



ROV-based monitoring of passive ecological recovery in a deep-sea no-take fishery reserve



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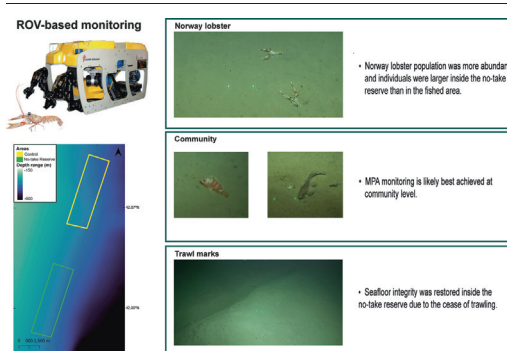
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HIGHLIGHTS

- Norway lobster population was more abundant within the no-take reserve.
- Norway lobster individuals were larger within the no-take reserve.
- Seafloor integrity was restored within the no-take reserve.
- MPA monitoring is likely best achieved at community level.
- ROVs are useful non-invasive tools for deep-sea MPA monitoring.

GRAPHICAL ABSTRACT



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ABSTRACT

In the context of marine conservation, trawl fishing activity is the most important ecosystem stressor in demersal Mediterranean waters. Limited management measures in bottom trawling have caused deep-sea stocks of the iconic Norway lobster *Nephrops norvegicus* to decrease over the last decade. This crustacean acts as an umbrella species for co-existing megafauna. Here, we used non-invasive Remote Operated Vehicle (ROV) video-surveys to investigate the status of a pilot deep-sea no-take reserve implemented in the northwestern Mediterranean by quantifying demographic indicators of Norway lobsters and the co-existing benthic community, seafloor restoration, and the presence of marine litter. The results revealed that in the no-take reserve the Norway lobster stock showed higher abundance and biomass, and slightly larger body sizes than in the control area without fishing prohibition. Some taxa, such as the fishes *Helicolenus dactylopterus* and *Trigla lyra* and anemones of the family Cerianthidae, increased in abundance. We also observed that all trawling marks were smoothed and most of the seafloor was intact, clear indicators of the recovery of the muddy seafloor. The accumulation of marine debris and terrestrial vegetation was similar in the no-take reserve and the fished area. On the basis of the results of this study, we suggest that the use of no-take reserves might be an effective measure for recovering the Norway lobster stock, its co-existing megafauna community, and the surrounding demersal habitat. We also suggest that ROV video-survey might be a useful, and non-invasive method to monitor megafauna and seafloor status in protected deep-sea environments.

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1. Introduction

The Mediterranean Sea is a biodiversity hotspot, constituting <1 % of the global ocean surface, but comprising up to 18 % of the world's marine species, 25–30 % of them being endemic (Bianchi and Morri, 2000; Coll et al., 2010; Regato, 2008). Fishing activity is one of the most important ecosystem stressors in Mediterranean waters, altering biodiversity and habitats (IOC-UNESCO, 2021). Fisheries play an important economic and social role in local and regional economies, representing nearly 20 % by weight and 35 % by value of European fishery production (Papaconstantinou and Farrugio, 2000). Although in 2019 the European Commission implemented a global management strategy for the whole western Mediterranean (WestMED initiative, European Commission, 2017a, 2017b), each country independently legislates its own fisheries, applying diverse management measures linked to the reduction of effort, such as a decrease in the number or fishing capacity of vessels, governing bottom otter trawl (trawling, hereafter), or restricting fishing activity seasonally or in particular areas (Aristegui-Ezquibela et al., 2021; Papaconstantinou and Farrugio, 2000).

Beyond the potential effects of global change on marine biodiversity and functioning (Denman, 2008; Levin and Le Bris, 2015; Trindade-Santos et al., 2020), the high-impact bottom trawling that has been used by Mediterranean Sea fisheries for >80 years (Palanques et al., 2006; Puig et al., 2012) is one of the main drivers of ecosystem change in deep-sea Mediterranean demersal communities (Danovaro et al., 2017). The main concern about applying management measures for fishery sustainability in the Mediterranean is related to the multi-specificity of fisheries preventing bottom trawl fleets from catching just the target species, rather than a relatively large number of unwanted species that are discarded (i.e., wasted), which may represent, on average, 25 % of the total catches (Blanco et al., 2023; Gorelli et al., 2016; Sánchez et al., 2004). Bottom trawling is a poorly selective fishing method with a great impact on demersal communities and deep-sea ecosystems. Consequently, most Mediterranean stocks (ca. 62.5 %) are being fished at their maximum sustainable yield or above their maximum reaching unsustainable levels (FAO, 2022; Papaconstantinou and Farrugio, 2000; Tsikliras et al., 2015). Moreover, bottom trawlers disturb and destroy seafloor habitats in their path, including seagrasses, coral reefs, or rock gardens, considered key habitats for multiple species (Stiles et al., 2010; Reed et al., 2007). Bottom trawling can also strongly modify seafloor morphology because of the resuspension and removal of a large amount of sediment by the action of wires, otter doors, sweeps, and nets (Palanques et al., 2006; Puig et al., 2012). As a result, historically intense commercial trawling has acted as a geological force flattening the surface of the continental shelf and slope margins in the Mediterranean, exposing its hardened substrate (Puig et al., 2012).

In the western Mediterranean Sea, the trawl fleet operates at a depth of between 50 and 800 m (Gorelli et al., 2011) targeting Norway lobster *Nephrops norvegicus* at a 300–500 m depth (Sardà, 1998). This demersal decapod is one of the most important demersal stocks for European fisheries, distributed on muddy bottoms along the northeast Atlantic Ocean and the Mediterranean Sea (Aguzzi et al., 2023; Aguzzi and Sardà, 2008; Bell et al., 2006; Ungfors et al., 2013). Nevertheless, due to high fishing pressure and ineffective management measures for the sustainable exploitation of the species, the catches of this iconic European crustacean have been decreasing over the last several years (from 2008 to 2016 there has been a decrease of 19 % in catches in the EU, EUMOFA, 2019; Letschert et al., 2021; Lolas and Vafidis, 2021). The species' dependency upon fragile silt and clay mud habitats, in which Norway lobsters dig their burrows, makes it highly vulnerable to trawling impacts (Campbell et al., 2009). Also, as a marine ecosystem engineer, the Norway lobster's burrowing behaviour increases habitat heterogeneity and provides structures for other co-existing megafauna, acting as an umbrella species (i.e., a key conservation target to protect the whole benthic community; Roberge and Angelstam, 2004).

