS	100%
	<i>Lepidorhombus whiffiagonis</i>	Megrim	(Walbaum, 1792)	LEPM WHS	100%
	<i>Psetta maxima</i>	Turbot	(Linnaeus, 1758)	PSET MAX	75%
	<i>Scophthalmus rhombus</i>	Brill	(Linnaeus, 1758)	SCOH RHO	95%
	<i>Zeugopterus regius</i>	Eckström's topknot	(Bonnaterre, 1788)	PHRY REG	60%
	<i>Buglossidium luteum</i>	Solenette	(Risso, 1810)	BUGL LUT	95%
	<i>Microchirus variegatus</i>	Thickback sole	(Donovan, 1808)	MICU VAR	85%
	<i>Monochirus hispidus</i>	Whiskered sole	Rafinesque, 1814	MONO HIS	80%
Soleidae	<i>Synapturichthys kleinii</i>	Klein's sole	(Risso, 1827)	SOLE KLE	75%
	<i>Solea solea</i>	Common sole	(Linnaeus, 1758)	SOLE VUL	100%

density (kg km⁻²) for each taxonomic group was used because many benthic invertebrates, such as sponges, are difficult to quantify in terms of numbers of individuals and are typically assessed using biomass or volume (Wulff, 2001). Rare subcategories, occurring in < 5% of all hauls, were excluded to remove extremely uncommon groups and reduce zero inflation in multivariate analyses (see statistical analysis below), finally retaining seven taxonomic groups (Table S2). Bottom temperature for each haul was extracted from the MEDITS database as the near-bottom temperature recorded at the time and depth of trawling and therefore corresponds to the standardized MEDITS hauls. Seafloor substrate types (mud, sandy mud, muddy sand, sand) were obtained from the EMODnet Geology Folk-7 sediment classification (data available at <https://emodnet.ec.europa.eu/en/geology>). Flatfish distributions are known to respond primarily to bottom temperature and substrate type (Abookire and Norcross, 1998; McConnaughey and Smith, 2000). Benthic organisms may also influence flatfish habitat selection by providing physical structure for refuge and potential food resources (McConnaughey and Smith, 2000; Ryer et al., 2004). Analyses therefore focused on these three environmental descriptors. Flatfish catch data and environmental data were then matched at the haul level for the last three MEDITS years (2021, 2023 and 2024), corresponding to 323 hauls, for which all the environmental data were available.

2.4. Statistical analyses

All analyses were carried out in R (version 4.5.1) using the packages *vegan* (Oksanen et al., 2025), *indicspecies* (De Cáceres and Legendre, 2009), and *ggplot2* (Wickham, 2016). For all multivariate community analyses, flatfish abundance data were fourth root-transformed. This transformation reduced the dominance of highly abundant species, which is appropriate for Bray–Curtis-based community analyses (Clarke and Warwick, 2001; Quinn and Keough, 2002).

Two complementary analyses were conducted: (i) an analysis of the overall assemblage structure of flatfish in the different bathymetric strata using the entire study period, and (ii) an analysis of habitat associations integrating flatfish abundances with environmental data (described above) at the haul level using the three most recent years.

2.4.1. Overall flatfish assemblage composition by stratum

This analysis used the entire study period to describe the spatial structure of flatfish assemblages across MEDITS strata in the western North–Central Adriatic Sea and to identify indicator species for each stratum.

Flatfish species abundances were averaged by year and stratum and converted to relative contributions (%) per species. Each combination of

year $\times$ stratum was treated as an independent observation, such that temporal variability was incorporated into within-stratum dispersion, thereby emphasizing long-term spatial organisation across strata rather than fine-scale interannual variation. Untransformed mean assemblage composition over the study period in each stratum was visualised as stacked bar plots, providing a preliminary representation of overall flatfish community composition in each stratum.

Potential differences in flatfish community composition among strata were explored using Principal Coordinates Analysis (PCoA) based on Bray–Curtis dissimilarity, implemented with *cmdscale()* in *vegan* (eig = TRUE, k = 2). Because Bray–Curtis dissimilarities can generate negative eigenvalues in principal coordinates analysis, the percentage of variation explained by each axis was calculated relative to the sum of positive eigenvalues. Ordination scores were plotted by stratum, and 95% confidence ellipses were drawn around group centroids to summarize within-stratum variability. Formal tests for differences in community composition among strata were conducted using permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) implemented with *adonis2()* in *vegan*, with depth stratum as a fixed factor and 10 000 permutations. Because significant PERMANOVA results may reflect differences in multivariate dispersion as well as differences in group centroids, homogeneity of multivariate dispersions among strata was evaluated using *betadisper()* followed by permutation tests with *permutest()* in *vegan*, using 10 000 unrestricted permutations and requesting pairwise comparisons among strata. This allowed us to assess whether the potential differences in community composition among strata reflected changes in multivariate centroids or differences in dispersion.

