

## ARTICLE OPEN ACCESS

# Recovery of Fish Assemblages After 10 Years of Enforced Trawling Ban in Two Natura 2000 Sites From Central Mediterranean Sea

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## ABSTRACT

Scientific literature supports the benefits of trawling bans for fish assemblages, particularly regarding species richness and fish size, besides the health of food webs and seafloor habitats. Length-based indicators are commonly applied to track the recovery, offering straightforward and sensitive metrics for detecting shifts in population structure. An Anti-Trawling Artificial Reef (AAR) was installed in 2013 along the lower boundary of *Posidonia oceanica* meadows, physically restricting access to illegal trawlers in two Mediterranean Natura 2000 sites (Special Areas of Conservation) located along Italy's central Tyrrhenian coasts. Over the subsequent decade, three fishing campaigns were conducted to assess the potential recovery of artisanal fishery's target fish species and to examine whether recovery patterns differed according to fish life history strategy. Most recorded species were categorized as either opportunistic or periodic, whereas the equilibrium strategy was less common in fish assemblage. A significant increase in fish length occurred in all functional groups, but equilibrium species exhibited a delayed response, with larger individuals appearing only 10 years after the protection. In contrast, opportunistic and periodic species rebounded more quickly, consistent with their respective growth, reproductive and survivorship trade-offs. Our findings suggest that the AAR approach can foster both biodiversity and small-scale fisheries recovery in the central Mediterranean, underscoring the value of combining spatial protection with effective physical barriers to deter destructive illegal fishing practices.

## 1 | Introduction

Bottom trawling has been widely recognized as one of the most impactful fishing methods on benthic ecosystems and demersal fish assemblages, causing both direct mortalities to target and non-target species and long-term alterations of benthic habitats (Collie et al. 2000; Steadman et al. 2021). Trawling bans or restrictions have been widely applied, aiming to safeguard local habitats and fish stocks while supporting the sustainability of

artisanal fisheries at the same time (Guyader et al. 2013; Lloret et al. 2018).

In the Mediterranean Sea, the enforcement of trawling bans has increasingly become a management measure through time, implementing spatial restriction strategies and generating a growing body of research on either the ecological or socio-economic effects of these prohibitions (Battaglia et al. 2010; Russo et al. 2019). Within the framework of Fishery Restricted

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Areas, both Marine Protected Areas (MPAs) and No Trawl Zones (NTZs) are widely adopted, although their scope and implementation can differ in many ways, leading to different ecological or socio-economic results (Fraschetti et al. 2018; Lloret et al. 2018; Ortega et al. 2023). MPAs are designated to protect marine habitats and species with broader objectives, encompassing habitat conservation, protection of vulnerable species and ecosystem resilience, and may include partial to complete fishing prohibitions in their management strategies (Boudouresque et al. 2020). NTZs are more specifically focused on prohibiting trawling gears while typically allowing other forms of fishing to reduce habitat destruction and facilitate the recovery of benthic and demersal communities (Pipitone et al. 2023). European countries implement a third kind of Fishery Restricted Areas, Natura 2000 sites, deriving from the European Union's Habitats Directive (92/43/CEE), which built up the world's largest conservation network to meet the target of halting (or at least significantly reducing) biodiversity loss (Fraschetti et al. 2018). As MPAs, these sites have wider aims than specifically regulating fishing pressure but may include fishing ban or restriction to protect either marine species or habitats. This strategy applies to *Posidonia oceanica* meadows in the Mediterranean Sea, which are protected under the Habitats Directive due to their ecological and fishing relevance as spawning, nursery and feeding grounds (Guidetti et al. 2019; Lattanzi et al. 2024).

Whatever the spatial strategy deployed, where compliance is low or illegal trawling persists, the positive impacts of protection can be greatly diminished, producing the so-called 'paper parks' (Roberts and Hawkins 2000). Even though in Mediterranean waters trawling at depths shallower than 50m is prohibited under EU Council Regulation No. 1967/2006, illegal trawling is still one of the main threats to many protected habitats and their associated biodiversity, including *P. oceanica* meadows (González-Correa et al. 2005). For this reason, Anti-Trawling Artificial Reefs (AAR) are often used in the Mediterranean Sea to block illegal trawling (Sánchez-Jerez et al. 2002). They both enforce environmental protection, boosting associated assemblages, and benefit local communities that practice small-scale fishing activity, thus providing case studies merging ecological and socio-economic sustainability (Pipitone et al. 2014; Lima et al. 2019). The literature on the subject overall highlights the positive results of this strategy (Reis et al. 2021), but some gaps are still present because fish-oriented studies are few, with much attention paid to the benthic community, and are frequently aimed at assessing the economic benefits, overlooking the ecological drivers behind timing and patterns of the recovery.

There is an overall agreement on the benefits of trawling bans on fish assemblages in terms of species richness and fish size, besides food webs and sea floor health (Fraschetti et al. 2022). However, the effects can vary with local environmental conditions, enforcement efficacy and socio-economic factors. Similarly, the timeline for ecological recovery can differ widely. Some studies note rapid improvements in fish assemblages within 2–5 years of a trawling ban, whereas others observe only gradual changes, especially when habitat-forming species (such as corals and seagrasses) have been extensively damaged (Steadman et al. 2021). This issue could be partly related to the metrics used to assess the recovery of the community after the ban, typically based on species richness and abundance and therefore changing at