The establishment of Marine Protected Areas (MPAs), such as legally recognized no-take reserves where fishery activity is prohibited, could be a useful management measure for not only recovering the over-exploited Norway lobster stock, in terms of density and body size, but also promoting

the co-existing benthic community (Melaku Canu et al., 2020; Vigo et al., 2022, 2021) and enhancing seabed quality and overall demersal richness (Cabral et al., 2020; Sala-Coromina et al., 2021; Sala and Giakoumi, 2018). The benefits obtained from MPAs could also be observed in adjacent areas, as a result of the spillover of adults and juveniles from the protected area (Lenihan et al., 2021; Sala-Coromina et al., 2021). Management evaluations within no-take fishery reserves have already been carried out on crustacean species, such as the European lobster *Homarus gammarus* and the spiny lobster *Palinurus elephas* (Follesa et al., 2011; Goñi et al., 2010; Padilla et al., 2022; Wiig et al., 2013). In the Mediterranean Sea, there are very few assessments of the use of no-take reserves for the recovery of Norway lobster populations, except for the Pomo Pit area in the Adriatic (Bastardie et al., 2017; Melaku Canu et al., 2020) and a no-take fishery reserve located at a deeper depth (375–400 m) in the northwestern Mediterranean (Order APA/753/2020; <https://www.boe.es/eli/es/o/2020/07/31/apa753To>; Vigo et al., 2021).

Monitoring strategies for the evaluation of the efficacy of no-take reserves for the recovery of Norway lobster stocks are a priority (Lester et al., 2009). Unfortunately, compared to shallow areas (e.g., Linares et al., 2012; Lloret et al., 2006), the monitoring of deep-sea stocks is a technological and operational challenge (Aguzzi et al., 2020). Experimental trawling remains the most common tool to quantify the abundance and biomass of deep-sea stocks (e.g., Fiorentini, 1999; Sánchez et al., 2007; Tuset et al., 2021). However, its use in an MPA is not desirable due to its intrinsic impact on benthic communities and habitats. As an alternative strategy to assess the status of demersal and benthic communities, visual monitoring through the use of Remotely Operated Vehicles (ROVs), Autonomous Underwater Vehicles (AUVs), and other systems is increasingly employed (Benoist et al., 2019; Chimienti et al., 2018; Huvne et al., 2016). In fact, there are regular underwater television (UWTV) surveys that are conducted to provide abundance estimates for Norway lobsters on the functional units (FUs) in the North Atlantic to assess their stocks (Dobby et al., 2021). Video-surveys can provide habitat assessments evaluating anthropogenic impacts at the level of seabed sediment integrity or the presence of marine litter (Bo et al., 2014; Mecho et al., 2020) defined as any persistent, manufactured or processed solid material discarded, disposed, or abandoned (definition by the United Nations Environment Programme; UNEP).

In this study, we used ROV video-surveys to investigate the ecological and morphological status of a pilot no-take reserve implemented in a deep-sea northwestern Mediterranean area 2.5 years after its establishment as well as the situation of a nearby control (fished) area. We followed an ecosystem-based approach, i.e., by quantifying the demographic indicators of abundance, biomass, and body size of Norway lobsters and other co-occurring benthic megafauna, including the main predators of Norway lobsters. We also examined the status of seafloor recovery as a metric for passive recovery from trawling impacts and the presence of marine litter and terrestrial vegetation in the reserve.

2. Materials & methods

2.1. Study area and ROV surveying procedures

This study was conducted in a deep-sea no-take fishery reserve with an area of 10 km² (hereafter referred to as no-take reserve), located along the continental margin from 351 to 475 m depth in the northwestern Mediterranean Sea (Fig. 1A). This no-take reserve was established on the northern flank of the Palamós canyon, where deep-sea trawling has taken place for around a century (Puig et al., 2012). In the whole slope region, the sediment is compact silt and clay mud suitable for the excavation of burrows by Norway lobsters (Maynou and Sardà, 1997). This reserve was created in 2020 by the Spanish Government (Order APA/753/2020; <https://www.boe.es/eli/es/o/2020/07/31/apa753To>) with the main objective of recovering the stock of Norway lobster in this Mediterranean area. However, before the designation as an MPA, fishing activity inside the no-take reserve was ceased in September 2017 through an agreement, i.e., not officially enforced, between two local fishermen's associations (Roses and