Associations between individual flatfish species and the main multivariate gradients were described by projecting species onto the PCoA ordination using vector fitting (*envfit()* in *vegan*). This procedure was applied to the same transformed flatfish abundance matrix used to construct the ordination. Because the ordination was derived from this species matrix, permutation *p*-values from *envfit()* were not used as a formal selection criterion. Instead, the squared correlation coefficient (*r*²) was used to interpret species–gradient relationships. Species with *r*² $\geq$ 0.50 were retained and plotted as vectors in the ordination. This threshold was chosen to focus on species strongly aligned with the main ordination axes and to avoid overcrowding the biplots. Species–stratum associations were assessed using Indicator Species Analysis (ISA) based on the generalised IndVal index, which is the product of two components: specificity and fidelity (Dufrêne and Legendre, 1997; De Cáceres et al., 2010). Specificity was calculated as the relative mean abundance of a species within a given stratum compared to its mean abundance across all strata, thus quantifying how strongly the species' abundance is

concentrated in that stratum. Fidelity was computed as the proportion of sampling units ($year \times stratum$ combination) in which the species was present, reflecting the proportion of years in which the species was recorded within a stratum (temporal frequency). The IndVal statistic was calculated using the function *multipatt()* in the R package *indicpecies*, considering only single strata and pairwise combinations of adjacent strata ($max.order = 2$). Statistical significance was assessed using 10 000 permutations, and species with $p \leq 0.05$ were retained as indicators. This restriction was applied a priori to enhance ecological interpretability and to focus on habitat-diagnostic species rather than widespread generalists associated with large multi-stratum combinations (Dufrène and Legendre, 1997; De Cáceres et al., 2010).

2.4.2. Flatfish habitat associations

This analysis used haul-level data from the last three MEDITS surveys (2021, 2023, and 2024) to describe habitat associations of flatfish assemblages along gradients of bottom temperature, seafloor substrate type, and benthic invertebrate biomass.

The spatial distribution of sampling effort was comparable among 2021, 2023, and 2024, with 120 hauls conducted in each survey year across the six depth strata. For the habitat-association analyses, hauls containing at least one flatfish were matched with the available benthic data, resulting in a final dataset of 323 hauls. All six depth strata were represented in each survey year ensuring consistent spatial coverage across years (Table S3).

Bray–Curtis dissimilarities based on haul-level flatfish abundances were subjected to PCoA using *cmdscale()* in *vegan* ($eig = TRUE, k = 2$), and the resulting ordination was used as a common multivariate space. Vector fitting (*envfit()* in *vegan*) was then applied to relate flatfish species and environmental variables (benthic invertebrate biomass, bottom temperature and substrate type) to this ordination. For flatfish, *envfit()* was applied to the transformed abundance matrix, and species with $r^2 \geq 0.30$ were retained and plotted as vectors. This threshold was chosen to focus on species showing at least moderate alignment with the main ordination axes. For benthic invertebrates, *envfit()* was used on the transformed biomass data, treating the biomass of each taxonomic group as a continuous environmental variable, and identified groups significantly associated with the ordination ($p \leq 0.05$), which were represented as vectors indicating correlations with flatfish community structure. Bottom temperature was likewise included as a continuous environmental variable in *envfit()*, producing a single vector representing the gradient of increasing temperature in ordination space. Seafloor substrate types (mud, sandy mud, muddy sand, sand) were represented by the centroids of hauls assigned to each class, computed as the mean PCoA scores (PCoA1, PCoA2) within each substrate category. These centroids were used for descriptive visualization of substrate-related patterns and were not subjected to formal significance testing in the same way as continuous *envfit* variables. Finally, a PERMANOVA with stratum as a fixed factor was used to test for differences in flatfish community composition among strata, using 10 000 unrestricted permutations.

Potential collinearity among depth, bottom temperature, and substrate type was evaluated. The association between depth and bottom temperature was first quantified using Pearson and Spearman correlation coefficients to assess their linear and monotonic relationships, respectively. A full distance-based redundancy analysis (dbRDA; *dbRDA()* in *vegan*) was then fitted to the Bray–Curtis dissimilarity matrix of flatfish abundances, with depth, bottom temperature, and substrate type included as explanatory variables. A square-root correction of the Bray–Curtis dissimilarities ($\sqrt{dist} = TRUE$) was applied to improve their Euclidean properties (Legendre and Anderson, 1999). Variance inflation factors (*vif.cca()* in *vegan*) were calculated from the full dbRDA model to assess multicollinearity among the three predictors. Variation partitioning (*varpart()* in *vegan*) based on adjusted R^2 values was then used to quantify the unique and shared fractions of explained variation among the three environmental predictors (Peres-Neto et al., 2006). The

significance of the unique fractions was assessed using partial dbRDA models with the remaining predictors included as conditioning variables (*Condition()*), using 9 999 permutations restricted within survey year to account for temporal dependence among hauls.

To evaluate whether results were sensitive to data spatial resolution, the ordination was replicated using $year \times stratum$ averaged flatfish abundances from the 2021, 2023, and 2024 surveys. The relative positioning of depth strata between haul-level and averaged ordinations was then compared using Procrustes analysis (*procrustes()* and *protest()* in *vegan*, 9 999 permutations).

3. Results

3.1. Overall flatfish assemblage composition by stratum

Mean flatfish assemblage composition based on untransformed mean abundances differed among strata (Fig. 2). Across most strata, assemblages were dominated by two or three species, whereas the central deep-shelf assemblage (stratum 21108) showed a more even distribution of abundances among multiple species. In all strata, except for the central upper slope stratum (21109), *A. laterna*, *A. thori* and *C. linguatula* accounted for a substantial fraction of the percentage composition. In the northern shallow shelf stratum (10–50 m; stratum 21101), the assemblage was strongly dominated by *A. thori* ($\approx 45\%$), with *A. laterna* and *C. linguatula* contributing a further $\approx 16\%$ and 13% , respectively. Other species such as *P. flesus*, *S. kleinii*, *B. luteum*, *M. hispidus* and *Z. regius* were present but individually contributed less than about 5% of the composition. In the central shallow shelf stratum (10–50 m; stratum 21106), *A. laterna* became the dominant species ($\approx 67\%$), followed by *C. linguatula* (14%), whereas other species were rare or absent. In the northern and central intermediate shelf strata (51–100 m; 21102 and 21107), *C. linguatula*, *A. laterna* and *A. thori* remained numerically important (each contributing roughly 15–30% depending on the stratum), with a predominance of *B. luteum* in stratum 21102. In the central deep-shelf-upper-slope strata (21108 and 21109), the assemblage was dominated by deeper-water species: in the deep shelf (21108), *A. rueppelii*, *L. whiffiagonis*, *L. boscii* and *S. nigrescens* together contributed about 50% of total abundance, whereas in the upper slope (21109) the community was strongly skewed towards *A. rueppelii* ($\approx 57\%$), followed by *L. boscii* and thereafter by *L. whiffiagonis* and *S. nigrescens* accounting for most of the remaining composition.