a quite slow pace (Coleman et al. 2015). Conversely, functional trait-based metrics may respond more readily due to the direct link between species traits and environmental conditions, including human impacts. These metrics can early signal a recovery, which would otherwise remain undetected if using species richness or biomass-based metrics alone (Mouillot et al. 2013; Aune et al. 2024). Within this context, length-based indicators are employed to assess the recovery of fish stocks, providing a simple metric for evaluating changes in population structure and being able to detect early signs of population recovery. Their reliability roots in a solid knowledge base showing that in heavily exploited fish populations, smaller size classes typically dominate catches, but once trawling pressure relieves, fish may grow to larger sizes (Kell et al. 2022). As more trait-based data become available, evidence suggests that multi-trait-based assessments are also effective in evaluating the efficacy of management actions in effectively rebuilding both the stocks and the ecological functions critical for long-term resilience, especially if they are complementing taxonomic and abundance approaches (Barnett et al. 2019; Costa et al. 2024). Also, functional traits linked to life strategies are increasingly gaining a role in providing insight into the recovery patterns of different species belonging to the same community and hence targeted by the same fishery. Life history strategies explain how, and how much, fish species may face environmental fluctuations, including those of anthropogenic origin such as climate change and fishing pressure (Hidalgo et al. 2011).

This study stems from the implementation of a conservation project dedicated to two Mediterranean marine Natura 2000 sites (Special Areas of Conservation [SACs]), located along the Italian coasts of the central Tyrrhenian Sea, where only artisanal and recreational fishing would be allowed. However, the trawling ban was poorly enforced, and, in response, an AAR was built in 2013 by submerging concrete structures along the lower limit of the *P. oceanica* meadows and closing the access to trawlers. The aim of the study was to explore the early ecological responses of fish communities to AAR deployment over the subsequent decade (2014–2023). A further objective was to assess whether and how the recovery patterns vary among target fish species in light of their life history strategies, an expectation supported by theory but so far rarely tested in marine fish communities (Hidalgo et al. 2011).

## 2 | Material and Methods

### 2.1 | Study Site

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

The SAC IT6000001 (hereafter SAC1) has an extension of 1762 ha and represents one of the most extensive meadows of *P. oceanica* in the central Tyrrhenian Sea. Its boundaries are marked by the mouths of the Chiarone River to the north and the Fiora River to the south. Mixed meadows of *P. oceanica* and *Cymodocea nodosa* are present between the coastline and the lower limit of the meadow, which is also characterized by the presence of sandy

patches. The SAC IT6000002 (hereafter SAC2) has an extension of 1112 ha, being characterized by an intricate bathymetry that generates a variety of microhabitats, and by a wide belt of matte along the lower bound of the meadow, at -30 m of depth, witnessing a marked regression.

In these areas, recreational and small-scale artisanal fisheries are allowed, whereas any other fishing activity is banned, including trawling. To fully enforce the trawling ban, in the aim to protect *P. oceanica* habitat, an AAR was deployed in 2013 within the frame of an EU LIFE project (LIFE09NAT/IT/00176) by submerging 550 concrete structures along the lower limit of the meadows and so precluding trawlers from illegally entering these areas (Figure 1). Since that moment, the state of fish assemblages associated with seagrass meadows has been surveyed through experimental fishing activities involving local fishermen along with research personnel.

## 2.2 | Experimental Fishing Plan and Data Collection

In the survey series, three campaigns were carried out in 2014–2015, 2019–2020 and 2022–2023 in both SACs, hereafter named Campaigns 1, 2, and 3 (C1, C2 and C3). The local artisanal

fishery fleet is based in the channel harbour located at the Fiora River mouth and has been involved in sampling campaigns. The number of vessels, between 7.5 and 8 m in length, decreased through the years, passing from 8 in 2014 to 5 in 2023. A total of 5 vessels per campaign carried out the experimental fishing activities, for a total of 32 hauls (5 h each) per SAC per campaign, subdivided among the two SACs.

An articulated sampling plan was designed to provide an accurate representation of catches on an annual basis. The local artisanal fishing fleet employs a variety of fishing gears to maximize catches based on the species most abundant in different seasons, requiring calibrated sampling in terms of both gear types and seasonality. Therefore, the hauls have been carried out all year long at a depth of 4–48 m, according to the seasonally used fishing gears, which are either trammel or gill nets with different mesh and structure (Table 1). In particular, ‘incastellata’ nets combine features of both trammel nets in the lower section and gillnets in the upper section, targeting species that inhabit different water column strata. ‘Barracuda’ are specialized gillnets, tailored to the behaviour and size of the target gregarious species that in this area are the shi drum (*Umbrina cirrosa*) and many sparids.

The sampling plan for the campaign 2019–2020 was affected by Covid restrictions, so 24 hauls were carried out instead of the 32