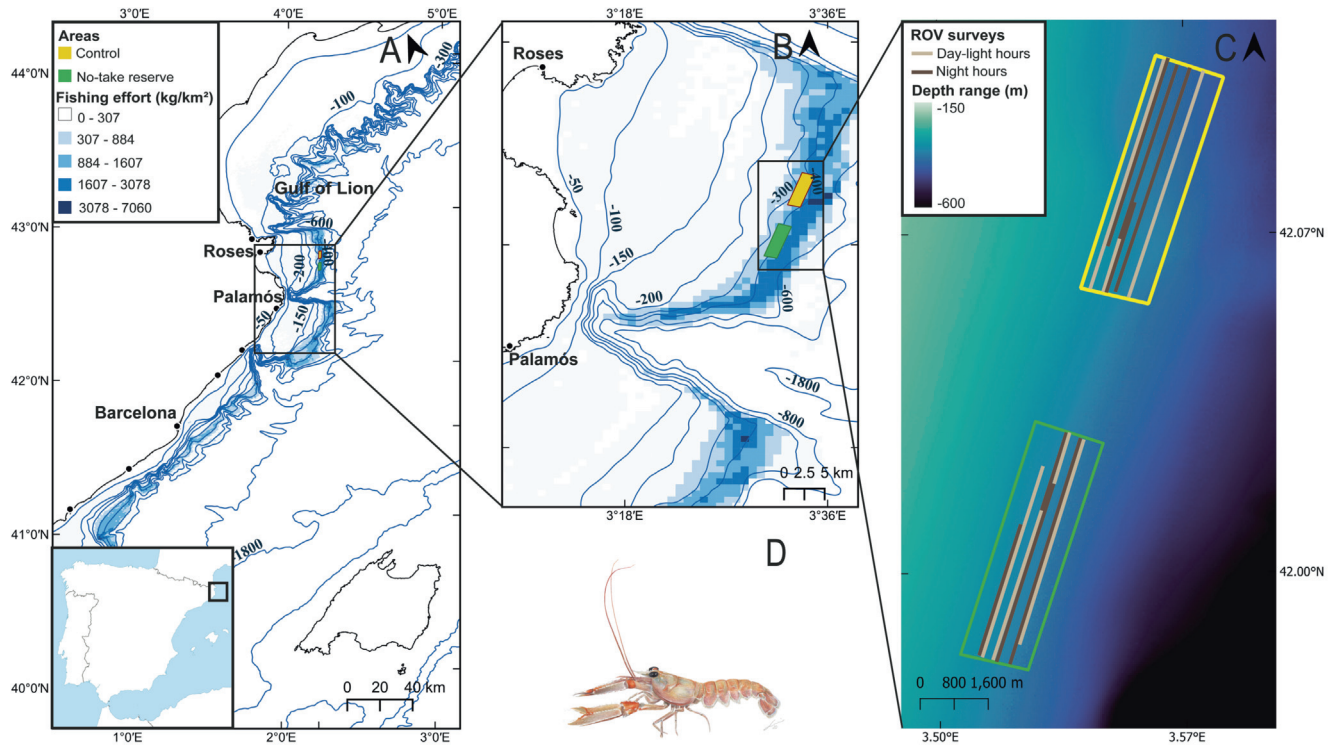


Fig. 1. The study area showing A) the spatial distribution of Norway lobster catches, B) the location of the no-take reserve and the control area, and C) the position of the ROV video-surveys. The spatial distribution of Norway lobster catches accumulated was obtained by combining vessel monitoring system information and official daily landing data in the time period 2005–2018 (European Commission, 2022). D) Norway lobster illustration by Joan Mir-Arguimbau.

Palamós). We used, for comparative purposes, an adjacent control area (i.e., ecologically, geomorphologically and bathymetrically equivalent) where bottom trawling was permitted, having the same dimensions as the no-take zone (Fig. 1B). The no-take reserve has a bathymetric range of 310–475 m and the control area has a range of 290–440 m depth (Fig. 1C).

Just prior to the cessation of fishing in the no-take reserve (August 2017), we conducted 4 experimental fishing surveys in the no-take area and 2 in the control area, using an otter bottom trawl net of a square

mesh size of 12 mm. All hauls were of 1 h of duration, with an average speed of 2.5 knots. The swept area (km²) of all hauls was estimated based on vessel speed (S, in knots), average horizontal opening of the net (BT, in m) and haul duration (H, in h) between the initial and final position of the gear on the bottom (Sparre and Venema, 1998). The preliminary results of these experimental trawling surveys (see Fig. 2) indicated that abundance (control area; mean = 1584.31; SD = 925.89 No.·km⁻²; no-take reserve; mean = 2789.56; SD = 1446.37 No.·km⁻²), biomass (control

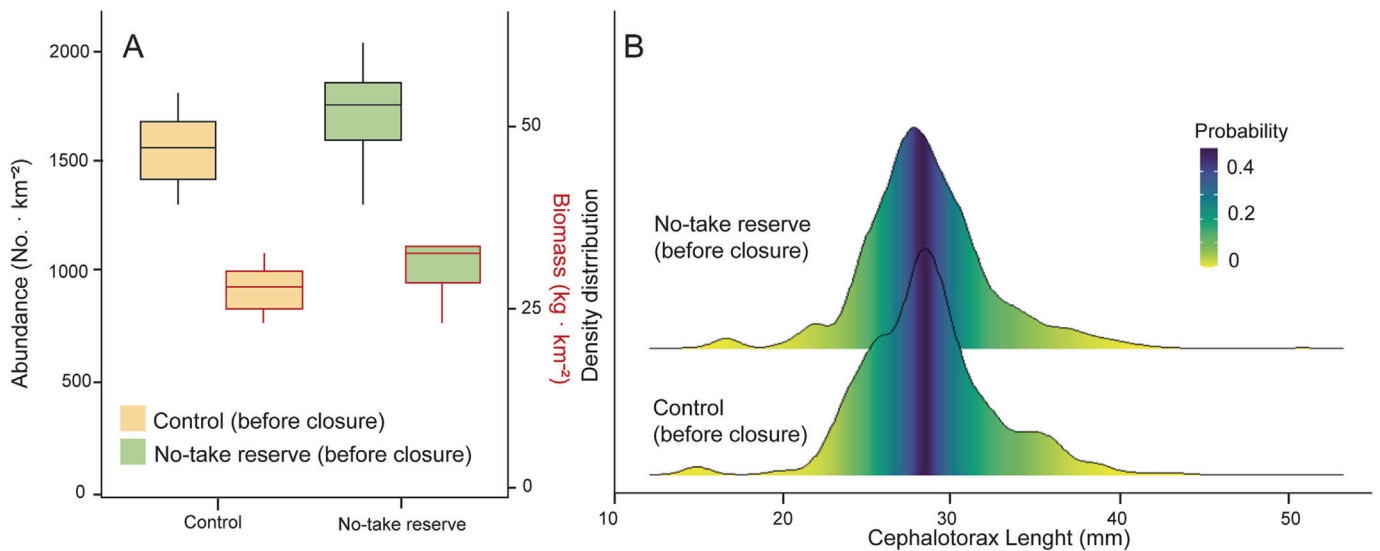


Fig. 2. A) Abundance and biomass of the Norway lobster in the no-take reserve and in the control area in August 2017 as determined by experimental trawl fishing. B) Body size density distribution determined by experimental trawl fishing in August 2017. Based on the color degradation, dark blue indicates the highest likelihood of sizes (CL, mm) coinciding with the mean size.

area; mean = 24.65; SD = 12.54 kg·km⁻²; no-take reserve; mean = 42.16; SD = 20.79 kg·km⁻²), and size distribution (control area; mean = 23.37; SD = 4.97 mm CL; no-take reserve; mean = 27.30; SD = 4.81 mm) of Norway lobster did not differ between both control area and no-take reserve (Abundance; $F_{1, 5} = 0.31$, $p = 0.61$; Biomass; $\chi^2 = 0.86$; $p = 0.35$; Mean size distribution; $\chi^2 = 0.05$, $p = 0.48$).

To monitor Norway lobster (Fig. 1D) abundance and biomass in a non-invasive way, ROV video-surveys were performed in both the no-take zone and adjacent control area in February 2020, 2.5 years after the implementation of the no-take reserve. In particular, we conducted six ROV video-survey transects in the no-take reserve (341–376 m depth) and six in the control area (327–424 m depth) (Fig. 1C, Supplementary Material Table A1). These surveys were performed on board the R/V *Sarmiento de Gamboa* with ROV Liropus 2000, a Super-Mohawk ROV. The ROV was equipped with a forward-facing video camera (HD Kongsberg OE14-502) positioned below four Halogen 250 W Deep Sea Power & Light (DSPL) lights. The ROV also had two parallel lasers with 10 cm separation, to provide a reference scale for animal sizing within the camera field of view. Underwater ROV positioning was measured by a High Precision Acoustic Positioning system (HiPAP; 350 P Simrad) with a spatial accuracy of 0.3 % and an error of range of detection <20 cm. This was linked to the Differential Global Positioning System of the R/V.