PCoA showed a separation of flatfish assemblages among strata (Fig. 3). The first two ordination axes explained 45.1% and 15.1% of the total variance, respectively. The first PCoA axis primarily reflected the separation between shallow-shelf and deep-shelf-upper-slope assemblages, whereas the second axis captured additional variation in community composition among samples, including spatiotemporal variation within individual strata. Samples from the northern and central shallow shelf strata (21101 and 21106; 10–50 m) were mainly positioned on the left side of the ordination plot, whereas samples from the central deep-shelf-upper-slope strata (21108 and 21109; 101–500 m) clustered toward the right side. Intermediate northern and central intermediate strata (21102 and 21107; 51–100 m) occupied transitional positions between the shallow and deep assemblages. The 95% confidence ellipses showed partial overlap between adjacent strata but remained largely separated across the full depth range. PERMANOVA confirmed that flatfish community composition differed among depth strata ($R^2 = 0.73$, $F_{5,114} = 63.20$; $p < 0.001$; Table S4), indicating significant separation in multivariate centroids. A permutation test for homogeneity of multivariate dispersions (PERMDISP) further revealed significant differences in within-stratum dispersion around centroids ($F_{5,114} = 13.97$; $p < 0.001$; Table S5A). Pairwise comparisons of dispersion showed that stratum 21106 had significantly higher dispersion than all other strata ($p \leq 0.002$), whereas dispersion did not differ significantly between the two deepest strata (21108 vs 21109) or between the northern and central intermediate shelf strata (21102 vs 21107; Table S5B). Thus, the

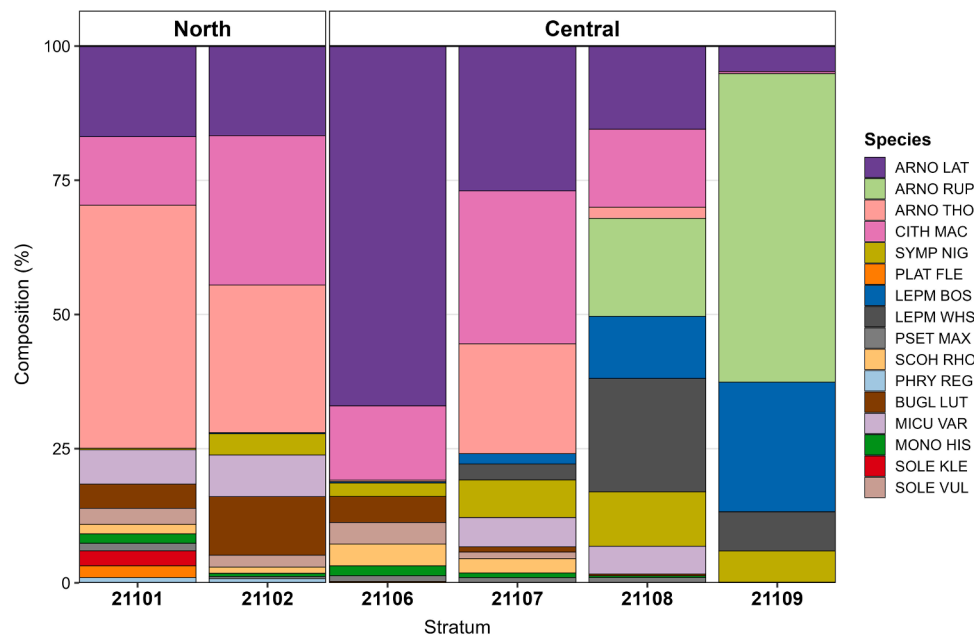


Fig. 2. Mean flatfish assemblage composition by depth stratum in the northern and central areas. Bars show the relative contribution (%) of each of the 16 retained flatfish species to total assemblage composition within each stratum. Percentages were calculated from untransformed mean abundances ($N\ km^{-2}$) averaged across all survey years included in the study within each stratum. Flatfish species abbreviations are defined in Table 2, and MEDITS stratum codes and corresponding depth ranges are provided in Table 1.