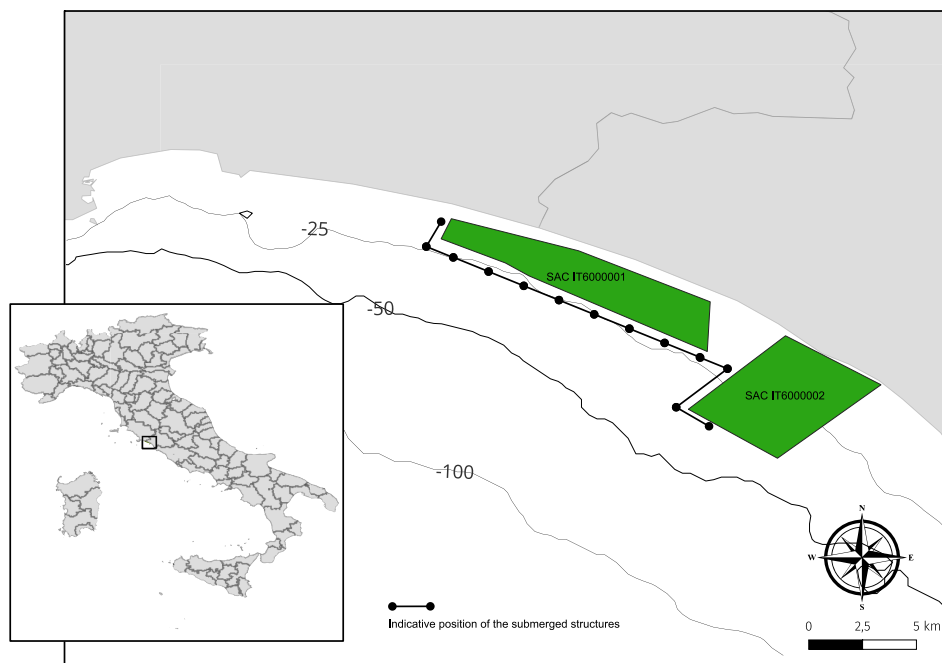


**FIGURE 1** | Geographic position of the two studied SACs (inlet) with the approximate distribution of the Anti-Trawling Artificial Reef.

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

| Net                                  | Mesh  | Season               | Hauls/SAC/campaign |
|--------------------------------------|-------|----------------------|--------------------|
| Trammel net + gillnet                | 22    | Spring/summer/autumn | 12-9-12            |
| Trammel net + gillnet                | 32–35 | All year long        | 8-6-8              |
| ‘Incastellata’ + “Barracuda” gillnet | 40–45 | All year long        | 8-6-8              |
| ‘Barracuda’ gillnet                  | 50    | Spring/summer/autumn | 4-3-4              |

for the other two campaigns. However, to provide a representative and comparable sampling, the proportion of the hauls using the various fishing gears was kept steady in the three campaigns and across seasons (Table 1).

As the main goal of the study was to compare the recovery patterns of different functional groups, we centered our data exclusively on fish species, although the cuttlefish (*Sepia officinalis*) and crustaceans such as lobsters and prawns (*Homarus gammarus*, *Palinurus elephas* and *Penaeus kerathurus*) were targeted by the fleet. Landings were analysed for bony and cartilaginous fish by identifying each specimen at the species level and recording both the total length and the wet weight of each specimen (Table S1).

## 2.3 | Statistical Analyses

Because the data did not follow a normal distribution (checked with the Shapiro–Wilk test), the non-parametric Kruskal–Wallis test and the Conover–Iman test for stochastic dominance were employed to highlight statistically significant differences in fish body size among both SACs and campaigns (Conover 1999; Kruskal and Wallis 1952). Analyses were performed using the package ‘conover.test’ in R (Dinno 2017; R Core Team 2024). Non-taxonomic size metrics and length-based indicators were calculated to describe the size structure of fish communities sampled in each SAC over the years: (i) the size spectrum parameters; (ii) the mean maximum length, MML; and (iii) the large fish index, LFI (Kell et al. 2022).

### 2.3.1 | Fish Size Spectra

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

We performed an ordinary least square linear regression (OLS model) between the midpoint of the size classes on the x-axis and the normalized fish abundance on the y-axis as the dependent variable at a  $\log_2$ – $\log_2$  scale using Cook’s Distance (Quinn and Keough 2002). Outliers were identified and removed through the `ols_plot_cooksd_bar` function from the ‘Olsrr’ package of R (Hebbali 2024) according to the thresholds and methods proposed by Bollen and Jackman (1985) and Sprules and Barth (2016).

To avoid collinearity between spectra coefficients (Spearman  $r_s = 0.94$ ;  $p < 0.001$ ), which may produce statistical artefacts of

increasing intercept with decreasing slope, the y-intercept of the log-x regression was centered so that the obtained elevation reflected the ‘height’ of the spectrum (Daan et al. 2005; Guet et al. 2016; Sprules and Barth 2016). Both the slope and elevation were extracted from the linear regression equation.

### 2.3.2 | Length-Based Indicators

The mean maximum Length indicator (MML) per species was calculated according to the ICES WGECo Report (ICES 2012) by assigning to each specimen an  $L_{\max}$  based on its species and averaging this across all individuals in a campaign (Piet and Jennings 2005).

The LFI expressed the proportion of total fish biomass sampled in each campaign exceeding a specified threshold length (Greenstreet et al. 2010). As the determination of a length threshold is prone to arbitrary choices, we calculated the LFI by applying a sixth-degree polynomial smoother to the LFI time series derived using threshold body lengths of 20, 25, 30, 35 and 40 cm and selected the threshold with the best fit (highest  $r^2$  value) as the ‘large fish’ threshold length (Modica et al. 2014). The measured threshold value was set at 35 cm.

## 2.4 | Functional Diversity of Fish Assemblages and Archetypal Analysis

To functionally characterize fish species, we selected 11 functional traits known to be involved in tolerance/sensitivity to overfishing and that can be grouped in three categories related to various life history strategies of the 61 sampled species (Ladds et al. 2018; De Juan et al. 2020). (1) Life history traits influencing the potential recovery of populations: age max, trophic level, k (the growth coefficient, a parameter of the von Bertalanffy growth function), generation time (the time from birth to average age of reproduction) and age at first maturity; (2) catchability traits influencing the probability of individuals to be caught: maximum length and sociability; and (3) resilience traits, which describe species’ reproductive potential, and thus their ability to recover after exploitation: fecundity, egg diameter, larval size at hatching and size at first maturity. We also calculated the PCI (Parental Care Index; Petrik et al. 2021), a composite index considering traits linked to reproductive investment: fertilization mode and reproductive guilds (*sensu* Balon 1990), the presence/absence of any type of parental care and the frequency of spawning.

