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PRIMARY RESEARCH PAPER

# Structural and functional variations in macrobenthic assemblages impacted by fishing dredges in the soft bottoms of the southern Adriatic Sea during the COVID-19 lockdown

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**Abstract** Macrobenthic assemblages on shallow soft bottoms exploited by fishing hydraulic dredges in the Gulf of Manfredonia (Southern Adriatic Sea) were investigated before the COVID-19 lockdown (2018–2019) and during the fishing closure caused by lockdown restrictions (June 2020). Standardized abundance data (N/100m$^2$) of benthic species from fishery-independent monitoring surveys were analysed. Fishing effort and environmental variables were obtained from fishermen's reports and the Copernicus Marine Service, respectively. Temporal changes in diversity, structural and functional traits were analysed through alpha diversity indices and Biological Trait Analysis. Benthic diversity increased in 2020, while the total abundance declined over time. Fishing effort influenced the macrobenthic assemblage in 2018 and 2019, while flooding and related environmental changes impacted soft bottoms in 2020, masking effects expected from the fishing ban due to COVID-19 restrictions, such as the recovery of commercial stocks. Species without protective structures were abundant in 2018, while shell-protected ones increased in 2019. By 2020, small and short-lived species were prevalent, while bioturbators, sessile species and suspension feeders declined. Overall, sudden and impactful natural events affecting seabed sediments appear to shape macrobenthic assemblages more than forced fishing closures, highlighting the need for an ecosystem-based management approach in the management of fishing benthic resources.

**Keywords** Commercial bivalves · Biological traits analysis-BTA · Benthic diversity · Hydraulic dredges

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## Introduction

Marine-coastal areas are subjected to multiple natural and anthropogenic pressures that interact in complex ways, affecting the ecological dynamics of marine ecosystems (Korpinen et al., 2021). Among human activities, the mechanical harvesting of shellfish from soft bottom habitats represents a significant socio-economic sector (Mora et al., 2009; Scarcella & Cabanelas, 2016), as well as a critical human driver of ecological change, influencing the structure and diversity of benthic communities and the stability of ecosystem functioning (Thrush & Dayton, 2002; Legare et al., 2020). In particular, the use of hydraulic dredges in bivalve fisheries on infralittoral soft bottoms is a critical factor in the alteration of benthic communities, which has direct and indirect impacts on their ecological status. Moreover, the overexploitation of commercial bivalve stocks can negatively affect the juvenile recruitment in wild populations, while mechanical damage caused by dredging can result in physical damage to other species in benthic communities, contributing to the alteration of the ecosystem functioning (Jennings & Reynolds, 2000; Løkkeborg, 2005). However, negative effects can also be induced by other natural and human factors, especially on the coastal marine seabeds, which are high-energy environments subject to multiple stressors, such as ocean warming, salinity variations and organic pollution (Carrier-Belleau et al. 2021). Benthic species are relevant bioindicators due to their sessile or sedentary habits and exposure to a wide range of pressures, such as high levels of organic matter and contaminants as well as human activities (Jayachandran et al., 2022). Their persistence makes them biological archives that integrate a wide range of environmental events and anthropogenic impacts over time. Therefore, benthic communities are very useful for assessing the Good Environmental Status of the marine-coastal ecosystems, as required by the European Water Framework Directive (Muxika et al., 2007).

In the Mediterranean Sea, benthic communities are subjected to significant fishing pressure, which interacts in complex ways with environmental variability and other human drivers at different temporal scales (Morello et al., 2006). This is particularly evident on shallow, soft bottom areas subjected to fishing, where benthic species are affected by mechanical stress due to fishing activities such as trawling (Mangano et al., 2014) and dredging (Urra et al., 2017; Baeta et al., 2021). The cumulative effects of environmental factors and fishing, acting at the ecosystem level with irregular patterns, could lead to structural changes in marine ecosystems, which may increase ecological complexity (Carrier-Belleau et al., 2021). In this sense, during the COVID-19 lockdown, the restrictions of human activities, including fisheries using towed gears, led to a temporary shift in anthropogenic pressures, affecting marine resources and the ecosystem traits (Russo et al., 2021; Mosbahi et al., 2022). Indeed, in the Adriatic Sea, positive effects were observed for several demersal commercial stocks (such as the common sole and mantis shrimp) in response to the decrease in fishing pressure (Scarcella et al., 2022). However, other commercial resources showed declining conditions after the COVID-19 lockdown, such as cuttlefish *Sepia officinalis* Linnaeus, 1758 and deep-water rose shrimp *Parapenaeus longirostris* (Lucas, 1846) stocks, signalling evidence of conflicting dynamics between the reduction in fishing pressure and climate variables acting on a large spatial scale (e.g. temperature, dissolved oxygen), which were therefore scarcely affected by the COVID-19 lockdown restrictions (Coro et al., 2022).

Considering the benthic resources, positive effects for the benthic fauna were observed in fishing grounds exploited by hydraulic dredges for clam harvesting in the northern Adriatic Sea in 2019 and 2020. This included an increase in benthic biodiversity and the recovery of the striped venus clam *Chamelea gallina* (Linnaeus, 1758) stocks from a condition of high exploitation (Nepote et al., 2022). Thus, the temporary fishing ban during the COVID-19 lockdown could be associated with positive changes in benthic communities previously impacted by mechanical harvesting on shallow soft bottoms. In particular, the reduction of impacts appears to favour an increase in taxonomical diversity of benthic assemblages. In addition, after a recovery period, benthic communities may be characterized by larger sessile organisms, mostly infauna, with medium and long lifespans, with a regular occurrence of several feeding guilds (Kaiser et al., 2006). However, the recovery time of benthic communities can also vary depending on the type, duration and intensity of the fishing impact, showing complex ecological responses (Lambert et al., 2014). Therefore, responses and changes in benthic assemblages should be further investigated, especially in shallow soft bottom habitats where multiple stressors co-occur with different patterns of combined impacts. Biological Trait Analysis (BTA) is a useful analytical approach to better understand the relationships between organisms and ecosystem functioning (Bremner et al., 2006, 2008; Gagic et al., 2015), especially in a multiple stressor context. BTA combines structural data of a faunal community (i.e. species abundances) with the information on functional features of the species (Törnroos & Bonsdorff, 2012). The use of species composition alone might be inadequate for investigating processes that sustain an ecological system (Diaz & Cabido, 2001), since the ecosystem processes are determined by the functional traits of the organisms involved, rather than by taxonomic identity (Grime, 1997). BTA relies on a comprehensive set of functional traits (e.g. feeding type, body size and reproductive technique), which can serve as indicators for ecosystem functioning (Nasi et al., 2018).

Commercial bivalve molluscs were historically exploited in the northern region of Apulia (Italy, Southern Adriatic Sea) until the late 1990s, particularly in the shallow waters of the Gulf of Manfredonia, where there is an important fishing area for striped venus and razor clams *Ensis minor* (Chenu, 1843) (Vaccarella et al., 1996). However, throughout the Apulian region, there has been a sharp decline in *C. gallina* landings over the last two decades likely due to a decrease in primary productivity (Romanelli et al., 2009) and a reduction in fishing effort in line with changes in European and national fisheries regulations (Carlucci et al., 2024a). In fact, a regulatory reduction in the number of vessels, the number of weekly fishing days (4 days per week) and daily catches (400 kg per day) was introduced in 2017 (DGPEMAC, 2019). However, despite the reduction in fishing effort, monitoring surveys carried out to assess the biomass status of commercial stocks of *C. gallina* have shown poor recovery throughout the Adriatic Sea over the last five years (STECF, 2023). Furthermore, in the southern Adriatic, negative trends were also observed in the period 2018–2020, when the COVID-19 lockdown further reduced fishing effort. This lack of a positive response by the commercial resource to the reduction in fishing pressure raises questions about the effectiveness of management measures based solely on reducing fishing effort, especially when marine-coastal ecosystems are undergoing significant environmental changes (Baeta et al., 2021). Indeed, benthic communities inhabiting shallow soft bottoms habitats are influenced by several environmental stressors (Carrier-Belleau et al., 2021). Some act at broader scale, such as temperature, salinity, and acidification, while others are strictly driven by local pressures and regime shift in human activities, such as nutrient load changes from river inputs during the COVID-19 lockdown (Braga et al., 2022). Therefore, identifying the strength of the effects attributable to fishing impacts with respect to those derived from fluctuations driven by natural variability (Vinebrooke et al., 2004), as well as those triggered by sudden events, becomes a fundamental challenge to effectively support biological resource management actions. Given the high ecological complexity of these habitats exploited by dredge fishing, it can be difficult to identify the responses of benthic communities to different environmental and anthropogenic pressures simply by analysing changes in the structure of the faunal assemblage. In this regard, a better understanding of the changes in benthic communities when different pressures alter their state could be identified through the analysis of functional traits expressed by the benthic assemblage (Bremner et al., 2006).

This study provides the first description of the taxonomical diversity, assemblage structure and functional trait composition of the benthic macrofauna inhabiting the poorly explored shallow soft bottoms of the Gulf of Manfredonia applied to the investigation of temporal changes in relation to fishing effort and environmental variability. Biological data on benthic species were collected as non-mandatory data during monitoring surveys targeting the striped venus clam in the study area before and during the COVID-19 lockdown (2018–2020). The study aims to: (i) assess the response of species diversity and composition to different fishing effort intensity (high, low, null); (ii) evaluate the influence of fishing effort and environmental variables on functional traits categories expressed by the benthic assemblage; (iii) examine the role of environmental variability, driven by human pressures at local (e.g. COVID-19 lockdown) or global (climate change) scale in structuring the assemblage and functional trait patterns.