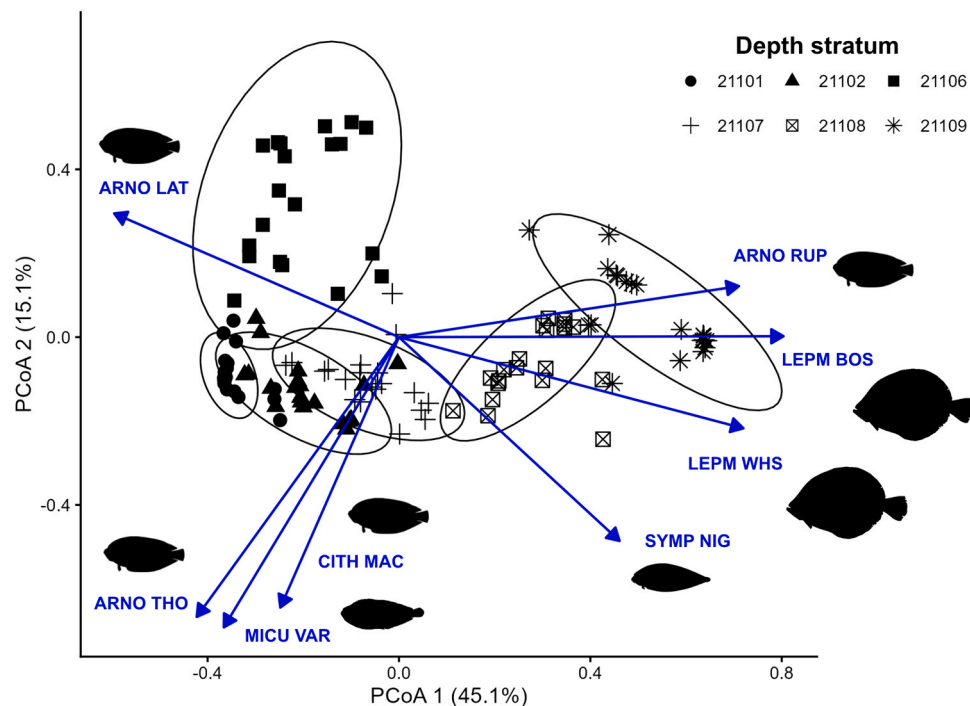


Fig. 3. Principal Coordinates Analysis (PCoA) of flatfish assemblages across MEDITS strata in the North–Central Adriatic Sea (GSA17), based on Bray–Curtis dissimilarities of abundance data. Each point represents one year, and ellipses denote 95% confidence intervals for each stratum. Flatfish species vectors were fitted using the *envfit* procedure. Blue arrows indicate flatfish species with coefficients of determination $r^2 \geq 0.50$; arrow direction represents the gradient of increasing relative abundance, and arrow length reflects the strength of the correlation with the ordination axes. Complete *envfit* results for all flatfish species are reported in Table S6. Flatfish species abbreviations are defined in Table 2, and MEDITS stratum codes and corresponding depth ranges are provided in Table 1. Icons were obtained from the PhyloPic database (<https://www.phylopic.org>, accessed 8 September 2026).

observed ordination pattern reflects both differences in assemblage centroids and uneven within-stratum variability.

The *envfit* projection of flatfish species onto the PCoA ordination indicated that the distribution of several species was well explained by

the main multivariate gradients (Fig. 3; Table S6). Among these, *C. linguatula*, *L. boscii*, *A. thori* and *L. whiffiagonis* displayed the highest coefficients of determination ($r^2 > 0.70$; Table S6).

Species associated with positive PCoA1 values included *L. boscii*,

L. whiffiagonis, *S. nigrescens* and *A. rueppelii*, corresponding to the region of the ordination space mainly occupied by the deepest strata (21108–21109). Although these species shared positive scores on PCoA1, they differed along PCoA2: *A. rueppelii* showed positive PCoA2 values, *L. boscii* was positioned near zero, *L. whiffiagonis* displayed slightly negative values, and *S. nigrescens* was oriented toward strongly negative PCoA2 scores. In contrast, species associated with negative PCoA1 values, corresponding to northern shallow and central intermediate shelf strata (21101–21107), included *A. thori*, *M. variegatus* and *C. linguatula*, which showed negative scores on both PCoA1 and PCoA2, whereas *A. laterna* combined negative PCoA1 with positive PCoA2 values.

Indicator Species Analysis revealed significant associations between flatfish species and specific strata or pairs of adjacent strata ($p < 0.001$; Table 3). The northern shallow shelf (10–50 m; stratum 21101) supported the highest number of indicators ($n = 6$). *S. kleinii* and *P. flesus* showed the strongest associations (IndVal = 0.87 and 0.78), with most of their abundance concentrated in this stratum (specificity = 0.94–1.00) and occurrence in the majority of years (fidelity = 0.65–0.75). Smaller flatfish such as *B. luteum* and *M. hispidus* exhibited moderate abundance concentration (specificity = 0.51–0.63) but high interannual frequency of occurrence (fidelity = 0.70–0.90). By contrast, *Z. regius* combined relatively high abundance concentration (specificity = 0.72) with lower frequency of occurrence (fidelity = 0.50), while *P. maxima* displayed the weakest association among the indicator species of this stratum (IndVal = 0.57).

Several species were associated with pairs of adjacent strata, reflecting transitional depth ranges. The northern shallow-to-intermediate shelf group (21101–21102) included *A. thori*, *M. variegatus*, and *C. linguatula* (IndVal = 0.70–0.84). *A. thori* showed relatively high abundance concentration together with complete frequency of occurrence (specificity = 0.70, fidelity = 1.00), whereas *M. variegatus* exhibited slightly lower values for both metrics (specificity = 0.59, fidelity = 0.80); *C. linguatula* also occurred in all years (fidelity = 1.00) but had the lowest abundance concentration among the three species (specificity = 0.48).

The combination of the northern and central shallow shelf strata (21101–21106) included *S. solea*, *S. rhombus*, and *A. laterna* (IndVal = 0.65–0.73). *S. solea* and *S. rhombus* showed moderate abundance concentration and frequency of occurrence (specificity = 0.64–0.70; fidelity = 0.72–0.77). In contrast, *A. laterna* occurred in all years (fidelity = 1.00) but displayed lower abundance concentration (specificity = 0.42).