Functional traits were derived from FishBase (Froese and Pauly 2024) using the R package ‘rfishbase’ (Boettiger et al. 2012). Additional trait data were obtained from searching both papers and reports, producing a dataset characterized by mixed variables, that is, categorical and continuous. We used the variance inflation factors (VIF; Dormann et al. 2013) to check for multicollinearity among explanatory variables and excluded size at maturity, larval size at hatching and generation time from the multivariate analysis due to their strong collinearity with age at maturity, k, and egg diameter. The correlation coefficients between the remaining nine functional traits were below 0.7 (Pearson coefficient). Before carrying out multivariate

analyses, continuous traits were log-transformed to approximate normality and reduce the impact of extreme values. Both quantitative and categorical data were weighted following Petrik et al. (2021).

Based on the selected traits, we performed an archetypal analysis (AA), an unsupervised learning method useful for characterizing life history strategies based on traits, resulting in a continuous grouping of species according to their functional strategies (Cutler and Breiman 1994; Pecuchet et al. 2017). The analysis was performed using the package ‘archetypes’ in R (Eugster and Leisch 2009). The ‘elbow criterion’ was employed to determine the optimal number of strategies, allowing us to minimize the residual sum of squares (RSS) while minimizing the number of strategies by assessing the number corresponding to a visually significant drop in the RSS (Pecuchet et al. 2017). The result of the AA, and notably the position in the traits space of the archetypes, was visualized using a principal component analysis (PCA) biplot. A two-way analysis of variance (ANOVA) was used to test for a significant effect of SACs and campaigns, as well as their interaction, on the average and range of total length within different functional strategy groups.

The patterns of temporal change in size structure of the three functional groups resulting from the AA were exemplified using the length frequency distribution (LFD) of 10 species representing each functional group, selected among the most abundant in terms of total catches across the three campaigns: five species for the opportunistic group (*Mullus barbatus*, *Mugil cephalus*, *Pagellus erythrinus*, *Diplodus annularis* and *Diplodus vulgaris*), four species for periodic (*U. cirrosa*, *Diplodus sargus* and *Scorpaena scrofa*) and two for equilibrium (*Mustelus mustelus* and *Raja clavata*). LFD per species was calculated by determining the class interval, the class midpoint and the frequency for each length group (Dimarchopoulou et al. 2018; Shin et al. 2005). A two-sample Kolmogorov–Smirnov test was used for a pairwise comparison of the LFD shapes between campaigns.

### 3 | Results

The dataset obtained is composed of 8504 fish belonging to 61 different species distributed into 31 families (Table S1). Sparidae was the most represented family with 15 species, followed by Carangidae (five species), Mugilidae (four species), Clupeidae and Serranidae, represented by three species each.

The number of sampled fish was higher in C3 ( $n = 3796$ ) and C1 ( $n = 2906$ ), whereas a quite lower number of fish was sampled in C2 ( $n = 1802$  records) because of the reduced sampling effort due to the COVID-19 pandemic. The minimum and maximum lengths observed per species were reported in (Table S1). The total length of sampled fish was significantly different in all the comparisons among SACs and Campaigns except for SAC2 C2 versus C3 (Kruskal–Wallis  $H = -0.498$ ,  $p = 0.309$ ).

The obtained size spectra provided a strong fit to the size distributions, according to  $R^2$  adjusted values (Table 2). A very similar trend can be identified in the two SACs, namely, negative slopes and positive elevations increased through time, resulting in steeper spectra and lower elevations in C1 than in the following C2 and C3 in both areas (Figure S1).

#### 3.1 | Length-Based Indicators

Length-based indicators showed concordant trends, with size increasing in both SACs. MML values increased over the years in both SACs, ranging from 24.68 to 46.43 in SAC1 and from 21.97 to 35.97 in SAC 2 (Table 2). Accordingly, the LFI grew in C1 versus C3 from 0.01 to 0.30 in SAC1 and similarly from 0.02 to 0.11 in SAC2 (Table 2), suggesting an increasing presence of larger individuals/species over the years.

#### 3.2 | Functional Characterization of Assemblages

Comprehensive data on all functional traits for the 61 recorded species were available and utilized in the AA. The optimal number of archetypes required to represent the spatial volume of trait-space was three, as pointed out by the largest drop in the RSS when passing from two to three archetypes. The three archetypal groups were superimposed on a principal component analysis (PCA) biplot, whose first two axes explained most of the trait variability (60.7%; Figure 2). The first axis (PC1) explained 40.1% of the total variability and was driven by egg diameter, age at first maturity and PCI (Parental Care Index), whereas the second axis (PC2) explained 20.6%, mostly driven by fecundity and maximum age. The three functional groups showed trait combinations closely corresponding to the life history strategies of the theoretical model of Winemiller and Rose (1992) and are henceforth referred to as opportunistic (O), periodic (P) and equilibrium (E) strategies, respectively (Table S1 and Figure 2). Both the O and P strategies were

**TABLE 2** | Length-based indicators per SAC and campaign: size spectra adjusted  $R^2$ , slope and elevation; mean maximum length (MML); and large fish index (LFI).

| SAC  | Campaign | Adjusted $R^2$ | Slope | Elevation | MML   | LFI  |
|------|----------|----------------|-------|-----------|-------|------|
| SAC1 | C1       | 0.94           | −2.75 | 2.65      | 24.68 | 0.01 |
|      | C2       | 0.74           | −1.01 | 4.49      | 36.38 | 0.23 |
|      | C3       | 0.64           | −0.32 | 5.53      | 46.43 | 0.3  |
| SAC2 | C1       | 0.83           | −2.71 | 3.39      | 21.97 | 0.02 |
|      | C2       | 0.57           | −1.52 | 4.85      | 32.61 | 0.09 |
|      | C3       | 0.79           | −0.56 | 7.02      | 35.97 | 0.11 |

prominent in the species pool, whereas three species only showed an E strategy: the smooth-hound *M. mustelus*, the thornback ray *R. clavata* and the common torpedo *Torpedo torpedo*.