## Materials and methods

### Study area

The Gulf of Manfredonia is a bay located southeast of the Gargano Promontory (southern Adriatic Sea,

Fig. 1). It represents a transition zone between the northern and southern Adriatic circulation, characterized by reduced water movement and a high sedimentation rate (Damiani et al., 1988). Continental inputs are mainly represented by the Ofanto River, the major river flowing into the Adriatic Sea, south of the Gargano Promontory. Other minor rivers, which are the Carapelle, Cervaro and Candelaro, show a seasonal and limited contribution to sediment deposition (Simeoni, 1992).

The study area is included in the bathymetric range of 2–6 m between the mouth of the Candelaro River and before the mouth of the Aloisa Canal that connects the open sea with the Margherita di Savoia saline basins. Sediments distributed at depths greater than 10 m in the Gulf of Manfredonia are mainly composed of silt and clay, while silty sands dominate the shallowest coastal areas (Cattaneo et al., 2003; Scirocco et al., 2019). Some fragmented and small areas around rivers mouths are characterized by coarser sediments (sand > 30%) (Spagnoli et al., 2008). The sediment grain size in the study area is affected by the local sea-water circulation combined with the flood events of rivers (Candelaro, Cervaro and Carapelle), which discharge debris and mud along the northwest–southeast direction of the coast (Simeoni, 1992). The sediment distribution shows an irregular mosaic pattern with no obvious gradients in the grain size on the mesospatial scale (5–10 km). This condition is also evident in the distribution of the benthic species collected in a monitoring survey conducted in 2013 to map the distribution of commercial bivalves (unpublished data). In particular, the biocenoses detected through the occurrence of the collected species showed a random distribution of Well-Sorted Fine Sands (WSFS), superficial muddy sands in sheltered areas (SVMC) and muddy debris (Fig. 1).

The study area was historically impacted by fishing dredging for the harvesting of commercial bivalves, such as striped venus and razor clams (Vaccarella et al., 1996; Carlucci et al., 2024a), and it is subject to potential threats of various pollutants resulting mainly from urban and agricultural activities (Guglielmi et al., 2023).

## Survey periods and sampling procedures of biological data

Samplings were conducted in September 2018, June 2019 and June 2020 under the dredgers molluscs surveys research programme (DRES). The purpose was to assess the status of the striped venus clams in the compartment of Manfredonia. The explored area extends approximately 15 km along the southern coast of the Gulf of Manfredonia, representing a sub-area where the fishing activities are mainly conducted by the Manfredonia dredge fleet. The sampling procedure was carried out using a hydraulic dredger (overall length of 12.46 m, gross tonnage of 11 GT, and engine power of 110 kWh) operating in the Manfredonia compartment. The survey layout consisted of a minimum of 5 linear transects each year, positioned perpendicularly to the coastline and spaced approximately 2 km apart in a depth range between 2 and 6 m (Fig. 1). Sampling was carried out in areas subject to dredge fishing activities over the past few years based on indications from local fishermen, and information reported in a previous fishery-independent monitoring conducted in 2013. Along each transect, sampling was carried out at up to four sampling stations parallel to the coastline and spaced approximately 0.25 nautical miles apart. The number of stations in each transect depended on the presence (or absence) of *C. gallina* in the catch, as the sampling operation moved to the next transect after the first station where the target species was not found. The operators on board collected information on the duration of the operation (min), depth (m), geographical position (latitude and longitude) and length of the haul (m) by means of a geographical positioning system (GPS, model Garmin 650). Over the three years of the survey, a total of 41 stations were sampled. The dredger used in the sampling procedure was characterized by a 3-m-wide opening. Inside the dredge cage, a sampling net 40 cm wide and 20 cm long, with 14 mm mesh was attached to collect the juveniles of *C. gallina* and associated macrobenthic fauna. The catches were stored at − 20°C. Samples were sorted, and organisms were identified to the lowest possible taxonomic level and counted. Abundance data for each taxon was standardized for all sampled species using the area swept at each sampling station (N/100 $m^2$).

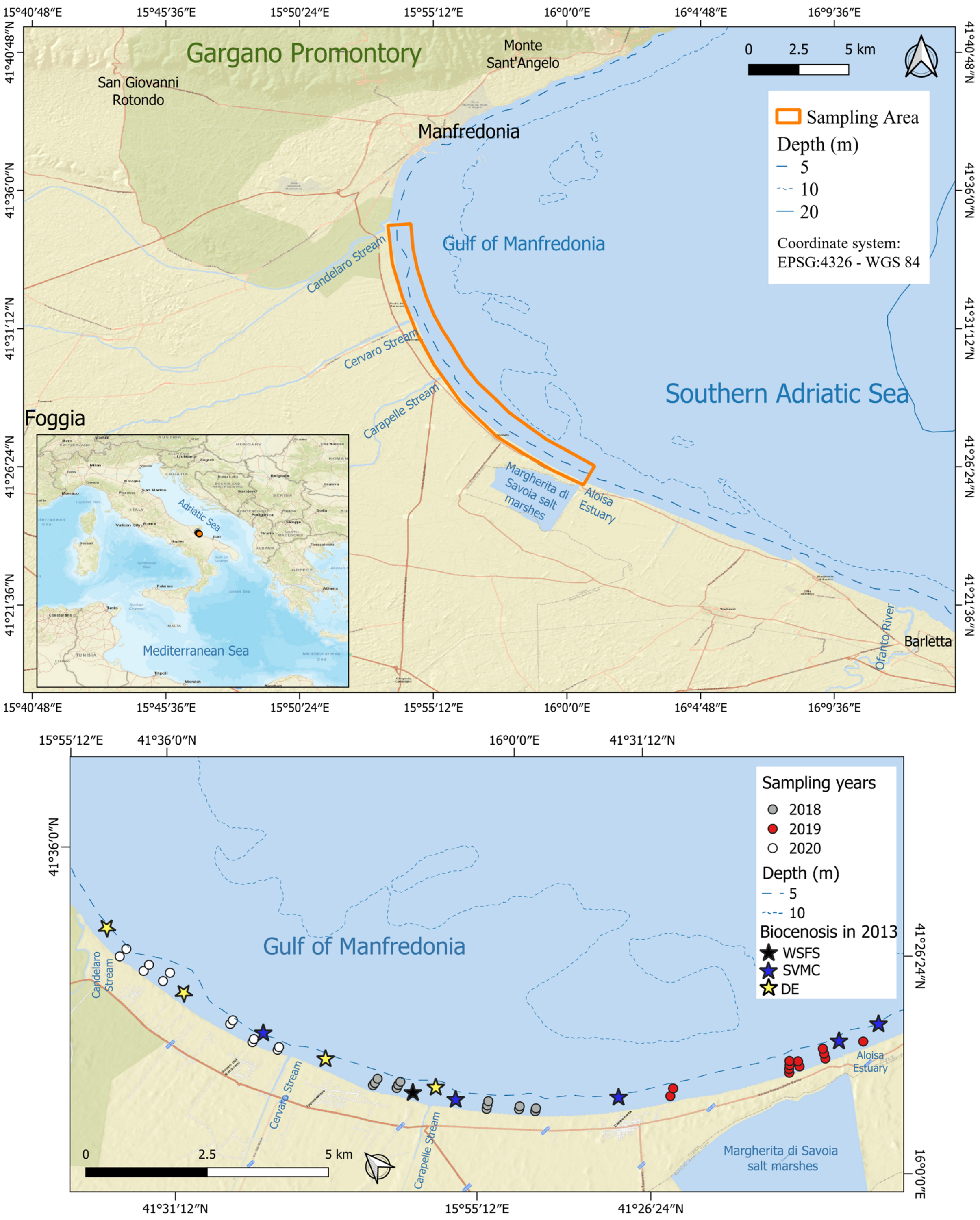


**Fig. 1** Study area in the Gulf of Manfredonia in the period 2018–2020 (upper panel) with investigated sampling stations (circles in lower panel). Information on biocenosis distribution acquired from an explorative monitoring survey of commercial bivalves, conducted in 2013, are represented by the coloured stars (lower panel): Well-Sorted Fine Sand (WSFS, black), superficial muddy sands in sheltered areas (SVMC, blue), muddy debris (DE, yellow)

### Fishing effort and environmental data

Data were collected using four hydraulic dredges with license to operate in the study area, which occasionally harvested species other than the striped venus clam, such as razor clams (*E. minor*, *Solen marginatus* Pulteney, 1799), purple dye murex *Bolinus brandaris* (Linnaeus, 1758) and rough cockle (*Acanthocardia tuberculata* (Linnaeus, 1758)) (Vaccarella et al., 1996). The absence of an official management consortium for fishing cooperatives in Manfredonia makes it very difficult to obtain fishing effort and catch data. Thus, the information on the fishing behaviour of the local hydraulic dredges fleet was collected directly from fishermen involved in the sampling activities. In 2018, fishing dredge activities occurred from the end of March up to July with 4 vessels working about 4–8 days each month; halted in August and resumed from the end of September to November In 2019, fishing activity in the area was less intense compared to 2018, with no more than two vessels operating between March and July, as well as in October. From January to June 2020, fishing activities were absent due to the restrictions of the COVID-19 emergency. According to the sampling periods and the fishing behaviour, the level of fishing impact was classified as: high in September 2018, medium in June 2019 and null in June 2020 (Fig. 2).