The ROV video-surveys were continuously recorded and conducted during consecutive 24 h cycles close to the bottom (50–100 cm of altitude above the seabed) at a constant speed of 0.6 m·s⁻¹ (Ayma et al., 2016; Grinyó et al., 2022; Mecho et al., 2020, 2018). The video-swept area was calculated from the ROV instantaneous velocity each second, multiplied by the width of the image as measured by the laser pointer (approximately 1.5 m width at a constant height of 1.8–2 m). Despite possible bathymetric and swept area differences between surveys, each ROV video-survey conducted was considered a replicate within each. We standardized by adjusting the resulting parameters according to the swept area. We also quantified the presence of other co-occurring megafauna species, marine litter, organic debris such as terrestrial vegetation, and the status and recovery of the seabed by categorizing the trawling impact marks (see below for a more detailed explanation).

2.2. Norway lobster evaluation

To estimate the abundance and biomass of Norway lobsters in the no-take reserve and in the control area, we conducted two complementary approaches: “burrow-system counting” and “animal counting”. In the burrow-system approach, we followed the assessment protocols of the Working Group on Nephrops Surveys (ICES, 2016; Dobby et al., 2021), counting all burrow-systems in the control area and the no-take reserve. Burrows of Norway lobster present characteristic features related to the shape and appearance of burrow openings that occasionally number two or three in a system, and are easily identified (e.g., Chapman, 1980; Froglija et al., 1997; Tuck et al., 1994; Supplementary Material Fig. A2). To standardize the counting of burrows from each video-transect, their abundance was standardized by the unit of video-swept seabed surface, obtaining a density estimate as the number of burrow-systems per km². We assumed that one burrow-system contained only one Norway lobster as this species is highly territorial and usually only one adult occupies the burrow-system (Johnson et al., 2008; Sbragaglia et al., 2017; Vigo et al., 2021). We also considered that all burrow-systems were occupied, as unoccupied burrows rapidly degrade and collapse (Marrs et al., 1996).

In the animal counting approach, we standardized the number of individuals counted in ROV transects per unit of video-swept area during 24 h cycles. The video-swept area was calculated in m² for each minute of video recording (given the constancy of cruising; see above), and then converted into km². Therefore, the data were presented as the number of individuals per km² (i.e., density). Only in the animal counting approach, we tested for differences considering the abundance of Norway lobsters during daylight hours and then during nighttime hours (considering sunrise at 8 am and sunset at 6 pm).

To test the differences between Norway lobster counting approaches, burrow-system and animal counting, between the control area and the no-take reserve, two-way ANOVA tests were conducted. The test allowed assessing the variance of the abundance of Norway lobsters with two fixed factors (“Area” for the control and no-take reserve, and “Activity” for presence in daylight hours and in nighttime hours). For burrow abundance, we conducted non-parametric Kruskal-Wallis tests in the R software version 4.1.2 (R Core Team, 2021) using the function *kruskal.test*. Statistical analyses were carried out beforehand to test for normality and homogeneity of variances for each variable using the functions *shapiro.test* and *bartlett.test* respectively of the package “stats”.

On the basis of the frames recorded in the ROV surveys, we measured the body size of Norway lobsters based on their cephalothorax length (Carapace Length = CL, in mm) using the software ImageJ V. 1.53q (Abràmoff et al., 2004) measuring individuals aligned within the field of view (i.e., whose cephalothorax was seen next to the two laser beams). We estimated the body size of each individual by averaging five repeated measures to minimize measurement bias. Then, a class-size frequency distribution was constructed (using the averaged CL measure for each individual) for both the control area and no-take reserve. We applied one-way ANOVA tests to compare body size between the control area and the no-take reserve.

The body mass (in g) of Norway lobsters was estimated from a length-weight relationship for the species, using a standard allometric model. We averaged the allometric coefficients from 1995 reported by Sardà et al. (1998), in the same area of this study (GSA06), between female and male coefficients for obtaining combined sexes coefficients (Sardà et al., 1998):

$$W = 0.00045 CL^{3.10}$$

where W is body weight in grams and CL is cephalothorax length (see above). The constants 0.00047 and 3.14 are the coefficients a and b of the allometric model. Weight was calculated from each measure of CL computed for both the control area and no-take reserve, and the average and standard deviation were also estimated. Subsequently, we estimated the biomasses along each video-transect in the no-take and control areas. For this, we converted the previously obtained weight into biomass (kg·km⁻²) with the following formula (Morello et al., 2007; Froglija et al., 1997):

$$B = \bar{W} \cdot A / 1000$$

where B is the biomass (kg·km⁻²), \bar{W} is the mean individual weight (g) from all the individuals that were possible to measure with ImageJ (we were only able to measure individuals aligned within the field of view), and A is the total abundance corrected by swept area (No.·km⁻²). We calculated a total of four biomasses depending on the A source: for the two areas, control zone and no-take reserve, and the two approaches, burrow-system and animal counting.

A non-parametric statistical approach was used to determine significant differences between groups for cases in which normality and homogeneity of variance were not met. The Kruskal-Wallis non-parametric test was used to compare estimated biomasses in the control area and the no-take reserve, and between burrow-system counting and animal counting of Norway lobster. To compare estimated biomasses from burrow-systems in different areas, we conducted parametric one-way ANOVA tests.

2.3. Community megafauna taxa evaluation

Taxonomic identification and counting of the co-existing megafauna taxa were performed for each ROV video-survey analyzing the recorded video frames. A video-catalog of best images of the detected taxa that appeared in the area was built as a reference for their classification (Supplementary Material Figs. A3–A9). All these individuals were then classified at the lowest possible taxonomic level according to identification guides (Froese and Pauly, 2022; Grinyó et al., 2022; Lloris, 2015; Fricke et al.,

2022; WoRMS Editorial Board, 2022) and by taxonomic specialists from the Institut de Ciències del Mar (ICM-CSIC). Due to the difficulty of correctly assigning cephalopods to particular species, we classified them into three larger taxonomic groups: Superorder Decapodiformes, Order Octopoda, and Order Sepiida. The community (dis)similarity of all co-occurring taxa was calculated via the video-swept area method (see previous section). We also identified the main predators of Norway lobster based on Vigo et al. (2022).