The central intermediate-to-deep shelf transition (21107–21108) was represented by *S. nigrescens* (IndVal = 0.70), which exhibited very high occurrence frequency (fidelity = 1.00) but only moderate

abundance concentration (specificity = 0.50). Finally, the central deep-shelf–upper-slope combination (21108–21109) included *L. boscii*, *L. whiffiagonis*, and *A. rueppelii* (IndVal = 0.88–0.94). *L. boscii* and *L. whiffiagonis* showed high abundance concentration and frequency of occurrence (specificity = 0.83–0.88; fidelity = 1.00–0.95), while *A. rueppelii* exhibited complete abundance concentration with slightly lower frequency (specificity = 1.00; fidelity = 0.77).

3.2. Flatfish habitat associations

At the haul level, flatfish assemblages sampled in 2021, 2023 and 2024 showed organisation along habitat gradients (Fig. 4). The first two PCoA axes, derived from Bray–Curtis dissimilarities, explained 32.3% and 17.6% of the total variation, respectively. Hauls from the northern and central shallow shelf strata (21101 and 21106; 10–50 m) were mainly located in the lower part of the ordination and towards negative values of PCoA1, whereas hauls from the deepest central strata (21108 and 21109; 100–500 m) clustered in the upper-left part of the plot, at high PCoA2 and negative PCoA1 scores. Northern and central intermediate shelf strata (21102 and 21107; 51–100 m) occupied transitional positions, overlapping partly with both the shallow and deep clusters. PERMANOVA confirmed that depth stratum significantly affected flatfish community composition at the haul level ($R^2 = 0.32$, $F_{5317} = 29.70$; $p < 0.001$; Table S7). Envfit identified four flatfish species that were strongly associated with the ordination ($r^2 = 0.32$ –0.76, $p = 0.001$; Fig. 4; Table S8). *C. linguatula* ($r^2 = 0.76$) and *A. laterna* ($r^2 = 0.76$) showed opposing gradients along PCoA1: *A. laterna* was linked to shallow coastal stations, whereas *C. linguatula* increased towards positive scores at more offshore shelf stations. *L. boscii* ($r^2 = 0.58$) and *L. whiffiagonis* ($r^2 = 0.32$) were mainly structured along PCoA2 and characterised hauls from the deepest strata (21108–21109).

Five benthic invertebrate subcategories were likewise significantly related to the ordination ($r^2 = 0.06$ –0.16, all $p = 0.001$; Fig. 4; Table S8). Vectors for decapod crustaceans (B) and gastropods (Emg) were oriented towards the lower-left sector, where shallow northern shelf hauls with negative PCoA1 scores and high *A. laterna* abundance predominated. In contrast, echinoderms (Eec), tunicates (Etu), and sponges (Esp) pointed towards the lower-right sector, overlapping mainly with northern and central intermediate shelf strata (21102–21107) and the *C. linguatula* vector.

Bottom temperature (envfit vector T; $r^2 = 0.11$, $p = 0.001$; Table S8) was significantly aligned with the ordination, increasing from the deepest strata (21108–21109), characterised by *L. boscii* and *L. whiffiagonis*, toward northern and central shallow shelf strata (21101, 21106), where *A. laterna* and *C. linguatula* were most frequent.

Table 3

Results of the indicator species analysis showing significant associations of flatfish species with individual or combined strata. Reported are stratum, species codes, specificity, fidelity, IndVal statistic, and associated p-values. Significance was assessed using 10 000 permutations. MEDITS stratum codes and corresponding depth ranges are provided in Table 1.

Stratum	Species	Code	Specificity	Fidelity	IndVal	p
21101	<i>Synapturichthys kleinii</i>	SOLE KLE	1.00	0.75	0.87	< 0.001
	<i>Platichthys flesus</i>	PLAT FLE	0.94	0.65	0.78	< 0.001
	<i>Buglossidium luteum</i>	BUGL LUT	0.51	0.90	0.68	< 0.001
	<i>Monochirus hispidus</i>	MONO HIS	0.63	0.70	0.67	< 0.001
	<i>Zeugopterus regius</i>	PHRY REG	0.72	0.50	0.60	< 0.001
	<i>Psetta maxima</i>	PSET MAX	0.51	0.65	0.57	< 0.001
21101 + 21102	<i>Arnoglossus thori</i>	ARNO THO	0.70	1.00	0.84	< 0.001
	<i>Microchirus variegatus</i>	MICU VAR	0.59	0.80	0.70	< 0.001
	<i>Citharus linguatula</i>	CITH MAC	0.48	1.00	0.70	< 0.001
	<i>Solea solea</i>	SOLE VUL	0.70	0.77	0.73	< 0.001
21101 + 21106	<i>Scophthalmus rhombus</i>	SCOH RHO	0.64	0.72	0.68	< 0.001
	<i>Arnoglossus laterna</i>	ARNO LAT	0.42	1.00	0.65	< 0.001
	<i>Symphurus nigrescens</i>	SYMP NIG	0.50	1.00	0.70	< 0.001
21107 + 21108	<i>Lepidorhombus boscii</i>	LEPM BOS	0.88	1.00	0.94	< 0.001
21108 + 21109	<i>Lepidorhombus whiffiagonis</i>	LEPM WHS	0.83	0.95	0.88	< 0.001
	<i>Arnoglossus rueppelii</i>	ARNO RUP	1.00	0.77	0.88	< 0.001