Lack of water column sampling was compensated by remote sensing data, available from physical reanalysis components of the Mediterranean Monitoring and Forecasting Centre on the Copernicus Marine Service portal (CMS, http://marine.copernicus.eu accessed on 1 June 2025). Environmental variables selected in the analysis were bottom temperature (T bottom,°C), salinity (PSU), dissolved oxygen ($O_2$, mmol m$^{-3}$), pH, dissolved phosphates ($PO_4$, mmol m$^{-3}$), dissolved ammonium ($NH_4$, mmol m$^{-3}$), dissolved nitrates ($NO_3$, mmol m$^{-3}$ – 3) and net primary production (NPP, mg m$^{-3}$ day$^{-1}$). Each environmental variable was derived from specific Copernicus products: bottom temperature and salinity were derived from the Mediterranean Sea Physics Reanalysis (CMS—MEDSEA_MULTIYEAR_PHY_006_004), while dissolved oxygen, nutrients and NPP were obtained from the Mediterranean Sea Biogeochemistry Reanalysis (CMS—MEDSEA_MULTIYEAR_BGC_006_008). The datasets were retrieved in the form of NetCDF files and projected into a 0.042 decimal degrees raster (Coordinate Reference System WGS84) using the R (v. R-3.6.3) package raster (version 3.5–2) in the R Studio environment (v. 1.3.1093). Environmental data were extracted for a total of 7 grid cells, which overlapped with the biological sampling sites (Table S1; Fig. S1). For each raster cell, the mean monthly value of each variable was calculated for the available depth strata from January 2018 to December 2020 (Table S2). In addition, given the lack of local studies on the relationships between coastal flash floods, seabed siltation, and biological responses of benthic species, a collection of information on the occurrence of extreme events, such as heavy rain during the investigated period, was carried out. This information may be indirect

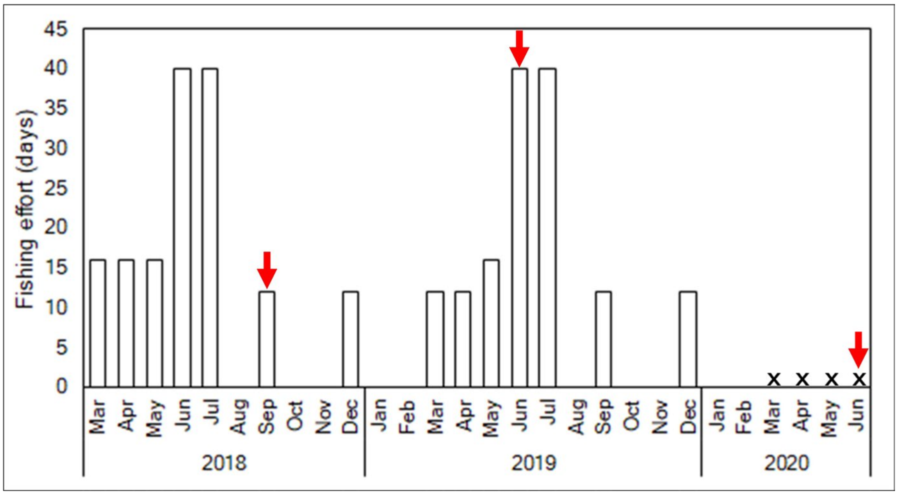


**Fig. 2** Distribution of monthly fishing effort (days at sea, bars) during the study period. The red arrows indicate the sampling month for each year. The 'X' marks represent fishing shutdown periods due to COVID-19

evidence of temporary flooding events in the coastal areas facing the study area, resulting in the transport of large quantities of muddy sediments to shallow bottoms. Data on the occurrence of heavy rainfall, defined as rainfall exceeding 35 mm per hour (criteria by ESWD, 2021), were obtained from the European Severe Weather Database (ESWD ver. 5.1, https://eswd.eu/en, accessed on 1 September 2025) by collecting spatial data (location) and event dates from the EWSD GIS support. Specifically, events occurring in the terrestrial area between the coastline facing the study area and a boundary set at a distance of 50 km were taken into consideration. This area overlaps with the river basins of the three rivers (Carapelle, Cervaro and Candelaro) that flow into the study area.

## Biological trait analysis (BTA)

BTA classifies the species through a list of selected biological traits (Table 1). The traits considered in this study (10 traits with 42 total categories) were selected based on their ecological importance, as indicated by previous studies that have used this technique for similar purposes (De Juan et al., 2020; Beauchard et al., 2023. In particular, biological traits were divided into two broad groups: (i) *response* traits (FRt), i.e. those that indicate a species response to changes in the environment, such as disturbance, resource availability or climatic shift; (ii) *effect* traits (FEt), i.e. those that express an effect by a species on the ecosystem properties, such as bioturbation activities, feeding habits and the environmental position (Bolam et al., 2016; Beauchard, 2023). Overall, the selected traits reflect the species life-cycle characteristics, morphology, ecological adaptations, behaviour and the fishing disturbance. Specifically, the fishing impacts were represented by the damage intensity (the Damage category in Table 1) due to the mechanical dredge impact, which were assigned according to the observations on the frequencies of undamaged/damaged discarded species reported in the literature (Urra et al., 2017; Baeta et al., 2021; Bargione et al., 2024).

The affinity of each species to all functional traits was assigned through the "fuzzy coding" procedure (Chevene et al., 1994), which allows species to be joined at multiple categories within each trait (0 = no affinity, 1 = low importance, 2 = moderate importance, 3 = dominant) (Bremner et al., 2006). Species, for example, were classified according to their feeding habits, such as suspension feeders, surface detritivores, or fossorial, herbivorous, predatory or scavenger organisms. For example: for exclusively suspension feeder organisms, a value of 3 was assigned for suspension-feeding and 0 for all other habits. For both suspension feeder and detritivore organisms, values of 1–2 were assigned for each of these habits (depending on the degree of affinity for these traits) and 0 for the rest of the habits. Thus, a Species-Traits matrix was realized by acquiring information of taxon traits from literature sources and from information available in online databases, as listed in Table S3. The Species-Traits matrix was combined with Abundance Species-Sites matrix (Table S4) to analyse changes in trait composition, calculating the Community-Weighted Mean (CWM) of each trait within the sampling stations (Table S5). CWM is a widely used index that reflects trait strategies given by the species pool and environmental conditions of a site (Muscarella & Uriarte, 2016). CWM values represent the expression of a trait by species in each community, weighted by the abundance of species with that specific trait. The analysis of the abovementioned indices adopted in the BTA was conducted using the FD library of the R programme ver. 3.1.3 (Laliberté et al., 2014; www.R-project.org/).

## Statistical analyses

To detected temporal variations in the environmental conditions, monthly mean values of environmental variables were evaluated using the Spearman's correlation coefficient (rs) for the study period. Before performing the temporal analysis, the presence of spatial gradients in the environmental variables was assessed by comparing the median values between the seven grid cells for each year using the non-parametric Kruskal–Wallis test (McDonald, 2014). No significant differences were detected in any environmental variable within each year (Table S1). Consequently, the entire study area was treated as a single spatial unit.

Standardized abundance data of each species (N/100 m$^2$) were organized into a species-station matrix (Table S4). Temporal differences in species diversity of the macrobenthic assemblage were analysed. Before the analysis, *taxa* that were not identified at least at the family level and those belonging to

**Table 1** Functional Traits divided into Functional Response trait (FRt) and Functional Effects trait (FEt) groups, categories and their codes adopted in Biological Trait Analysis (BTA)

| Group | Traits | Categories | Code |
|---|---|---|---|
| Response (FRt) | Size (mm) | 5–50 | Size_S |
| | | 50–100 | Size_M |
| | | 100–200 | Size_L |
| | | > 200 | Size_XL |
| | Protection | No protection | Prot_No |
| | | Tube | Prot_Tub |
| | | Case | Prot_Cas |
| | | Shell | Prot_Shl |
| | Regeneration | Regeneration increases survival of the species | Reg_Y |
| | | The absence of regeneration reduces the probability of survival | Reg_N |
| | Damage | High | Dh |
| | | Medium | Dm |
| | | Low | Dl |
| | Longevity | ≤ 1 year | Al-1 |
| | | 1–3 years | Al-3 |
| | | 3–6 years | Al-6 |
| | | 6–10 years | Al-10 |
| Effect (FEt) | Environmental position | Infauna | EP_Inf |
| | | Epifauna | EP_Epif |
| | | Interface | EP_Interf |
| | | Epibiont | EP_Epib |
| | Mobility | Sessile | Mob_Sess |
| | | Semi-motile | Mob_S-mot |
| | | Motile | Mob_Mot |
| | Movement method | No movement | MovM_No |
| | | Swimmer | MovM_Swim |
| | | Crawler | MovM_Craw |
| | | Tube-builder | MovM_Tubl |
| | | Burrower | MovM_Bur |
| | Bioturbation | No bioturbation | BT-No |
| | | Surface modifier | BT-Smod |
| | | Biodiffuser | BT-Biodif |
| | | Regenerator | BT-Regen |
| | | Conveyor | BT-Conv |
| | Feeding habit | Suspension feeder | Feed_Susp |
| | | Surface deposit feeder | Feed_Sdep |
| | | Subsurface deposit feeder | Feed_SSdep |
| | | Herbivore | Feed_Herb |
| | | Predation | Feed_Pred |
| | | Scavenger | Feed_Scav |