To examine the differences between the control area and the no-take reserve in the composition and abundance of taxa, we generated a nonmetric Multi-Dimensional Scaling (nMDS) ordination analysis in the R software version 4.1.2 (R Core Team, 2021) using the function *metaMDS* of the package “vegan”. The abundances were previously square-root transformed to achieve normality, and a Bray-Curtis similarity matrix was calculated. Once we visualized the grouping, we conducted a one-way permutational multivariate analyses with *adonis* from the package “vegan” (PERMANOVA tests; Anderson, 2001) using one fixed factor (‘area’, with two levels) to test for differences in community (dis)similarity between transects from the control area and the no-take reserve. As for Norway lobsters, we compared all taxa abundances between the control area and the no-take reserve with PERMANOVA and a pairwise multilevel comparison with Bonferroni-based adjusted *p*-values by using the package “pairwiseAdonis” and *pairwise.adonis* (Martinez Arbizu, 2020). Moreover, Shannon's diversity index (H' , log 10 base) (Shannon and Weaver, 1948) was calculated to measure species diversity in each community (control area and no-take reserve). To test for differences between areas, one-way ANOVA tests were performed for each biodiversity index.

We constructed two taxa accumulation curves (Thompson and Withers, 2003; Ugland et al., 2003) to record the cumulative number of species in each study area (control and no-take reserve) as a function of the cumulative effort expended searching for them (hours of video recorded by ROV surveys). The taxa accumulation curves allowed us to assess and compare diversity across the two areas and to evaluate the adequacy of the ROV video-surveys in representing the benthic and demersal fauna in each area. We also calculated the Chao estimator in the R software version 4.1.2 (R Core Team, 2021) using *specpool* from the package “vegan” for assessing species richness in the two communities, the control area and the no-take reserve. This estimator indicates how many species or different taxa would be registered if the effort sampling was increased or how many species we did not record with our effort (Béguinot, 2016; Chao, 2006).

2.4. Marine litter and terrestrial vegetation

We classified marine litter as plastic, metal, glass, and the remains of fishing nets (GESAMP, 2021; Mecho et al., 2020; Ramirez-Llodra et al., 2011). We also counted terrestrial vegetation items (such as tree branches) to analyze all organic inputs coming from terrestrial sources (Galimany et al., 2019). The abundance of the different types of litter and terrestrial debris were also standardized by the swept area (km²). The differences in the abundance of anthropogenic debris between the control area and the no-take reserve were tested using two-way ANOVA tests with two fixed factors (“Area” with two levels for the control and no-take reserve, and “Type of Debris” with five levels). The difference in the abundance of terrestrial debris between the control area and the no-take reserve was also tested with non-parametric Kruskal-Wallis tests in the R software version 4.1.2 (R Core Team, 2021) using the function *kruskal.test*.

2.5. Seafloor integrity and recovery

We examined seafloor integrity in the control area and the no-take reserve by assessing the perturbations of trawling marks (by bottom trawl metal doors and trawl nets). We classified them into six different categories according to the degree of alteration (see description in Table 1, Fig. 3). We recorded the duration of their appearance in each ROV video-survey, classifying them as stated in Table 1, and then a percentage was calculated considering the total time recorded at each transect. Finally, we estimated the

Table 1
Categories of seafloor impact due to trawling.

Categories	Description
1	Seafloor with no perturbations. No signs of trawling effects.
2	Perceptible trawling marks, probably old trawling marks in recovery.
3	Smoothed door mark from the trawling gear.
4	Flattened seafloor due to the net of the trawling gear.
5	Flattened seafloor with door marks and berming of the muddy sediment.
6	Deeply altered seafloor due to a profound door mark of the trawling gear.

overall average and standard deviation of the control area and the no-take reserve.

We tested for differences in the variance of presence of each category of alteration between areas and also among all six categories defined in Table 1. We conducted the non-parametric test of Scheirer Ray Hare in the R software version 4.1.2 (R Core Team, 2021) using the function *scheirerRayHare* of the package “rcompanion”. The post-hoc tests were performed using multiple comparisons with Dunn's Test using the function *dunn.test* from the package “dunn.test” and “FSA”.

3. Results

In total, we recorded 72 h in all the ROV surveys, corresponding to a total swept area of 83.82 km² (Supplementary Material Table A1). We covered a similar time and area in the control area (time = 32 h; area = 40.18 km²) and the no-take reserve (time = 39 h; area = 43.64 km²).

3.1. Norway lobster evaluation

ROV surveys showed significantly higher numbers of Norway lobsters in the no-take reserve than in the control area, independent of the approach used (burrow-system or animal counting; Figs. 4–5). Regarding the abundance of Norway lobster based on burrow-system counting, although the average number of burrows in the no-take reserve (mean = 7513; SD = 2951 No.km⁻²) was higher than in the control area (mean = 4411; SD = 3203 No.km⁻²), the difference was not statistically significant ($\chi^2 = 3.10$; $p = 0.07$). With the animal counting approach, during nighttime, we found a similar (Fig. 4A; $F_{1,6} = 23.22$, $p = 0.95$) abundance of Norway lobster in both areas (control area; mean = 1022.94; SD = 954.9 No.km⁻²; no-take reserve; mean = 1658.47; SD = 1529.01 No.km⁻²). In contrast, during daylight hours, we found that the abundance of Norway lobster in the no-take reserve was significantly higher than in the control area (Fig. 4A; $F_{1,6} = 11.59$, $p = 0.002$).

In relation to the body size of Norway lobsters, we measured 169 out of a total of 299 individuals detected. Testing for differences in body size (CL in mm), we found that individuals from the no-take reserve were significantly larger than the ones from the control area (Fig. 4B; control area; mode = 19, SD = 6 mm; no-take reserve; mode = 23, SD = 8 mm; $F_{1,166} = 14.44$, $p < 0.01$). Moreover, larger-sized individuals were found in the no-take reserve (maximum body size of 51 CL in mm) compared to the control area (maximum body size of 35 mm) (Fig. 4B).

The estimated body mass (g) considering all individuals counted in the two areas was lower in the control area (body mass = 5.51 ± 5.76 g) than in the no-take reserve (body mass = 10.21 ± 12.78 g) (Table 2). Both the burrow-system counting and animal counting approaches showed a higher biomass of Norway lobster in the no-take reserve than in the control area (burrow-system method: $F_{1,11} = 16.88$, $p < 0.01$; animal counting method: $F_{1,18} = 5.14$, $p = 0.03$; Fig. 5). Nevertheless, we found significant differences between the burrow-system and animal counting methodologies. By using the burrow-system approach, the biomass of Norway lobster in both the control area and the no-take reserve was higher than the biomass estimated with the animal counting approach ($\chi^2_{1,30} = 4.23$, $p = 0.04$; Fig. 5A). In contrast, the abundance of Norway lobsters did not differ significantly between burrow counting and animal counting approaches ($\chi^2_{1,30} = 3.95$, $p = 0.05$; Fig. 5B).