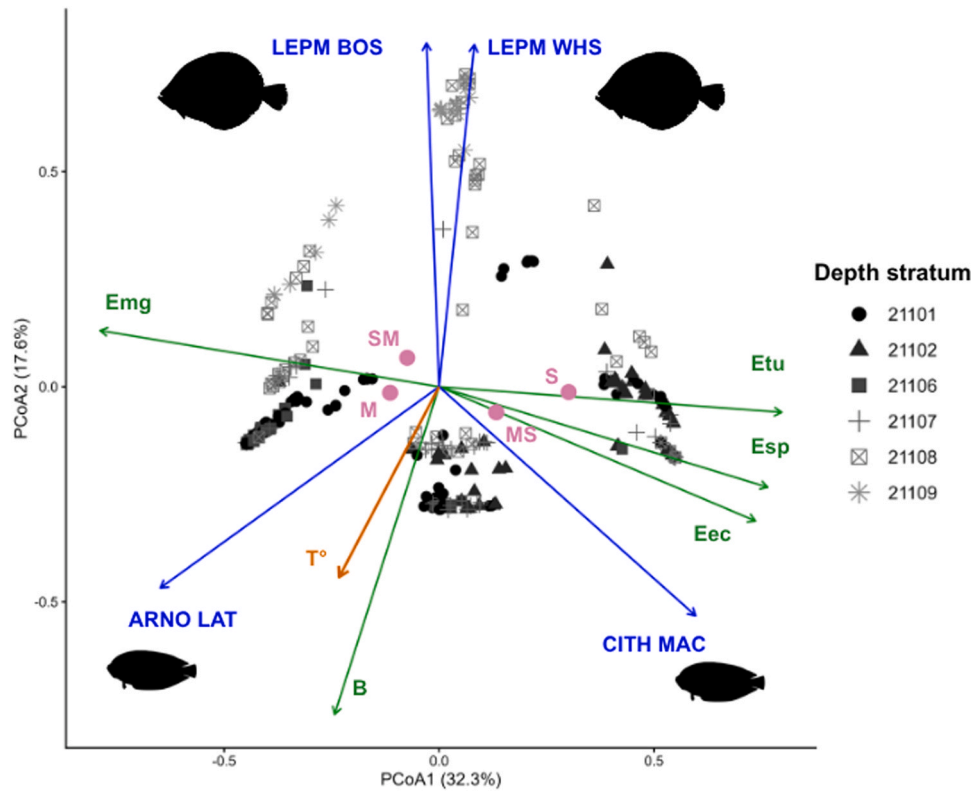


Fig. 4. Principal Coordinates Analysis (PCoA) of flatfish assemblages based on haul-level abundances ($N\ km^{-2}$) from the 2021, 2023, and 2024 MEDITS surveys in the North–Central Adriatic Sea (GSA17). Each point represents a haul, with symbols indicating spatial strata. Envfit vectors are fitted for flatfish species (blue arrows; CITH MAC, ARNO LAT, LEPM BOS, LEPM WHS, retained based on $r^2 \geq 0.30$), benthic invertebrate subcategories (dark green arrows: B = Decapoda, Emg = Mollusca Gastropoda, Etu = Tunicata, Esp = Porifera, Eec = Echinodermata; $p \leq 0.001$), substrate-type centroids (magenta circles: M = mud, SM = sandy mud, MS = muddy sand, S = sand), and bottom temperature ($T^\circ C$; orange arrow). For envfit vectors, arrow direction indicates the gradient of increasing fitted values, and arrow length is proportional to the strength of association with the ordination (r^2). Full envfit results and substrate centroids are reported in Table S8. Icons were obtained from the PhyloPic database (<https://www.phylopic.org>, accessed 8 September 2026). Flatfish species abbreviations are defined in Table 2, benthic invertebrate abbreviations in Table S2, and MEDITS stratum codes and corresponding depth ranges are provided in Table 1.

Centroids of seafloor substrate types showed a consistent spatial arrangement along PCoA1 (Fig. 4; Table S8). Mud and sandy mud centroids were located on the left side of the ordination, overlapping with hauls where *A. laterna*, *L. bosci* and *L. whiffiagonis* were most frequent, whereas muddy sand and sand were positioned on the right side, in the sector associated with intermediate–depth hauls characterised by higher occurrence of *C. linguatula*. Because substrate categories were represented as multivariate centroids, they were not associated with envfit r^2 or p -values, and their role is therefore descriptive rather than based on formal significance tests.

Depth and bottom temperature were moderately negatively correlated (Pearson $r = -0.53$; Spearman $\rho = -0.79$), whereas variance inflation factors indicated limited multicollinearity among environmental predictors (maximum VIF = 1.47; Table S9A). The full dbRDA model explained 19.1% of the variation in flatfish assemblage composition (adjusted $R^2 = 0.18$). Variation partitioning showed that depth, bottom temperature and substrate each explained significant independent fractions of assemblage variation (all $p < 0.001$), whereas shared fractions were small, with the largest occurring between depth and bottom temperature (Table S9B).

The sensitivity analysis comparing the PCoA positions of stratum centroids between haul-level and $year \times stratum$ averaged ordinations for the 2021, 2023 and 2024 surveys indicated a relatively high Procrustes correlation ($r = 0.77$). Although the test fell just above the conventional significance threshold ($p = 0.054$; Table S10), the magnitude of the correlation suggested similar overall structure across resolutions.