the non-dredge fish category were excluded, as they could not be effectively classified as benthic. Considering the lack of information on the granulometry of the seabed, an indirect estimate of the sediment type at each sampling station was made by calculating the affinity of the biocenoses (Pérès & Picard, 1964). The calculation considered the characteristic species (exclusive and preferential) of soft bottom biocenoses, as well as generalist species associated with conditions of high ecological variability. Species not associated with a specific biocenosis, or lacking attribution in the scientific literature, were excluded from the analysis (Table S4). This calculation is based on a correction coefficient ($C$), which corresponds to the relative percentage occurrence of the species characteristic of biocenosis $j$ in relation to the total of species belonging to other biocenoses within a sampling station. Thus, the absolute affinity ($A_j$) is calculated as:

$$A_j = n_j \times \left(100 - C_j\right)$$

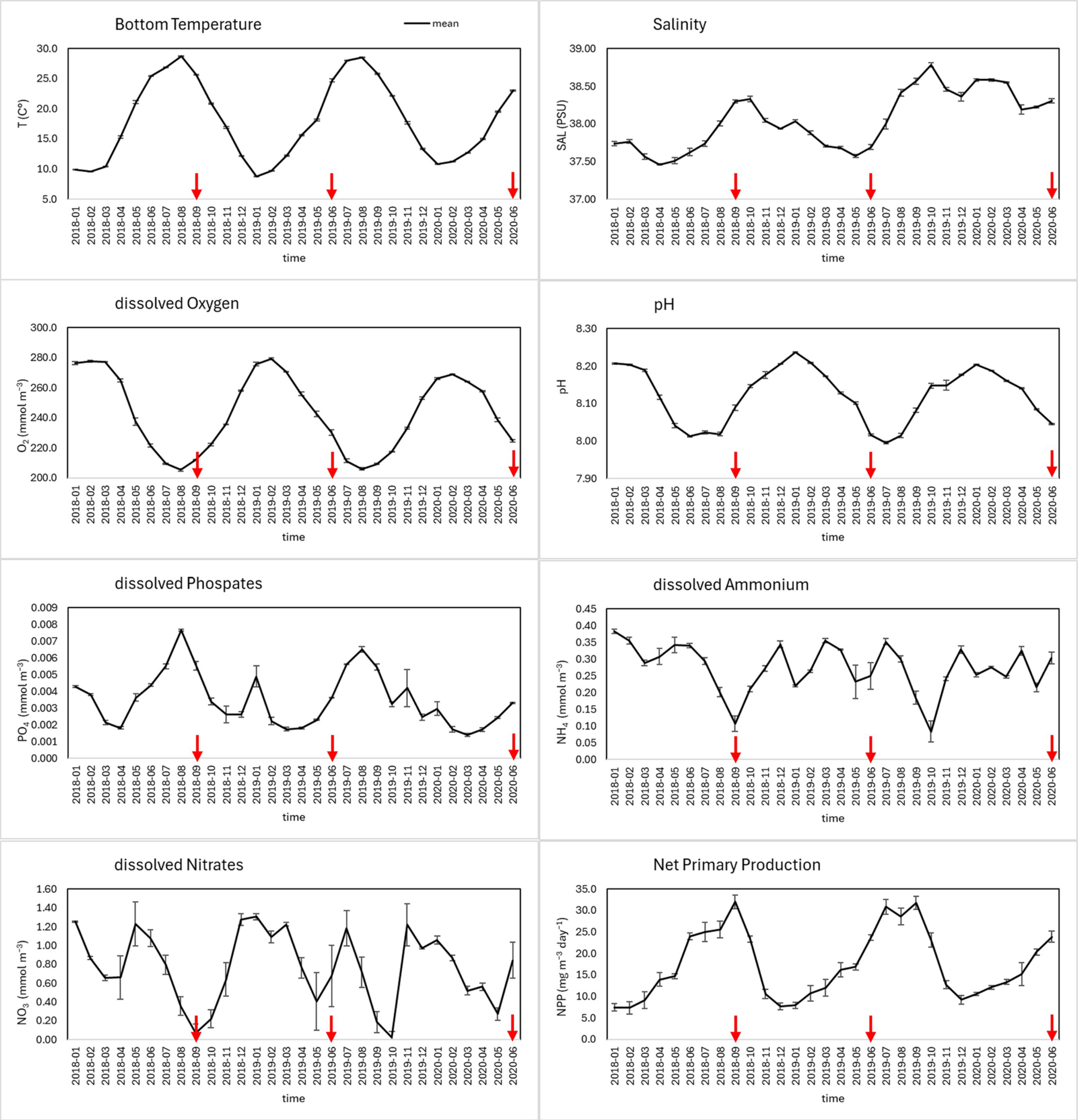
where $n_j$ is the number of characteristic species of biocenosis within the considered sampling station. The biocenosis affinity was expressed as percentage values calculated within each sampling station. Moreover, the same calculation was carried out considering the number of characteristic species of biocenosis in each investigated year to assess the temporal variation of the biocenosis affinity.

For the Total Abundance ($N$) and alpha diversity indices (Shannon-Weiner, $H$'; Margalef's, $d$; and Pielou's, $J$) median, minimum–maximum values, 1st and 3rd quartiles were calculated for each year, and temporal differences were tested using the non-parametric Kruskal–Wallis (KW) test, and a *post-hoc* multiple comparison based on the Mann–Whitney ($U$) test with Bonferroni correction (McDonald, 2014). The choice of this test was due to the non-normal distribution of diversity indices data and the absence of variance homogeneity of sampling, checked using Shapiro–Wilkinson and Levene's tests. Statistical tests were performed using PAleontological STatistics software (PAST ver. 4.14, Hammer et al., 2001). The analysis of the macrobenthic assemblage structure was carried out on a standardized species-station abundance matrix. All data were then transformed into fourth root to balance the contribution of the very abundant species and keep information on relative abundances intact (Legendre & Legendre, 2012). Temporal differences in the abundance composition of the assemblage of selected benthic species and CWM values were analysed through a multivariate analysis of variance by permutations (PERMANOVA, Anderson, 2001). The fixed factor 'Year' is characterized by 3 levels (2018, 2019 and 2020). The permutation method adopted to calculate the probability values (*P-value*) through 9999 permutations was conducted by an unrestricted permutation of raw data. The significance level of the test was set at $P < 0.05$. Differences between factor levels were subsequently analysed with a Pairwise t-test combined with the Monte Carlo test. To visualize temporal differences in the analysed species assemblage, the unconstrained ordination method of the Principal COordinate analysis (PCO, Gower, 1966) was adopted, based on the Bray–Curtis similarity applied to the species-station matrix. To identify the contribution of *taxa* to the differences between years, a Similarity Percentage (SIMPER; Clarke, 1993) analysis was carried out using a Bray–Curtis similarity on transformed data, as part of multivariate analyses performed with PRIMER v.7 using the PERMANOVA routine (Anderson et al., 2008; Clarke et al., 2014).

## Results

### Environmental changes in the period 2018–2020

No significant linear trends were detected for environmental variables, except for salinity, which showed a significant positive trend over time ($rs = 0.685$; $P < 0.001$) (Fig. 3; Table S2). A sharp increase in salinity was observed starting in July 2019, with values in 2020 averaging about 0.6 PSU higher than in 2018 (Table S1). Bottom temperature showed similar seasonal trends in all years, but a warmer winter period was observed in 2020, with a mean value in January of 10.8°C, higher than the values estimated in the same month in 2019 (8.7°C) and 2018 (9.9°C). The average net primary production in the first semester of 2018 (12.8 ± 6.35) was lower than those in 2019 (14.5 ± 5.60) and 2020 (15.9 ± 5.15). In particular, the mean values in the summer months of 2019 were higher than those in 2018. Dissolved oxygen showed similar variations in all years with minimum and maximum values detected in August 2018 and 2019 (205 mmol $m^{-3}$) and February 2019 (279.4 mmol $m^{-3}$), respectively. Moreover, the winter



Bottom Temperature

Salinity

dissolved Oxygen

pH

dissolved Phospates

dissolved Ammonium

dissolved Nitrates

Net Primary Production

**Fig. 3** Environmental variables reported as monthly mean value (bars = standard deviation) for the investigated period. Sampling periods are indicated by red arrows

values of 2020 were lower than those of previous years. Dissolved phosphates showed the maximum values in summer periods up to 0.008 mmol m$^{-3}$, and the minimum value of 0.002 mmol m$^{-3}$ in early springs of each year between March and April. In autumn of 2019, irregular oscillations of $PO_4$ values were observed with the highest monthly variation in November. For nitrogen nutrients, irregular oscillations were exclusively detected for dissolved nitrate values, with a sharp increase between October (0.004 mmol m$^{-3}$) and November (0.922 mmol m$^{-3}$) 2019.