Both the range size and average length of species within different functional groups (O, P and E) did not differ between

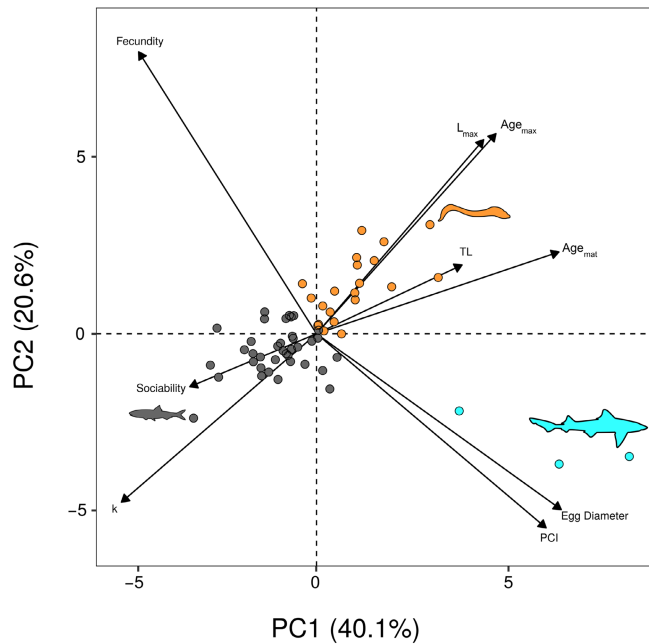


**FIGURE 2** | Biplot of the principal component analysis based on the 9 selected traits. Colours correspond to species life history strategy (see main text). Silhouettes show the three extreme archetypes of the trait space: the smooth hound *Mustelus mustelus*, equilibrium strategy (blue); the European anchovy *Engraulis encrasicolus*, opportunistic strategy (grey); the European conger *Conger conger*, periodic strategy (orange). Fish silhouettes were downloaded from PhyloPic (<https://www.phylopic.org>) under Creative Commons licenses. Traits' abbreviations: Age<sub>mat</sub> = age at first maturity, Age<sub>max</sub> = maximum age, L<sub>max</sub> = maximum length, TL = trophic level.

SACs (two-way ANOVA  $F < 1.79$ ,  $p > 0.1$  in all cases) while significantly increasing over the years (two-way ANOVA  $F > 9.1$ ,  $p < 0.05$  in all cases), with the only exception of the average length of periodic species (two-way ANOVA  $F = 7.5$ ,  $p = 0.071$ ). The post hoc Tukey test confirmed that most of this difference was attributable to the significant increase in fish size between C1 and C3 (adjusted  $p < 0.05$ ).

The violin plots evidence a larger bandwidth and a flattened shape for the first campaign for all the groups (Figure 3). The violin bandwidth becomes narrower, and the maximum size recorded increases through time for all the functional groups, but the violin shapes change in different ways. Opportunistic species pass from a unimodal distribution of the total length to a skewed one. Periodic species show a change in the kernel probability density, reaching a bimodal distribution of sizes in C3, with large outlier specimens ( $> 50$  cm) becoming more frequent. Equilibrium species show a delayed change in the violin shape, passing from a nearly unimodal distribution of the length in both C1 and C2 to a more skewed one in C3, due to the presence of large outlier specimens never recorded before ( $> 80$  cm).

The LFD shapes were significantly different among the three campaigns for all the 10 selected species representing the three life history strategies, as shown by the significant Kolmogorov–Smirnov tests ( $p < 0.05$ ) (Figure S2). The only exceptions were the red mullet, flathead grey mullet and smooth hound in C1 versus C2; the annular seabream in C1 versus C3; and the axillary seabream in C2 versus C3. The opportunistic species showed a unimodal distribution across the three campaigns, with the larger classes increasing their frequency through time and with some even larger individuals appearing in C3 (Figure 4). The red mullet showed a different pattern, with specimens following a unimodal distribution across the size classes without any significant difference across the three campaigns (Figure S2). All three periodic species showed a skewed distribution towards smaller size classes in C1, becoming progressively unimodal and including larger