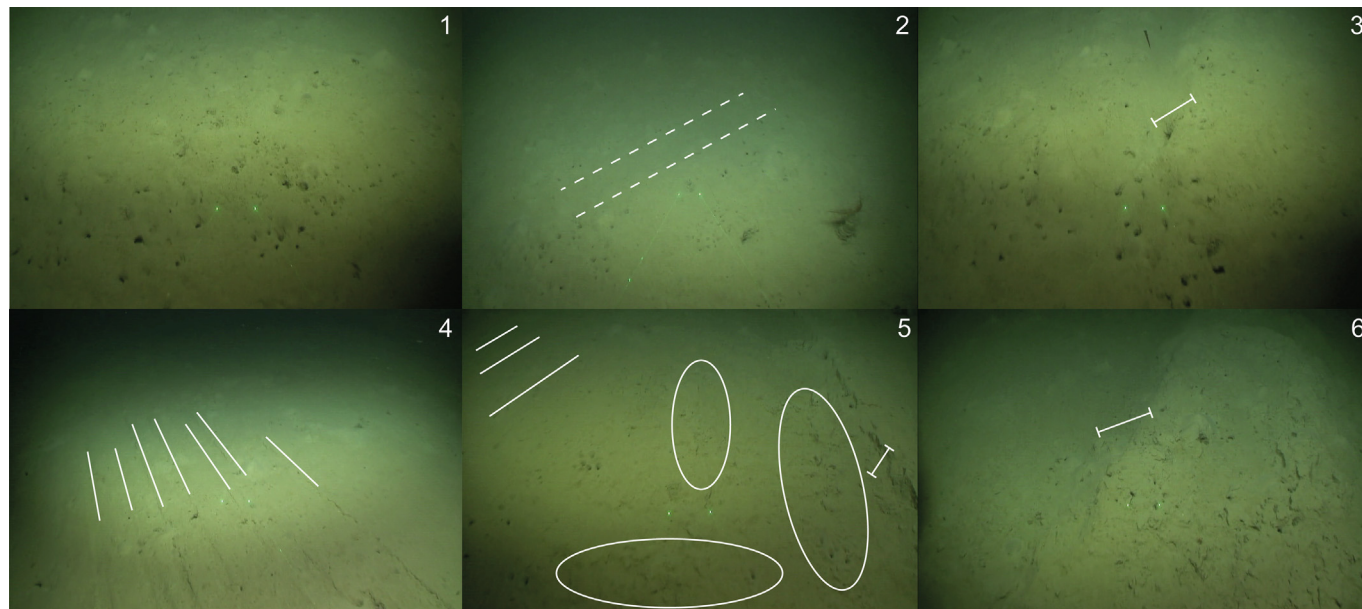


Fig. 3. Trawl mark categories used to evaluate the seafloor state following the descriptions in Table 1. 1: No signs of trawling effects, 2: perceptible trawling marks, 3: smoothed door marks from trawling gear, 4: flattened seafloor due to the trawling gear net, 5: flattened seafloor with door marks and the berming of muddy sediment, 6: deeply altered seafloor due to deep door marks from trawling gear.

3.2. Community megafauna taxa evaluation

We identified a total of 43 taxa from seven major taxa groups: Cephalopoda, Cnidaria, Crustacea, Echinodermata, Elasmobranchii, Porifera, and Teleostei (see Figs. A3–A9 and Table A10 of the Supplementary Material). Diversity indexes showed a similar composition of taxa between the benthic community found in the control area and in the no-take reserve, with Teleostei being the most diverse taxon group in the benthic community followed by Crustacea (Fig. 6A). The Bray-Curtis matrix of distances obtained from the abundances of the demersal community was represented in a nMDS (Fig. 6B). The ordination had a relatively low stress value (0.13) and showed no obvious separation of transects between areas, as was corroborated with a PERMANOVA test (pseudo- $F_{1,18} = 1.61, p = 0.06$).

After comparing the abundance of all identified taxa between the control area and the no-take reserve, we found that only the fishes *Helicolenus dactylopterus* and *Trigla lyra*, and the anemones of the Family Cerianthidae, showed higher abundances in the no-take reserve than in the control area (Table 3; Fig. 6C). The other recorded taxa did not differ in abundance between the control area and the no-take reserve (Table 3). In relation to the predators of Norway lobster, we found that their abundance was similar between the control area and the no-take reserve (Table 3). We did not observe an increase in predators in terms of abundance as a result of the protection provided by the no-take reserve.

The taxa accumulation curves indicated that nearly all taxa were recorded in both areas suggesting a good sampling effort. In the control area, we recorded a total of 40 different taxa, while the Chao estimator was 43, only three more taxa compared with our observations. Similarly,