During the investigated period, four extreme heavy rainfall events were detected in 2019: on 10th July in Manfredonia, on 02nd and 03rd September in Foggia

**Table 2** List of taxa collected and identified in the study and their faunal groups, coded as follows: Bivalves = Biv; Bony fish = Bonf; Decapod Crustaceans = Cru; Echinoderms = Echi; Elasmobranchs = Elasm; Gastropods = Gast; Polychaetes = Poly; Sipunculidae = Sip

| Faunal group | Species | Faunal group | Species |
|---|---|---|---|
| Biv | *Acanthocardia tuberculata* (Linnaeus,1758) | Cru | *Polybius depurator* (Linnaeus,1758) |
| Biv | *Bosemprella incarnata* (Linnaeus,1758) | Cru | *Penaeus (Marsupenaeus) japonicus* Spence Bate, 1888 *1888* |
| Biv | *Chamelea gallina* (Linnaeus,1758) | Cru | *Upogebia pusilla* (Petagna, 1792) |
| Biv | *Donax semistriatus* Poli, 1795 | Echi | *Astropecten bispinosus* (Otto, 1823) |
| Biv | *Dosinia lupinus* (Linnaeus,1758) | Echi | *Astropecten* Gray, 1840 |
| Biv | *Ensis megistus coseli* Vierna, 2014 | Elasm | *Raja asterias* Delaroche, 1809 |
| Biv | *Mactra stultorum* (Linnaeus,1758) | Gast | *Acteon tornatilis* (Linnaeus,1758) |
| Biv | *Moerella pulchella* (Lamarck, 1818) | Gast | *Bolinus brandaris* (Linnaeus,1758) |
| Biv | *Peronaea planata* (Linnaeus, 1758) | Gast | *Hexaplex trunculus* (Linnaeus,1758) |
| Biv | *Peronidia albicans* (Gmelin, 1791) | Gast | *Naticarius stercusmuscarum* (Gmelin, 1791) |
| Biv | *Pharus legumen* (Linnaeus,1758) | Gast | *Neverita josephinia* Risso, 1826 |
| Biv | *Polititapes aureus* (Gmelin, 1791) | Gast | *Tritia mutabilis* (Linnaeus, 1758) |
| Biv | *Solen marginatus* Pulteney, 1799 | Gast | *Tritia reticulata* (Linnaeus, 1758) |
| Biv | *Spisula subtruncata* (da Costa, 1778) | Poly | *Diopatra neapolitana* Delle Chiaje, 1841 |
| Bonf | *Callionymus maculatus* Rafinesque, 1810 | Poly | *Eunice aphroditois* (Pallas, 1788) |
| Bonf | *Deltentosteus quadrimaculatus* (Valenciennes, 1837) | Poly | *Glycera unicornis* Lamarck, 1818 |
| Bonf | *Lithognathus mormyrus* (Linnaeus,1758) | Poly | *Lumbrineris latreilli* Audouin & Milne Edwards, 1833 |
| Bonf | *Monochirus hispidus* Rafinesque, 1814 | Poly | *Nothria conchylega* (Sars, 1835) |
| Bonf | *Solea solea* (Linnaeus,1758) | Poly | *Owenia fusiformis* Delle Chiaje, 1844 |
| Cru | *Diogenes pugilator* (Roux, 1829) | Sip | *Sipunculus nudus* Linnaeus, 1766 |
| Cru | *Ilia nucleus* (Linnaeus,1758) | | |

and Monte Sant'Angelo, respectively and on 24th November in San Giovanni Rotondo. No extreme events were recorded in 2018 or 2020. These events were recorded in locations less than 32 km from the study area.

## Diversity and structure of the shallowest macrobenthic assemblage

During the three years of sampling, a total of 41 *taxa* were collected and identified: 5 crustaceans, 2 echinoderms, 21 molluscs (14 bivalves, 7 gastropods), 1 sipunculid, 6 polychaetes, 5 bony fishes and 1 elasmobranch (Table 2; Table S3). The assessment of biocenosis affinity showed a high occurrence of species associated with WSFS with values ranging between 50% in 2018 and 42% in 2020 (Table S4). Species associated with SVMC were exclusively detected in 2020 (24%) indicating an increase in mud content in the sediments. The characteristic species of Superficial Fine Sands (SFS) were detected with a percentage of 15% in 2019 and 9% in 2020. In all years, the occurrence of species associated with high ecological variability was detected, with percentage values of 50% in 2018, 38% in 2019 and 24% in 2020. This suggests that the soft bottoms were affected by relevant environmental variability.

During the three years, the total abundance showed a significant difference between 2018 (median value = 25 N/100m$^2$, interquartile range IR = 16) and 2020 (median value 4 N/100m$^2$, IR = 2.75; $U$ test = 0, $P < 0.001$) (Fig. 4). In addition, the total abundance in 2019 showed a median value of 4.5 N/100m$^2$, with the highest variability of data (IR = 24). All the diversity indices analysed ($H'$, $d$ and $J$) showed significantly higher median values in 2020 than in previous years ($P < 0.001$)

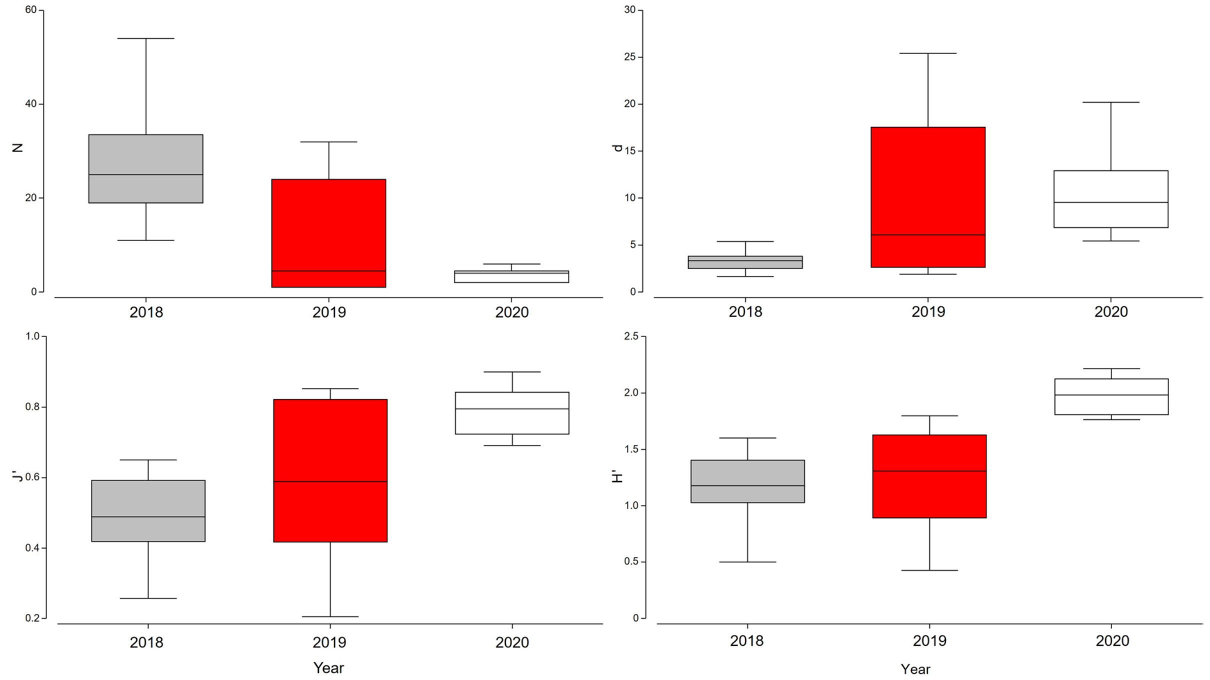


**Fig. 4** Boxplots of Total Abundance (*N*) and alpha diversity indices (Shannon-Weiner *H*', Margalef's *d*, Pielou's *J*) calculated in the investigated years. Values are indicated as medians (lines in the boxes), minimum and maximum values (lower and upper whiskers) and quartiles (boxes limits), respectively

**Table 3** PERMANOVA results based on the Bray–Curtis similarity matrix of the benthic assemblages (abundance by *taxa*) tested according to factor "Year", and PAIRWISE t-test obtained for factor levels (2018, 2019, 2020)

| Source of variation | Df | SS | MSS | Pseudo-F | P(perm) | perms |
|---|---|---|---|---|---|---|
| Year | 2 | 28,447 | 14,223 | 14.41 | 0.0001 | 9912 |
| Residuals | 32 | 31,583 | 986.98 | | | |
| Total | 34 | 60,030 | | | | |

PAIRWISE test – Year

| Year | T | Perms | P(MC) | Av. S % |
|---|---|---|---|---|
| 2018, 2019 | 3.072 | 9891 | 0.0002 | 36.7 |
| 2018, 2020 | 4.917 | 9925 | 0.0001 | 39.2 |
| 2019, 2020 | 3.633 | 9869 | 0.0001 | 29.0 |

The degrees of freedom (Df), Sum of Squares (SS); Mean Sum of Squares (MS); Pseudo-F test; p-values by permutations (P) and number of permutations (perms) are reported for the factor Year. In the PAIRWISE t-test, the T value, Monte Carlo p-values (P(MC)) and the average similarity (Av. S. %) are reported between Year pairs

(Fig. 4, Table S6). Specifically, *H*' showed an increase in median value from 1.02 in 2018 to 1.80 in 2020, the Margalef index from 3.35 to 9.54 and the *J* index was between 0.41 and 0.72.