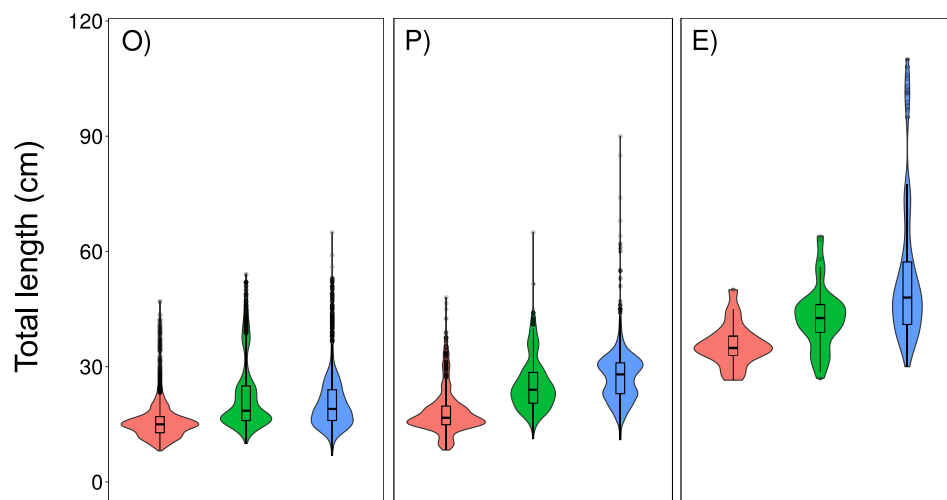


**FIGURE 3** | Violin plots showing the distribution of the total length (in cm) in the three groups corresponding to different life history strategies (E = equilibrium; O = opportunistic; P = periodic) in different campaigns (light red, C1; green, C2; blue, C3). The violin contours represent the kernel probability density, with thicker areas indicating a higher density of observations. Horizontal lines represent the median, whereas dots indicate outliers.

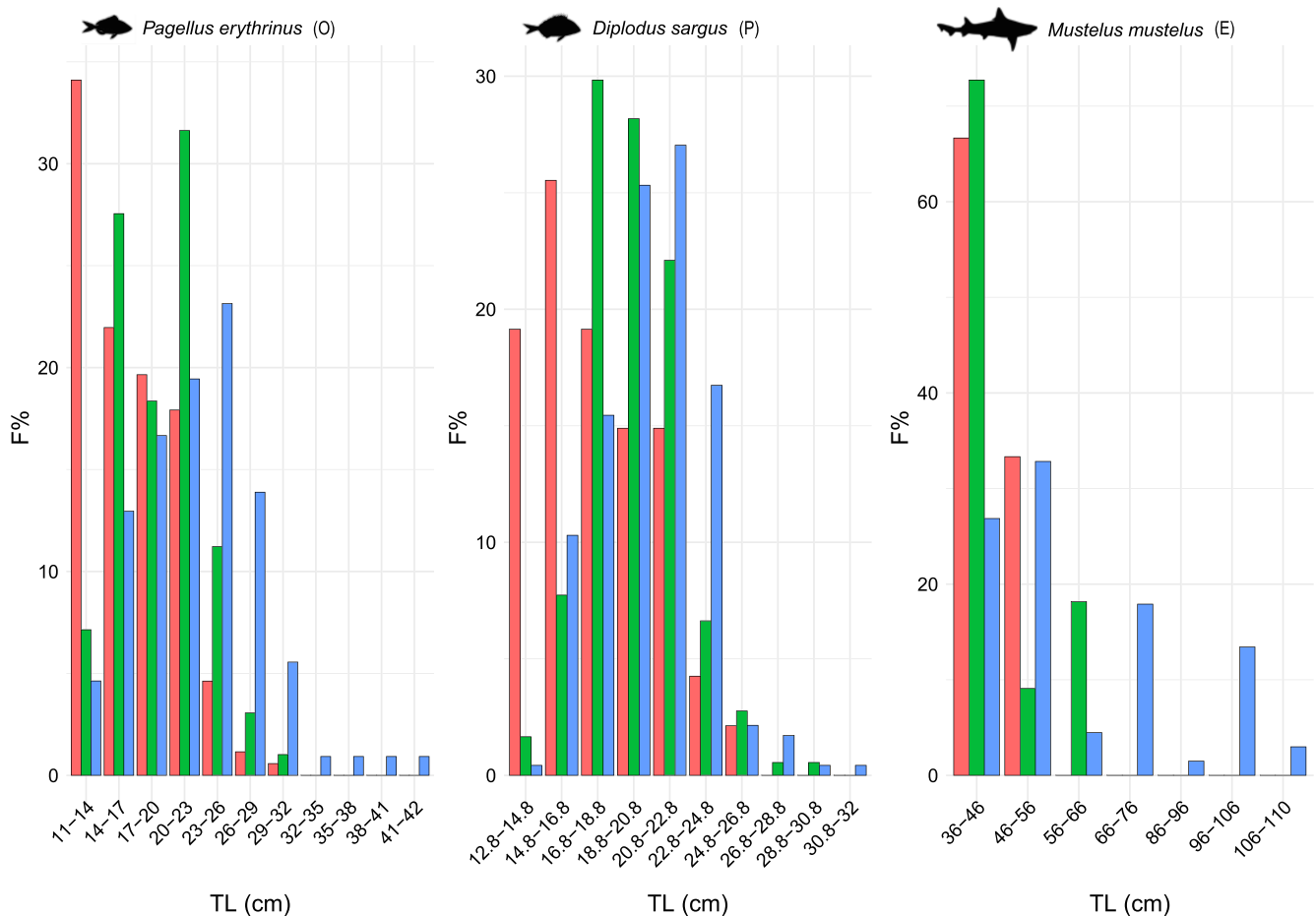


**FIGURE 4** | Length frequency distribution across the three campaigns for three species representing life history strategies: O = opportunistic, P = periodic, E = equilibrium. TL = total length. Red bars: C1; green bars: C2; blue bars: C3.

size classes over the following campaigns. The two equilibrium species showed a marked increase in the frequency of large to very large size classes, with a marked increase of these latter in C3 for the smooth hound (Figure 4).