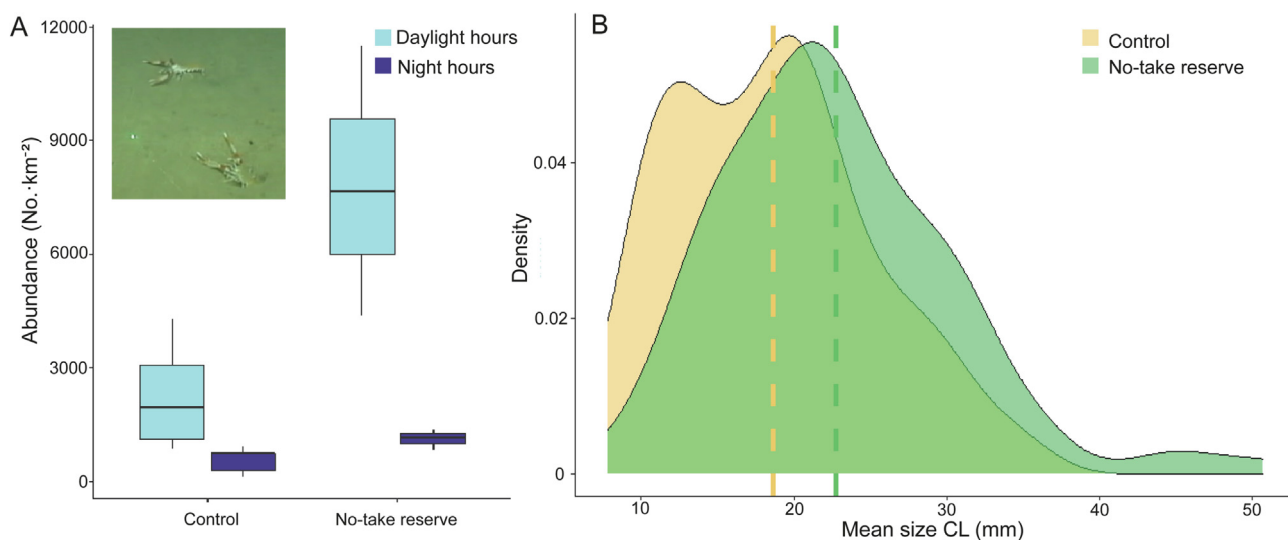


Fig. 4. A) Abundance (animal counting in each transect corrected per the swept area covered) of Norway lobster in the control area and the no-take reserve during daylight and nighttime hours by ROV surveys. The picture shows two individuals of Norway lobster, one outside a burrow and the other inside with only the cephalothorax visible. Box length represents interquartile range, bar length represents range and horizontal lines represent median values. B) Body size distribution of Norway lobsters for the control area and the no-take reserve by ROV surveys. The dashed line represents the individual mean size for each compared area.

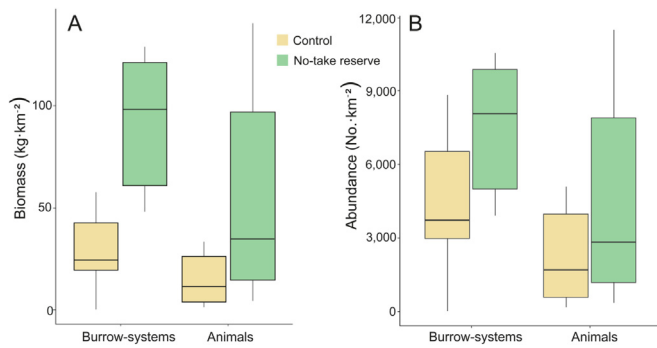


Fig. 5. A) Abundance (counts in each transect corrected per the swept area covered) and B) biomass of Norway lobster calculated with both methodologies (burrow-system counting and animal counting referred in the Figure as “Burrow-systems” and “Animals” respectively) in the no-take reserve and in the control area. Upper and lower 95 % confidence limits are represented by the extent of the vertical bars in the boxplots, indicating the quantiles and the median.

in the no-take reserve, we recorded a total of 43 taxa, while the Chao estimator was 47. In both cases, the saturation curve was reached at approximately 15–20 h of time effort and the estimator indicated that only 3–4 taxa were unrecorded (Fig. 6D).

3.3. Marine litter and terrestrial vegetation

The abundance of anthropogenic debris and terrestrial vegetation debris were similar between the control area and the no-take reserve (Fig. 7A). We did not find significant differences between the control area and the no-take reserve concerning the abundance of anthropogenic debris, ($F_{1,14} = 0.45, p = 0.52$), among types of different debris ($F_{3,14} = 0.72, p = 0.57$), or the abundance of terrestrial vegetation ($\chi^2 = 0.04; p = 0.84$). The diversity of anthropogenic debris was higher in the control area (fishing net, glass, metal, and plastic) than in the no-take reserve (plastic and metal) (Fig. 7B).

3.4. Trawl marks

All ROV video-surveys conducted in the control area showed high percentages of seafloor impacted (Fig. 8A). In the no-take reserve, more intact patches (Category 1) showed the highest average percentage ($97.24 \pm 3.61\%$), with the rest of the perturbations being $<4\%$ or not present. In the control area, Category 1 ($41.17 \pm 27.55\%$) and Category 4 ($38.21 \pm 26.91\%$) showed a similar average percentage, followed by Categories 5 and 6 with approximately 10 % coverage in the control area (Fig. 8B). Statistical comparisons showed differences between areas (control area and no-take reserve), categories and the interaction among areas and categories ($H_{1,71} = 13.41, p < 0.05$; $H_{5,72} = 28.27, p < 0.05$; $H_{11,72} = 22.29, p < 0.05$), indicating the presence of more intact patches (Category 1) in the latter and more deeply ploughed patches (Category

Table 2

Population parameters of Norway lobster in the control area and the no-take reserve based on ROV surveys. Biomass was obtained from the total density and the mean weight of individuals calculated from an allometric model, which considered the mean size (CL) of individuals. Body mass was calculated from the mean body size of each area of study.

	Control	No-take reserve
Burrow-systems abundance (No.km ⁻²)	4411 ± 3203	7513 ± 2951
Individual abundance (No.km ⁻²)	2227 ± 1849	4518 ± 4248
Body size (CL length, in mm)	19 ± 6	23 ± 8
Body mass (g)	5.51 ± 5.76	10.21 ± 12.78
Biomass from burrow-systems abundance (kg.km ⁻²)	28.81 ± 20.92	91.82 ± 36.06
Biomass from animal abundance (kg.km ⁻²)	12.27 ± 9.71	46.13 ± 43.37

6) in the former. The only categories of impact that appeared in the no-take reserve were smoothed door marks (1 ± 1.12) and slightly perceptible trawl marks (1.52 ± 2.62) (Fig. 8).

4. Discussion

Here, we investigated the effects of passive ecological recovery of a deep-sea no-take reserve from the western Mediterranean Sea using non-invasive ROV video-surveys. We examined the recovery state of the overexploited Norway lobster stock and assessed how their densities and biomasses differed in this no-take reserve compared to an adjacent control area in which bottom trawl fisheries operate. The results revealed that in a relatively short period of time (2.5 years) after ceasing trawling activity, the Norway lobster population showed higher abundance, biomass, and larger mean individual size in the no-take area than in the control area. Moreover, we also found that some community species, such as the Teleostei *H. dactylopterus* and *T. lyra* and sessile marine species from the family Cerianthidae, were more abundant in number inside the no-take reserve. We also observed how trawling marks on the seafloor in the no-take reserve were nearly absent.

4.1. Norway lobster recovery

The recovery of overexploited stocks of Norway lobster has been suggested to take between four to six years (Sardà et al., 1998) and some habitats may require at least 10 years to detect signals of recovery (McClanahan and Mangi, 2000). Here, after only 2.5 years, we found that the population of this crustacean in the no-take reserve was recovered in comparison with the control trawled area. This result suggests that MPAs may offer quick benefits in locations near fishing grounds where fishing mortality is elevated and stocks are below sustainable fishing levels (Halpern, 2003; Hart, 2006), corroborating the fact that the Norway lobster stock is being highly overexploited in the study area (Field et al., 2006; Sarda, 1998). The recovery rate of this species depends upon the rate of successful recruitment (Sardà, 1998). Since small juvenile Norway lobsters remain hidden inside burrows during the first year of life (Powell and Eriksson, 2013; Tuck et al., 1994), the present study refers to the population after their first year of life, or those individuals that already exhibit burrow emergence behaviour.