Significant differences in the abundance of the macrobenthic assemblage were observed between all investigated years according to the PERMANOVA test (Pseudo-F $=$ 14.41; $P < 0.0001$, Table 3) and observed through the PCO plot (Fig. 5). Specifically, there was a clear separation between the years with different degrees of dispersion among the sampling stations. In 2018, the stations were moderately dispersed and

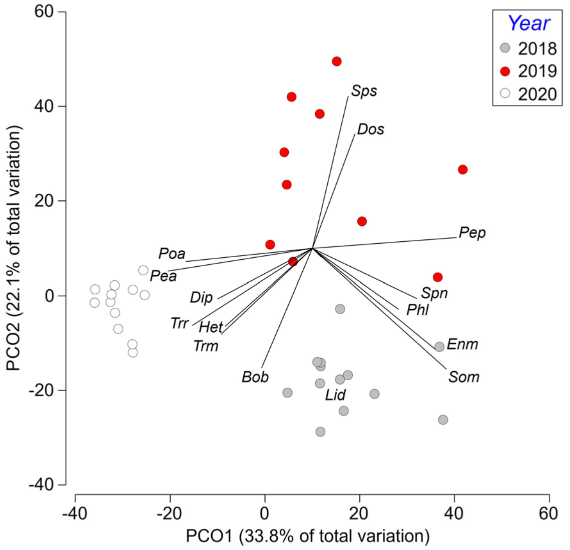


**Fig. 5** PCO ordination plot of sampling stations by years based on the Bray–Curtis similarity calculated by fourth root transformed taxa abundance data. Length and direction of vectors (black lines) indicate the correlation of taxa to the PCO axes according to Pearson's correlation coefficient ($r > 0.5$). Taxa are coded as: *Bolinus brandaris* (Bob), *Diogenes pugilator* (Dip), *Donax semistriatus* (Dos), *Ensis megistus coseli* (Enm), *Hexaplex trunculus* (Het), *Polybius depurator* (Pod), *Peronea planata* (Pep), *Peronidia albicans* (Pea), *Pharus legumen* (Phl), *Polititapes areus* (Poa), *Solen marginatus* (Som), *Spinculus nudus* (Spn) *Spisula subtruncata* (Sps), *Tritia mutabilis* (Trm), *Tritia reticulata* (Trr)

mainly characterized by the occurrence of *Polybius depurator* (Linnaeus, 1758), *S. marginatus*, *Ensis megistus coseli* Vierna, 2014, *B. brandaris*, *Pharus legumen* (Linnaeus, 1758) and *Sipunculus (Sipunculus) nudus* Linnaeus, 1766. In 2019, the stations appeared highly dispersed and diverse, characterized by *Peronaea planata* (Linnaeus, 1758), *Donax semistriatus* Poli, 1795 and *Spisula subtruncata* (da Costa, 1778). Finally, in 2020 the stations were much more grouped and homogeneous, characterized by the occurrence of *Hexaplex trunculus* (Linnaeus, 1758), *Peronidia albicans* (Gmelin, 1791), *Polititapes aureus* (Gmelin, 1791), *Tritia reticulata* (Linnaeus, 1758), *Tritia mutabilis* (Linnaeus, 1758) and *Diogenes pugilator* (Roux, 1829).

SIMPER results confirmed observations from the PCO, highlighting the high abundance of *S. marginatus* and *E. megistus coseli* in 2018, contributing to the difference in benthic assemblage structure between the first year and the following ones (Table 4). On the other hand, *P. planata* was characteristic of sampling stations in 2019, while *P. albicans* and *T. reticulata* stood out in 2020.

## Functional traits of the shallowest macrobenthic assemblage

Temporal differences in the composition of biological traits of the macrobenthic assemblages were detected both for Functional Response (FRt) and Effect (FEt) traits through PERMANOVA tests (Table S7). The PCO plot based on FRt showed good separation of the stations between 2018 and 2020 on the PCO1, which explained 56.6% of the total variation (Fig. 6). The main FRt correlated to the 2018 stations were Longevity Al-6 and Al-10, Size M and L and the absence of protection structures. In contrast, the occurrence of organisms with Case as protection, low Longevity Al-3, and Size S was observed within the stations sampled in 2020. In 2019, stations showed a high dispersion in the multidimensional space with partial overlaps with the 2018 and 2020 stations, indicating a transition phase. In this period, the FRt mainly detected in the stations of 2019 close to those of 2018 were Size XL-L, Longevity Al-6. On the other hand, Damage (Dl, Dm, Dh), Shell protection and Size S were the main FRt correlated to the 2019 stations closer to those of 2020.

PCO plot based on FEt showed lower separation between the 2018 and 2019 stations, while those of 2020 were clearly separated from other stations along the PCO1, which explained 64.5% of the total variation (Fig. 7). The main correlated FEt to stations of 2018 were those of sessile organisms of infauna, suspension feeders characterized by burrowing movements (MovM_Bur) and biodiffuser (BT-Biodif). In 2019, BT_Smod was a characteristic trait of several stations. In addition, several traits (Feed_Sdep, Mob_Smot, EP_Epif and the absence of bioturbation), increased their importance from 2019 to 2020, and organisms with traits belonging to Feed_Scav and Feed_Pred with MovM_Craw were more abundant. Some traits were found to be common between the macrobenthic assemblages of 2018 and 2020, such as BT_Regr, MovM_Swim and EP_Interf.

**Table 4** SIMPER results on the dissimilarity by species between three investigated periods.

*Years: 2018–2019*

| Species | Av. Ab 2018 | Av. Ab. 2019 | Av. Diss | Cont.% | Cum.% |
|---|---|---|---|---|---|
| *Solen marginatus* | 2.05 | 0.36 | 10.34 | 16.3 | 16.3 |
| *Polybius depurator* | 0.94 | 0.17 | 5.05 | 8.0 | 24.3 |
| *Ensis megistus coseli* | 0.92 | 0.23 | 4.44 | 7.0 | 31.3 |
| *Bolinus brandaris* | 0.71 | 0.15 | 3.79 | 6.0 | 37.3 |
| *Peronaea planata* | 0.76 | 0.88 | 3.47 | 5.5 | 42.8 |
| *Sipunculus nudus* | 0.58 | 0.51 | 3.42 | 5.4 | 48.2 |
| *Tritia mutabilis* | 0.73 | 0.35 | 3.18 | 5.0 | 53.2 |
| *Mactra stultorum* | 0.78 | 0.9 | 2.95 | 4.7 | 57.8 |
| *Chamelea gallina* | 0.12 | 0.51 | 2.92 | 4.6 | 62.4 |

*Years: 2018–2020*

| Species | Av.Ab 2018 | Av.Ab. 2020 | Av.Diss | Cont% | Cum.% |
|---|---|---|---|---|---|
| *Solen marginatus* | 2.05 | 0 | 11.34 | 18.7 | 18.7 |
| *Ensis megistus coseli* | 0.92 | 0 | 5.09 | 8.4 | 27.0 |
| *Peronaea planata* | 0.76 | 0 | 4.18 | 6.9 | 33.9 |
| *Sipunculus nudus* | 0.58 | 0 | 3.15 | 5.2 | 39.1 |
| *Polybius depurator* | 0.94 | 0.61 | 2.93 | 4.8 | 43.9 |
| *Peronidia albicans* | 0.31 | 0.77 | 2.85 | 4.7 | 48.6 |
| *Hexaplex trunculus* | 0.28 | 0.55 | 2.79 | 4.6 | 53.2 |
| *Bolinus brandaris* | 0.71 | 0.58 | 2.61 | 4.3 | 57.5 |
| *Tritia reticulata* | 0.25 | 0.57 | 2.36 | 3.9 | 61.4 |