4. Discussion

The analyses revealed a clear compositional turnover in flatfish assemblages in late spring–summer across the North–Central Adriatic Sea, consistently observed both in long-term stratum-averaged data and in haul-level samples from the most recent surveys. Although depth-related distribution in selected Mediterranean flatfish species has already been recognised (Sartor et al., 2002), our study shows that flatfish assemblage turnover in the North–Central Adriatic Sea is not explained by bathymetry alone. Bottom temperature and seafloor substrate type were also associated with flatfish assemblage organisation, and contributed mostly independently, despite some collinearity among predictors. Flatfish assemblages were also significantly associated with gradients in benthic invertebrate biomass, highlighting the additional influence of biotic characteristics on fish community organisation. Along the habitat gradients considered in this study (bathymetry, bottom temperature, substrate type, benthic invertebrate biomass composition), assemblages shifted from productive river-influenced shallow shelf communities, largely characterised by shallow-water soleids, pleuronectids, bothids and scophthalmids, to increasingly specialised central deep-shelf and upper-slope assemblages, where deep-water scophthalmids and cynoglossids became more prominent. Differences also emerged between the northern and central shallow shelf communities, with the central shelf area characterised by a comparatively less differentiated assemblage despite the same depth range.

The northern shallow shelf (stratum 21101, 10–50 m) supported the highest number of indicator species. Their identification as indicator species reflects their generally higher relative abundances and more

consistent occurrence in this stratum, rather than their complete absence from other strata. This area is strongly influenced by Po River discharge and is characterised by fine muddy and sandy-mud substrates, high nutrient inputs, seasonal stratification, and recurrent near-bottom hypoxia (Degobbi et al., 2000; Cozzi and Giani, 2011). During late spring-summer, bottom temperatures are relatively warm (Artegiani et al., 1997), and the elevated productivity (Degobbi et al., 2000) may contribute to favourable feeding conditions for benthophagous flatfish. At the same time, muddy and sandy-mud shallow bottoms may provide favourable feeding and resting habitat for species associated with river-influenced shallow grounds (Cabral, 2002; Amara et al., 2004; Amaral and Cabral, 2004). The taxonomic composition of stratum 21101 is consistent with a shallow habitat under strong riverine influence, where substrate characteristics, elevated productivity, and marked seasonal environmental variability likely favour taxa able to exploit productive but fluctuating conditions. Despite this environmental dynamism, the northern shallow shelf provides a recurrent habitat template that supports a comparatively consistent flatfish assemblage through time.

Moving southward, the central shallow shelf (stratum 21106, 10–50 m) shared much of the species pool with the northern shelf but displayed a different balance among families and substantially higher interannual dispersion, indicating stronger temporal variability in assemblage structure. This shallow stratum is also characterised by warm bottom waters in late spring-summer (Artegiani et al., 1997) and moreover influenced by the southward-flowing coastal plume generated by multiple Italian rivers and by intense bottom-trawling disturbance, resulting in fluctuating environmental conditions (Russo and Artigiani, 1996; Cozzi and Giani, 2011; Eigaard et al., 2017).

Both shallow strata (21101 and 21106) were associated with gastropods and decapod crustaceans, suggesting similarity in their soft-bottom invertebrate community composition. However, this similarity did not correspond to equivalent flatfish assemblages. Three taxa associated with shallow soft-bottom habitats, *A. laterna*, *S. solea*, and *S. rhombus*, consistently characterised the combined shallow-shelf domain. Nevertheless, the northern shallow shelf (stratum 21101) supported a more differentiated assemblage and greater species richness, whereas the central shallow shelf (stratum 21106) showed comparatively higher temporal variability and lower assemblage specificity and diversity. These differences may reflect variation between the two shallow shelf domains in environmental stability and disturbance regimes. In particular, the central shallow shelf may be more susceptible to environmental fluctuations and anthropogenic disturbance, including bottom trawling, which is widespread in the region (Eigaard et al., 2017), potentially contributing to its lower assemblage diversity. However, the differences between these two strata may also partly reflect sampling design, as the northern shallow shelf covers a substantially larger area than the central shallow shelf and is sampled by a greater number of hauls, increasing the likelihood of detecting rare species and identifying a larger number of indicator taxa. Taken together, the contrast between the two shallow shelf strata indicates that flatfish habitat associations in the Adriatic are not explained by depth alone; rather, similar bathymetry may correspond to distinct habitat settings and different flatfish assemblage organisation.

A. thori, *C. linguatula*, and *M. variegatus* were the species most closely associated with shallow and intermediate northern shelf grounds (strata 21101–21102), a pattern consistent with their broader occurrence on soft-bottom continental-shelf habitats, particularly muddy and sandy-mud substrates, across the Mediterranean (Sartor et al., 2002; Bayhan et al., 2009).

Northern and central intermediate shelf strata (21102 and 21107, 50–100 m) formed a transitional area between shallow and deep assemblages. These two strata supported broadly similar flatfish assemblages, although the central stratum (21107) also included a small component of species associated with deeper habitats. Along this portion of the gradient, substrates shifted towards muddier sand habitats,

bottom temperatures became more moderate than in the shallow shelf and benthic communities showed increased contribution of echinoderms, sponges, and tunicates. This pattern likely reflects a broader transition in habitat conditions along the intermediate shelf, where changes in substrate texture, benthic composition, and bottom hydrology jointly define suitable habitat conditions.

Further along the gradient, the occurrence of *S. nigrescens* in the transition between central intermediate and deep shelf strata (21107–21108) is consistent with its association with outer shelf environments and fine substrates (Bustos-Salvador et al., 2015), supporting its role as a transitional species between shelf and deep-slope assemblages.