#### 4 | Discussion

In the Mediterranean Sea, as across the world, trawling bans have been largely proved to be positive for both marine biodiversity and small-scale fishery revenues, providing a valid option in the sustainable management of marine resources (Dimarchopoulou et al. 2018; Pipitone et al. 2023). AARs are increasingly used worldwide, and particularly in European countries, with the aim of both protecting and enhancing biodiversity, by either enforcing trawling bans or increasing habitat complexity, and to sustain small-scale fisheries by reducing the competition with other fishing fleets (Lima et al. 2019; Vivier et al. 2021).

To date, few studies have assessed the effectiveness of the trawling ban implemented by AAR, and even fewer have utilized a sampling design based on small-scale fishery gears, particularly in the Mediterranean Sea. This situation creates a gap in the evaluation of this conservation strategy (Coll et al. 1998; Charbonnel et al. 2002; Iannibelli and Musmarra 2008; Bodilis et al. 2011). Our data contribute to such a case study by

analysing how enforcing a ban on illegal trawling through the deployment of an AAR reflects on target species for small-scale fisheries across a decade and how the fish's functional strategies influenced their recovery. To this end, we used length-based indicators that provide a straightforward metric for evaluating changes in population structure, being able to detect early signs of population recovery. In heavily exploited fish populations, smaller size classes typically dominate catches, but once trawling pressure relieves, fish may grow to larger sizes so that length-based indicators may be reliably used even in data-poor cases (Kell et al. 2022). This approach also allowed us to skip a caveat of this study due to COVID-19 restrictions that affected the C2 sampling, which occurred in 2019–2020: The lower fishing effort of this campaign would make abundance-based indices poorly comparable, whereas the increase in fish length could be evidenced even in the presence of a lower number of hauls (and fish), in any case representative of both seasons and gears.

Our results indicated that the fish reached a significantly greater length through the 10 years of the post-ban survey, suggesting a generalized improvement of the assemblage. Both the LFI and MML significantly increased from C1 to C2 to C3. This post-ban growth is attributed to the rising abundance of larger, slower-growing fish, suggesting a potential shift in age structure towards older and larger individuals that were previously depleted by fishing activities. Both indices responded quite readily, showing significant increases in the 5 years that occurred between C1

and C2, as well as between C2 and C3, corroborating the idea that a time span of 5–10 years is appropriate for their effective use (Shin et al. 2005). Length-based indicators applied to data from C2 resulted in alignment with this trend, confirming that the sampling plan of C2 was qualitatively consistent with those of the other campaigns.

The size spectra analysis showed that regression lines in both SACs flattened and increased their elevation across the 10 years of observation. The elevation of the spectra serves as a proxy of the community abundance across the entire size range and has been inversely correlated with the fishing pressure in many case studies (Trenkel and Rochet 2003; Daan et al. 2005; Shin et al. 2005; Gristina et al. 2006). The slope of size spectra is related to the frequency of small-bodied specimens so that if fish are allowed to survive and grow large, their abundance in higher size classes can increase, causing the slope to flatten. Flattening then suggests a more balanced or restored community size structure, with relatively more large individuals than before. As a historical example, in the North Sea, the rising fishing pressure recorded in the 1973–1993 period was correlated to the increasingly steeper slope of the size spectra (Rice and Gislason 1996). Within this framework, our findings agree with the bulk of data showing that size spectra modifications of both slope and height are directly related to fishing pressure, either while increasing or decreasing.

Recent papers have evidenced the relevance of functional traits in characterizing the fish community inhabiting Mediterranean seagrasses, particularly *P. oceanica*, providing information unevidenced by taxonomic diversity (Lattanzi et al. 2024; Bellisario et al. 2025). Fish functional assemblages have been shown to be non-randomly structured, showing a core of functionally similar fish species characterized by *r-like* reproductive strategies and low-to-intermediate trophic levels (Bellisario et al. 2025). However, fish species poorly fit along a linear *r-like* to *K-like* continuum, because they frequently show a mix of traits belonging to both strategies, and due to the fact that although functional group definitions rely on selected traits, life history strategies rather emerge from the combined influence of several key traits that interact with and place constraints on each other (Winemiller et al. 2015). Therefore, fish life history strategies are more frequently represented as a triangle in trait space, with each endpoint representing a unique life history strategy characterized by a combination of key traits: opportunistic, periodic and equilibrium (Winemiller and Rose 1992; Pecuchet et al. 2017). Trademarks of the opportunistic strategy are early maturation, small adult size, short generation time and high reproductive output over short intervals, whereas the periodic strategy is characterized by delayed maturation, large adult size, high fecundity and low offspring survival. Finally, the equilibrium strategy features moderate to late maturation, low fecundity, greater parental investment and comparatively stable juvenile survival. Ongoing comparative studies show that these life history patterns are useful for predicting responses to fishing pressure, alongside habitat disturbance and climate change (Hidalgo et al. 2011).

Our results showed that the bulk of species are classified as opportunistic, representing 59% of the total, followed by the periodic at 36%, whereas the equilibrium strategy is represented by

three species only, 5%. This was an expected finding because a relevant part of the Mediterranean fish species are classified as opportunistic (Pecuchet et al. 2017). Also, *P. oceanica* fish assemblages have been shown as characterized by small-sized, rapidly growing and low trophic level species, exhibiting traits typical of an opportunistic strategy (Bellisario et al. 2025). Accordingly, the sampled species belonging to this group are from families both highly associated with seagrass meadows and targeted by coastal fisheries, such as sparid or mugilid, besides the red mullet (*M. barbatus*) (Lattanzi et al. 2024). Among the periodic, we found highly fished species such as the shi drum (*U. cirrosa*), the red scorpionfish (*S. scrofa*) and large sparids like the common pandora (*P. erythrinus*). Sharks and skates, representing equilibrium species, are quite rarely recorded in Mediterranean seagrasses, in accordance with our results (Lattanzi et al. 2024).