*Years: 2019–2020*

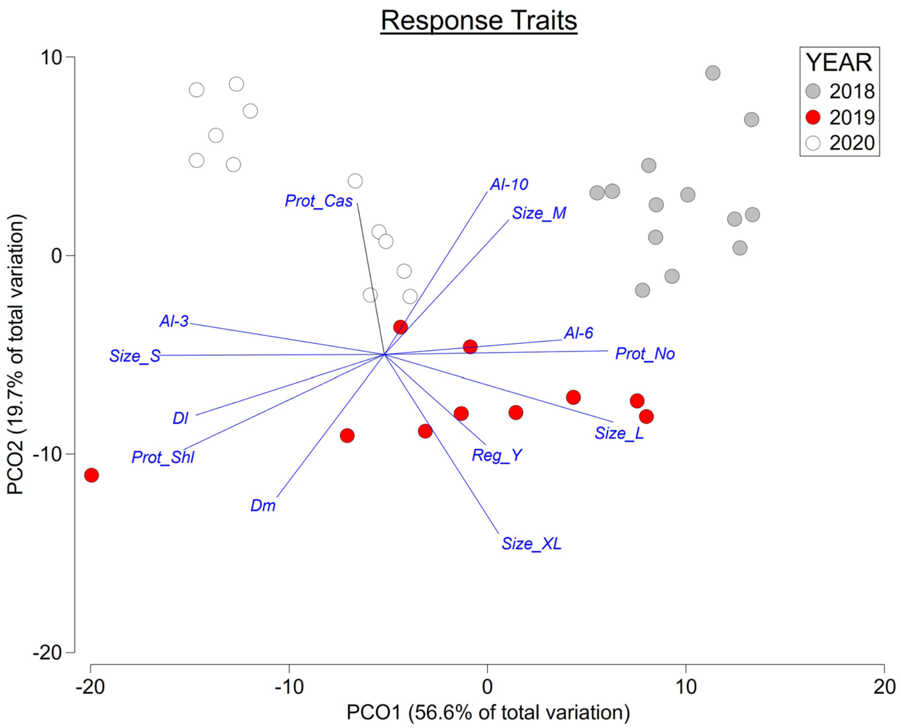
| Species | Av.Ab 2019 | Av.Ab. 2020 | Av.Diss | Cont% | Cum.% |
|---|---|---|---|---|---|
| *Peronaea planata* | 0.88 | 0 | 5.91 | 8.3 | 8.3 |
| *Peronidia albicans* | 0.2 | 0.77 | 4.39 | 6.2 | 14.5 |
| *Tritia reticulata* | 0 | 0.57 | 4.11 | 5.8 | 20.3 |
| *Polybius depurator* | 0.17 | 0.61 | 3.97 | 5.6 | 25.9 |
| *Hexaplex trunculus* | 0 | 0.55 | 3.93 | 5.5 | 31.4 |
| *Tritia mutabilis* | 0.35 | 0.82 | 3.93 | 5.5 | 37.0 |
| *Bolinus brandaris* | 0.15 | 0.58 | 3.82 | 5.4 | 42.4 |
| *Sipunculus nudus* | 0.51 | 0 | 3.38 | 4.8 | 47.1 |
| *Chamelea gallina* | 0.51 | 0.09 | 3.3 | 4.7 | 51.8 |
| *Donax semistriatus* | 0.47 | 0.03 | 3.07 | 4.3 | 56.1 |
| *Diogenes pugilator* | 0.28 | 0.66 | 3.02 | 4.3 | 60.4 |

For each year pair, average abundance (Av. Ab.), average dissimilarity (Av. Diss.), contribution to dissimilarity in percentage values (Cont.%) and cumulative values (Cum%) are reported for the species contributing over 60% of dissimilarity

## Discussion

Marine ecosystems are host to a great variety of species affected by several anthropogenic stressors. According to ecosystem-based fishery management (EBFM, Pikitch et al., 2004), the sustainable management of these ecosystems requires knowledge of the target species of fishery, those that are key elements to the stability of ecological communities, and the impacts of multiple and potentially interacting threats. For this reason, it is crucial to collect ancillary data on ecologically important species that are

**Fig. 6** PCO plot based on Bray–Curtis similarity of Functional Response traits (FRt, expressed as Community-Weighted Mean values) for investigated years (2018–2020). Vectors (black lines) indicate the correlation of FRt with the ordination axes in the multidimensional space, according to the Pearson's correlation coefficient ($r > 0.5$). FRt codes are reported in Table 1



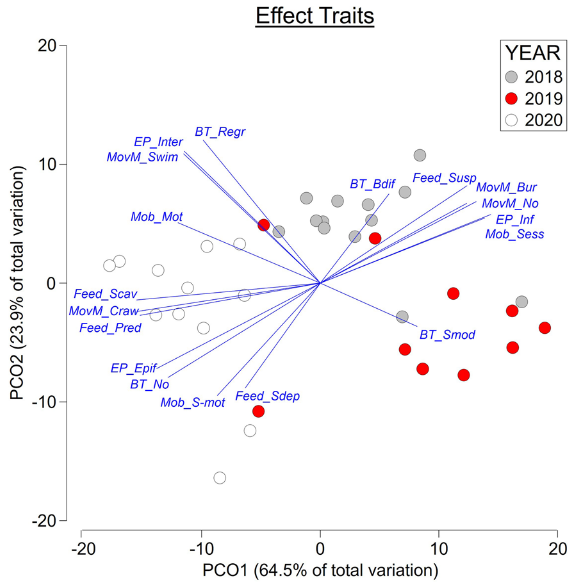


**Fig. 7** PCO plot based on Bray–Curtis similarity of Functional Effect traits (FEt, expressed as Community-Weighted Mean values) for investigated years (2018–2020). Vectors (black lines) indicate the correlation of FEt with the ordination axes in the multidimensional space according to the Pearson's correlation coefficient ($r > 0.5$). FEt codes are reported in Table 1

not the target of monitoring activities, especially in understudied areas.

The investigated benthic assemblages occur in shallow soft bottoms shaped by multiple drivers, mainly the inputs from rivers (Cattaneo et al., 2003), which contribute to a distribution of sediments and associated biocenoses in a random mosaic pattern (Spagnoli et al., 2008; Scirocco et al., 2019). This pattern seems to be persistent over time, with no clear spatial gradients emerging from the analysis conducted on the environmental variables. A similar mosaic pattern of sandy biocenoses has already been detected in a monitoring survey conducted in 2013 in the same area, where WSFS, SVMC, muddy sands and *Cymodocea nodosa* (Ucria) Ascherson, 1870 meadows were found to be distributed between depths of 2–6 m (unpublished data). This variability in sediment composition was consistent with the results obtained from the assessment of the biocenosis affinity, stressing the dominance of sandy bottoms in highly dynamic environment. Similar patterns of mixed association of biocenoses characterized by several opportunistic species (*B. brandaris*, *Astropecten*, *D. pugilator*) were observed in nearby areas of northern Gargano and Barletta during the summer season (Cascione et al., 2022; Carlucci et al., 2024a). Although data on the sediments grain sizes are not directly available from sampling activities, the biocenosis affinity assessment indirectly confirmed a mixed composition of sediments with a random distribution. Furthermore, sampling stations covering a distance of at least 5 km along the coast appear to be sufficiently wide to incorporate spatial variations in benthic assemblages at micro scale (< 1 km; Legendre et al., 1997) and mesoscale (1–3 km; Wlodarska-Kowalczuk & Weslawski, 2008). In fact, it has been shown that multiple environmental factors (e.g. depth, wave exposure) have more prominent effects on the distribution of benthic species at the mesoscale level, contributing to high heterogeneity of soft bottoms macrobenthic communities (Morrisey et al., 1992; Kotta & Möller, 2009).

## Fishing and environmental variability during the period of COVID-19 lockdown

The results obtained from the analysis reflect a complex ecological dynamic of benthic assemblages, due to fishing impacts in the period 2018–2019 and to environmental factors in 2020.

The variation in fishing effort corresponded to two different sampling periods, which fall at the end (September 2018) and beginning (June 2019) of the fishing season. In 2018, the benthic assemblage was observed after a month of a fishing ban and two months at high fishing intensity. This pattern of fishing effort and bans is usually adopted in the southern Adriatic Sea, where the highest fishing pressure is exerted in the early summer and the fishing ban months are displaced in September and October (Carlucci et al., 2024a). In 2019, the assemblage was investigated at the onset of the fishing season, when its disturbance on the bottoms was still exerting low to moderate impacts. These different conditions of fishing pressure are reflected in the species composition of the assemblage explored through the PCO analysis, where the sampling stations investigated during the fishing activities in 2019 showed a larger dispersion than those in 2018, that they were characterized from a higher similarity. Indeed, the fishing ban in 2018 could represented a sufficient recovery time for the stability of the macrobenthic assemblages, as reported for the benthic communities affected by medium-term impacts by fishing dredges in the central Adriatic Sea (Morello et al., 2006).

In 2020, the benthic assemblage showed the greatest difference in terms of diversity, species composition and functional traits, from the previous years. Given the absence of fishing activity due to the restrictions imposed by the COVID-19 lockdown, a recovery of commercial resources (e.g. clams and striped clams) distributed on sandy bottoms was expected. However, this phenomenon was not observed, in contrast to what was reported for other fishing areas of Ancona (Central Adriatic Sea), where *C. gallina* catches recovered after the COVID-19 period (Nepote et al., 2022). In addition, the new pattern of benthic assemblages comprised species typical of muddy-sand bottoms. This change could be linked to flash floods which occurred in the early summer and autumn of 2019 (after the sampling period), associated with heavy rainfall events Similar flash floods were recorded during 2009, stressing the hydrological instability of the study area (Apollonio et al., 2020). The impact of flash floods in the coastal bottoms may explain the change in macrobenthic assemblages observed in 2020, which was characterized by a recolonization of soft bottoms by the benthic species, after an intense physical disturbance during the autumn. The discharge of large amounts of muddy sediments initially has negative effects on the benthic fauna, but the event can positively affect the opportunistic species with faster growth rates within 1–3 months, as observed in polychaete assemblages of coastal marine environments affected by Rhone River inputs in the north-western Mediterranean Sea (Hermand et al., 2008). Similarly, in estuarine environments, recovery of different trophic groups (e.g. detritivores, small deposit feeders) occurred six months after a flooding event, while the total biomass of the benthic community declined (Cardoso et al., 2008).