At the opposite end of the gradient, the central deep-shelf and upper-slope strata (21108–21109; 101–500 m) were characterised by predominantly muddy or sandy-mud substrates, colder late spring-summer bottom water and reduced seasonal variability typical of the deep shelf and upper slope (Artegiani et al., 1997). These strata supported comparatively species-poor assemblages dominated by deep-water specialist taxa. However, this pattern may also partly reflect the lower number of hauls compared with the other strata. The concentration of *Lepidorhombus* spp. and *A. rueppelii* within this habitat domain is consistent with their known affinities for deeper shelf and upper-slope environments (Sánchez et al., 1998; Sartor et al., 2002; Vassilopoulou, 2006). The co-occurrence of both *Lepidorhombus* species within the same strata suggests shared habitat preferences. Within this habitat, reported differences in diet composition between the two species (Morte et al., 1999; Vassilopoulou, 2006) may facilitate resource partitioning. More broadly, the association of these assemblages with comparatively cooler and environmentally stable habitats suggests that future changes in bottom thermal conditions could alter the spatial organisation of deep-shelf flatfish communities in the Adriatic Sea.

In contrast to the substantial overlap observed within the genus *Lepidorhombus*, the three species of the genus *Arnoglossus* showed a more distinct spatial arrangement along habitat gradients, suggesting fine-scale partitioning within the Adriatic shelf system. Within the genus, *A. thori* and *A. laterna* showed partial spatial overlap but distinct habitat associations, with the former more closely linked to northern shallow and intermediate shelf grounds and the latter to shallow muddy northern and central shallow shelf habitats. By contrast, *A. rueppelii* was separated more clearly by depth, where it occurs on muddier habitats at greater depths than its congeners (Froese and Pauly 2024). Together, these patterns suggest that assemblage organisation within this genus is maintained through a combination of fine-scale habitat differentiation and bathymetric segregation.

Comparable depth-related turnover in demersal fish assemblages has been widely documented, for example in the central Mediterranean Sea (Colloca et al., 2003), the northern Aegean Sea (Labropoulou and Papaconstantinou, 2004), and the northwestern Mediterranean (Gaertner et al., 2005). In the Adriatic, such turnover is expressed not only across depth strata, but also within the same depth range, especially on the shallow shelf. Our findings indicate that demersal assemblage organisation within productive shelf ecosystems cannot be inferred from bathymetry alone, as similar depth domains may support distinct flatfish assemblages associated with different local conditions, including the degree of riverine influence and potentially disturbance regimes. For example, bottom trawling is known to modify benthic habitats and influence demersal community composition (Jennings and Kaiser, 1998). The Adriatic Sea is among the most intensively bottom-trawled areas in European waters, with spatially heterogeneous fishing pressure across soft-bottom habitats (Eigaard et al., 2017; Russo et al., 2020). However, available studies do not provide fishing-pressure estimates at a spatial resolution directly corresponding to the depth strata considered here, preventing us from assessing whether fishing disturbance differs among strata.

In our study, environmental descriptors each explained only a moderate fraction of the multivariate variation, but together they

contributed to the consistent spatial organisation of flatfish assemblages. Such moderate proportions of explained variation are expected in heterogeneous shelf ecosystems, where community structure emerges from the combined influence of multiple environmental drivers together with local variability (Pranovi et al., 2000; Simonini et al., 2004; Djakovac et al., 2015). The inclusion in future studies of additional parameters, such as fishing effort, known to impact benthic communities (Jennings and Kaiser, 1998; Pranovi et al., 2000; Eigaard et al., 2017), could potentially increase the explained variation of the models and improve our understanding of the spatial organisations of flatfish communities in the Adriatic Sea.

By moving beyond single-species analyses and adopting an assemblage-level framework, our results help define the broader structure of flatfish communities, their co-occurrence patterns, and the environmental factors with which these assemblages are associated, in line with the view that community-level approaches are particularly useful for describing collective ecological patterns and shared environmental responses (Wisiz et al., 2013; Ovaskainen et al., 2017). This study also provides an ecosystem-oriented baseline for interpreting future reorganisation of demersal communities in the Adriatic Sea. In the context of ongoing environmental change and increasing anthropogenic pressure on Mediterranean shelf ecosystems, long-term standardized surveys such as MEDITS may play an increasingly important role in detecting shifts in assemblage composition, habitat associations, and community turnover through time.

The present results represent a snapshot of the flatfish assemblages in late spring-summer, while the situation may differ at other times of the year, given the life cycle of the species and the marked seasonal hydrographic variability of the Adriatic Sea (Artegiani et al., 1997). Extending standardized sampling to other periods would be especially valuable for testing potential seasonal spatial redistribution and different habitat associations. Future studies could also expand this framework by incorporating additional environmental descriptors, such as productivity proxies or fishing pressure metrics, to further explain the relative contribution of physical and anthropogenic drivers to flatfish community structure.

These findings highlight the importance of assemblage-level approaches for interpreting habitat heterogeneity and ecosystem organisation, as well as for establishing monitoring baselines under ongoing climate and anthropogenic change in productive and heavily exploited shelf ecosystems.

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CRedit authorship contribution statement

Erica Genoni: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Alessandra Anibaldi:** Writing – review & editing, Data curation. **Chiara Manfredi:** Writing – review & editing, Data curation. **Michele Casini:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors have no conflicts of interest to declare.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.rsma.2026.105459](https://doi.org/10.1016/j.rsma.2026.105459).

Data availability

The survey data were collected within the EU Data collection Framework and are available upon official request to the Ministero dell’Agricoltura, della Sovranità Alimentare e delle Foreste (MASAF).

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