Studies are increasingly demonstrating that reduced fishing impacts may differentially benefit fish community components because of the interplay between life history strategies, disturbance nature and environmental conditions (Otero and Hidalgo 2023). Our data indicated that over the 10-year survey period, local populations exhibited recovery, as evidenced by significant increases in all fish length-based indicators across functional groups, albeit with varying patterns. Equilibrium species showed a delayed recovery, with outlier longer specimens appearing only in the last survey, 10 years after the protection from illegal trawling, whereas opportunistic and periodic species responded more quickly. This is somewhat expected, because it is known that when looking at length indicators, a transition from a rapid but size-limited recovery to a delayed but steady increase in length measures is predicted along the opportunistic to equilibrium gradient. These differences stem from trade-offs in each strategy's growth, reproduction and survivorship patterns. Opportunistic species may proliferate quickly, thanks to their high fecundity and short generation times. However, as these fish do not typically attain large body sizes, increases in length-based metrics may be less remarkable. Periodic species have quite longer generation times and delayed maturity, sometimes showing pulses in recruitment success due to fluctuations of environmental conditions (e.g., suitable temperature or abundant food). After these pulses, an uptick in the proportion of bigger individuals can drive shifts in size-based metrics. The recording of a bimodal distribution in the distribution of the total length for periodic species in C3 may suggest a role for environmental factors in producing the observed pattern of recovery. Equilibrium strategists' life history attributes (e.g., parental care and stable juvenile survival) lead to a methodical rebound, but their low growth rate takes more time to redistribute a significant rate of the biomass in the higher size classes. This is evidenced by the modification of the LFD of the smooth hound, showing higher classes being populated only in the C3. Accordingly, nearly all the outliers recorded in the C3 violin plot are smooth hounds, likely due to their greater body length and lower growth rate with respect to the two ray species belonging to the equilibrium group.

Our results align with those presented by the few other Mediterranean case studies. As to assemblage recovery, fish number, size and biomass increased for all the studied species in the case of the two AARs submerged in Salerno Bay, with a stronger effect for the AAR associated with the seagrass meadows

with respect to that placed on sandy bottoms (Iannibelli and Musmarra 2008). A 20-year study conducted in the MPA of Golfe-Juan, located in the NW Mediterranean, from 1988 to 1998, demonstrated a pattern of increasing fish richness and density, particularly among commercial species. Between 1998 and 2008, a reversal of the prior positive trend likely resulted from insufficient surveillance post-2002 and the resumption of fishery activities for 1 year in 2004 (Bodilis et al. 2011). Although general patterns have been documented, only a limited number of studies have linked functional traits to recovery patterns following a trawling ban in marine environments, and none have incorporated life history strategies. This is the case of one of the most studied trawling ban examples in the Mediterranean Sea, although not involving an AAR: A year-round trawl ban has been imposed since 1990 in Castellammare Gulf, allowing a long-time series of data to be collected according to a Before-After-Control-Impact (BACI) design (Pipitone et al. 2023 and references herein). Here, demersal species showed a significant increase in biomass compared to data collected both before the ban and in other trawled areas, particularly for highly commercial species at depths used by artisanal fishermen (Pipitone et al. 2023). According to our findings, the size structure recovery showed larger median sizes and an increased proportion of larger individuals compared to trawled areas; however, whereas mesopredators boosted, sharks and rays still had a low biomass, suggesting that the recovery was still taking place for these species (Pipitone et al. 2023).

## 5 | Conclusions

Our findings contribute to the growing body of evidence indicating that, in addition to the overall recovery pattern resulting from the trawling ban, the factors affecting both the magnitude and duration of recovery are numerous and interconnected. Although environmental parameters were not included in the analysis, the pattern of length increase shown by periodic species suggests a role for environmental fluctuations in boosting waves of recruitment. Furthermore, an AAR intrinsic effect may also play a role and could not be split from that of the enforced illegal trawling ban, because it has been shown that artificial reefs themselves may increase fish abundance, even in the absence of fishing pressure mitigation (Vivier et al. 2021).

The metrics employed indicate a clear recovery of the effectively protected fish assemblages. The patterns observed in relation to the life history strategies align with expected species traits when fishing pressure is relieved. This supports the notion that AAR may effectively enhance both biodiversity and the recovery of small-scale fisheries, particularly in the context of central Mediterranean coasts (Iannibelli and Musmarra 2008; Vivier et al. 2021).

### Author Contributions

R.C. and G.N. conceived the ideas and designed the methodology. All authors contributed to collect the data. A.L. and B.B. analysed the data. R.C. led the writing of the manuscript. R.C. and G.N. provided resources and supervised the work. All authors contributed critically to the drafts and gave final approval for publication.

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### Ethics Statement

No animal testing was performed during this study. No permits were required for samplings that were carried out under an allowed small-scale fishery regime.

### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

The authors have provided data information in the [Supporting Information](#) section at the end of this article (see Table S1).

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Fish species sampled with their family, life history strategy and minimum and maximum values of total length recorded. Life history strategies: E, equilibrium; P, periodic, O, opportunistic. See the main text for further explanations. **Figure S1:** Size spectra per SAC and Campaign. The lines represent the linear fitting of the size spectrum related to C1 (light red), C2 (green) and C3 (blue). **Figure S2:** Length frequency distribution across the three campaigns for seven representative species of the life history strategies: O=opportunistic, P=periodic, E=equilibrium. TL=total length. Red bars: C1; green bars: C2; blue bars: C3.