Assessing the recovery pattern of benthic communities after sudden flooding events is challenging to assess in field studies (Dernie et al., 2003), and the interpretation proposed in this study should be considered preliminary and further investigated. However, flooding events could be considered a primary factor in changes in the sediment structure and benthic assemblages, given the absence of trends in the variation of oceanographic and chemical-physical variables during the study period. Indeed, the only significant positive trend was found for the salinity, and similar variations in salinity were detected in the nearby area of the northern Gargano, in correlation with the changes in benthic communities on shallow soft bottoms (Carlucci et al., 2024b). However, although salinity can act as a key stressor and has been reported to be positively correlated with benthic species diversity (McLaverty et al., 2020), the variation of 0.6 observed between 2019 and 2020 would seem to be too small to impact the structure of the benthic assemblage. Some irregular oscillations in nutrients observed in autumn 2019 could be associated with flooding events (Zoppini et al., 2019). However, the monthly temporal resolution adopted in the analysis does not allow for more detailed insights into the dynamics of these biophysical processes. Thus, the evolution of environmental patterns in the study area should possibly be investigated by increasing the temporal scale resolution of the analysis (e.g. weekly scale).

Overall, this case study highlights how sudden extreme events can mask the expected responses of benthic communities and associated commercial species to the reduction of fishing impacts. The flash flood occurred randomly in overlap with the regime shift of human activities during the COVID-19 lockdown, outweighing the impact of fishing activities. These changes in the structure of the benthic assemblage are also influenced by the broad spatial–temporal scale of ecological processes linked to oceanographic variables, such as the primary production oscillation in the North Adriatic Sea (Braga et al., 2022), and water circulation changes with contrasting effects in salinity and temperature variations between coastal and offshore areas (Tojčić et al., 2024).

### Structure of the shallowest macrobenthic assemblage in the Gulf of Manfredonia

Benthic assemblage diversity and structure showed variations over time, with a significant increase in diversity and decrease in total abundance observed in 2020 in comparison to the previous years. The results highlight the absence of significant impacts on diversity due to changes in fishing pressure between 2018 and 2019, while a different composition in characteristic species emerged within the assemblage between the two years. In particular, the high abundance of commercial bivalves (*E. minor, E. megistus coseli* and *S. marginatus*) in 2018 compared to 2019 confirms that fishing impacts were focused in the first year. Moreover, the occurrence of scavenger species (*B. brandaris* and *P. depurator*) is consistent with a condition of intense impacts of dredges over time (Vasapollo et al., 2020; Carlucci et al., 2024b). As previously described, the 2018 sampling occurred after months of fishing activities and one month of a fishing ban, resulting in the emergence of species more tolerant to a regular mechanical impact. Species correlated to these moderate fishing impacts were also *P. legumen*, similarly to the observations reported by Morello et al. (2006), and *S. nudus* that has been observed in moderate disturbed benthic assemblages in the Tyrrhenian Sea (Vasapollo et al., 2020). In contrast, in 2019 the benthic assemblage was observed at the start of the fishing period, after a prolonged time of fishing inactivity, showing a high dissimilarity of the assemblage structure across the sampling sites. This pattern was clear from PCO output conducted on *taxa*, where the stations in 2019 showed a higher multivariate dispersion than those in 2018. In addition, the highest variance (expressed as range interquartile values in the boxplots) of all diversity indices in 2019 was consistent with this pattern. The occurrence of species such as *D. lupinus* and *S. subtruncata* in 2019 was associated to low or negligible fishing impacts, consistent with the pattern observed for these species in the Central Adriatic Sea (Morello et al., 2006).

The benthic assemblage in 2020 was characterized by the high occurrence of small gastropods and *D. pugilator*, as well as the bivalves *P. albicans* and *P. aureus*. These bivalves are positively associated with conditions of low fishing impacts and high organic matter (Derbali & Jarbouii, 2021; Vesal et al., 2023), which could be linked to the mud sedimentation after the intense flooding event. This kind of event can reduce the total abundance of the species and diversity, as well as favour the selection of specific faunistic groups (Cardoso et al., 2008). However, benthic communities are characterized by high resilience after the cessation of a disturbance (Dauvin, 2025), thus environmental stress that contributes to increasing environmental heterogeneity can promote the emergence of new ecological niches, especially for the most tolerant and opportunistic species of soft bottoms (Vesal et al., 2021). These observations appear to be consistent with the detection of SVMC biocoenosis and high benthic diversity in 2020, but a better understanding of these ecological dynamics emerges from the results of functional traits, as reported below.

### Functional traits pattern of the shallow macrobenthic assemblage

Response traits showed a clear separation between the macrobenthic assemblage of each year, while the Effect traits stress a difference in the assemblages between 2018–2019 and 2020. This is consistent with the higher sensitivity of response traits to changes in benthic communities due to anthropogenic and environmental impacts (Beuchard O 2023). The difference in fishing impacts between 2018 and 2019 was reflected in a selection of Response traits characterized mainly by medium-size organisms and longer life cycles in 2018, but a mixed composition of sizes from small to extra-large occurred in 2019. Species with no protection structures were predominantly associated with sampling stations in 2018 and to a lesser extent in 2019, while small size and shell-protected species increased their occurrence in 2019. In addition, the highest abundance of species with a low and medium sensitivity to dredge damage occurred in 2019, confirming the results obtained by the analysis of the macrobenthic assemblage structure. Shell and case protections arise as characteristic response traits of 2019 and 2020, respectively. The high occurrence of species with shell in 2019 can be explained by the overlap between the sampling event and the ongoing period of fishing dredging, with the increasing fishing pressure intensity from March to June (Fig. 2). On the other hand, species without protective structures were associated to conditions of soft bottoms in 2018, where the macrobenthic assemblage was favoured by a one-month recovery phase after the entire fishing season. The recovery of benthic communities seems to be usually rapid, occurring in range of two-six months from the interruption of the mechanical disturbances, as observed in the Central Adriatic Sea by Morello et al., (2006). In our study case, the recovery seems to occur in less time likely because the fishing pressure in the study area (35–40 fishing days) is about 10 times lower than the pressure in the case study of the Central Adriatic Sea (about 400 fishing days). In 2020, the high abundance of the small-sized organisms with short life cycles highlights a change of benthic assemblage, which did not seem to benefit from the fishing ban due to the COVID-19 lockdown. These functional traits seem to reflect a recolonization process of the soft bottoms predominantly impacted by several environmental stressors, such as those associated flooding events.

The results of Effect traits more clearly showed the separation between the assemblage shaped by the fishing impacts with respect to the effects of the flooding event. Temporal changes in the modalities of Effect traits showed a decrease in infauna, bioturbators and sessile species, as well as the low occurrence of suspension feeders in 2020. The strong decrease in bioturbation activities in 2020 can be explained by the impact of the flooding events on the vertical displacement of infauna. The negative effects may be linked to changes in sediment composition or salinity that affect the seabed surface, causing an extreme burrowing of the infauna and consequent death of organisms (Laurino et al., 2020). The pattern showed by feeding habit traits seem to be consistent with the changes induced by the disturbances associated to the flooding event. Suspension-feeders were detected as species positively associated to medium and lower fishing dredge pressures in 2018 and 2019, and similar findings were observed for filter feeders polychaetes, such as *O. fusiformis*, in areas with medium disturbance by dredging (Carlucci et al., 2024b). It has been observed that the dredging of soft bottoms conducted for several scopes (e.g. fishing, excavation) induces a low sediment resuspension, increasing the water turbidity, with potential positive effects for some filter-feeder species (Todd et al., 2015). However, high rates of sedimentation and excessive water turbidity could have negative effects on some faunal groups based on filter-feeding behaviour, favouring the selection of tolerant and pioneer species (Cardoso et al., 2008). Similarly, variations in the oscillation patterns of other environmental variables (net primary production or nutrients) could be responsible for selection of traits belonging to species acting as pioneers in transitional systems (Nasi et al., 2018).

## Conclusions

Information on the impacts of hydraulic dredges on benthic habitats is crucial for the sustainable management of fishery resources (Baeta et al., 2021), as well as for the integration of holistic approaches to assess the cumulative effects of anthropogenic and environmental drivers (Lambert et al., 2017).

The results showed a lack of recovery of the commercial species populations, such as striped and razor clams, during the period of absence of fishing pressure due to the COVID-19 lockdown. However, the recovery of bivalve stocks does not exclusively depend on the fishery management actions (Baeta et al., 2021), and the analysis of functional traits variation in the benthic assemblage of the study area recognizes other potential stressors, such as the sudden flooding events in autumn 2019. These events could have affected environmental conditions of water quality and sediment composition that negatively impact the recruitment processes of commercial bivalve stocks and other benthic species. In particular, the absence of fishing activity in the first six months of 2020 showed an expected response from the benthic assemblage, namely an increase in species richness and diversity, but the pattern of functional traits shows changes that contrast with the reduction in fishing impact, such as the absence of bioturbation, sessile organisms and infauna.

The use of biological traits was a useful tool to detect variations in the benthic communities driven by fishing impacts and climate changes, as observed in bentho-demersal communities exploited by the bottom trawls (Dupaix et al., 2021). Therefore, the implementation of the BTA in the assessment of benthic communities exploited by fishing dredges could be a useful approach to develop in support of EBFM.

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**Data availability** The data that support the findings of this study are available in the main text and in the supplementary materials.

### Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

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