In the last few decades, UWTV surveys have become the primary assessment method used by the WGNPEPS focusing on burrow counting, as they are static and relatively constant (Bell et al., 2018; Sardà and Aguzzi, 2012). However, the burrow counting method has uncertainties such as the persistence of empty burrows or exclusion from tunnel occupation by other fish and crustacean species that maintain its structural integrity (Aguzzi et al., 2021). To address this issue, we foresaw an opportunity to improve current stock assessment methods by applying two different approaches to estimate stock abundance and biomass, namely “burrow-system counting” and “animal counting”, which showed contrasting results. With the burrow-system approach, we observed similar abundances in the control area and the no-take reserve. Therefore, similar counts in both areas demonstrate that burrows can resist trawling, indicating equivalent numbers/densities of remaining individuals that rebuild the burrow systems after trawling disturbance, assuming that all are occupied only by Norway lobsters, as other species may opportunistically occupy and maintain Norway lobster tunnels (reviewed by Sardà and Aguzzi, 2012). Considering that juveniles initially occupy burrows linked to those of adults (Chapman, 1980; Tuck et al., 1994), the maintenance of high burrow densities could indicate a suitable habitat for good recruitment (Chapman and Howard, 1988; Johnson et al., 2013). Nonetheless, tunnel counts present several levels of uncertainty. Burrows can offer some protection from trawling; however, intense impacts on burrows destroy system integrity (Hiddink et al., 2006; Tillin et al., 2006). We did not measure the size and shape of burrow systems, although we generally noticed that burrow systems from the control area were more flattened and without the muddy mounds characteristic of well-structured systems in the no-take reserve

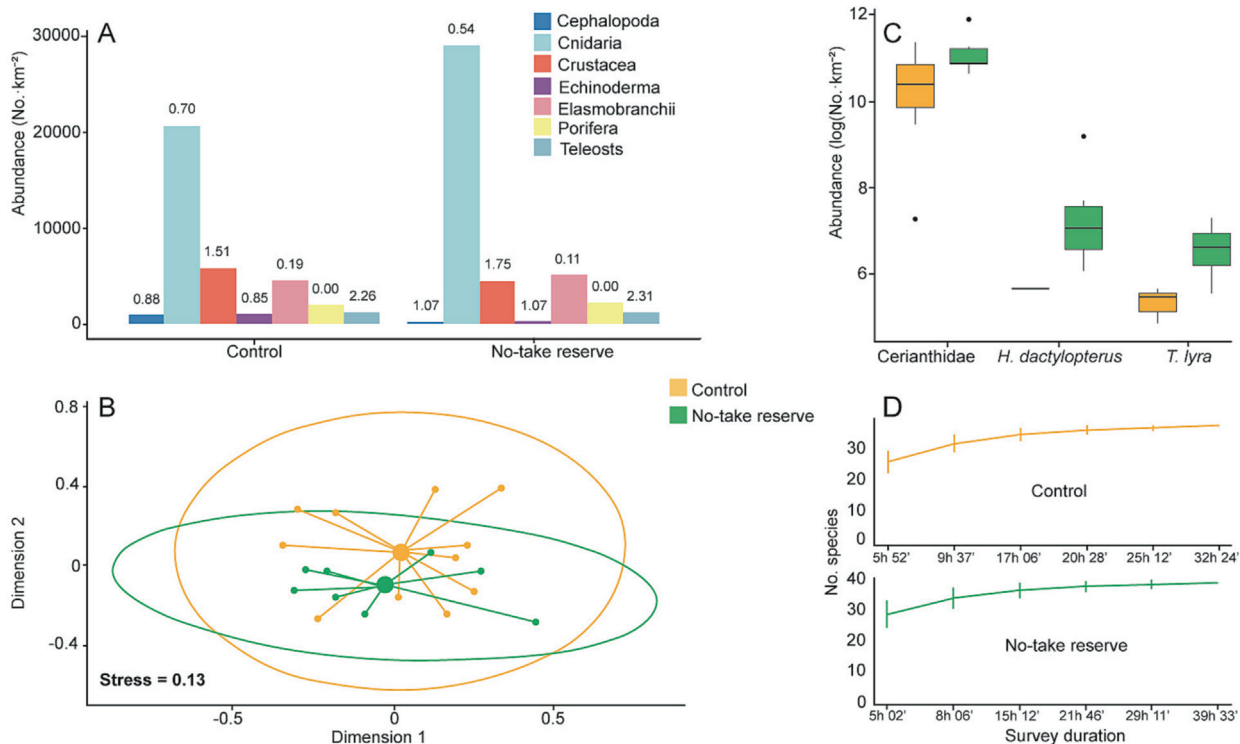


Fig. 6. A) Abundance of all megafauna taxa observed separated into six groups (Cephalopoda, Cnidaria, Crustacea, Echinoderma, Elasmobranchii, Porifera, and Teleostei) indicating the Shannon diversity values from each group in both the no-take reserve and the control area. B) Non-metric multidimensional scaling representation which indicates the similarities in terms of abundance and species composition (counts of all species corrected per the swept area covered in each transect) between the no-take reserve and the control area by overlapping both areas. Ordination ellipses represent 95 % confidence, and spiders connect the species composition variability to the centroid of each area, control area (in yellow) and no-take reserve (in green). C) Violin plots representing the densities of Family Cerianthidae, *Helicolenus dactylopterus*, and *Trigla lyra* individuals in the control area (in yellow) and in the no-take reserve (in green). D) Species accumulation curves for the no-take reserve and the control area, the hours accumulated for each transect are also specified. The error bars represent the standard deviation of the accumulation curve.

(Supplementary Material, Fig. A2). In addition, the stability of burrow systems per se also depends on the composition of the sediment in relation to currents (Campbell et al., 2009). In our case, differences in both habitat variables were not studied (as currents were not measured), since both surveyed areas are just small parcels of a much larger and homogenous slope area (Palanques et al., 2005; Send et al., 1999). In this scenario, we did not observe species other than Norway lobster close to tunnel system entrances in either area. Norway lobster juveniles usually occupy burrows already created by adults to avoid predation (Chapman, 1980).

Here, we suggest a complementary and more reliable approach to counting all individuals of Norway lobster, classifying them according to their activity, as an alternative method of ICES stock assessment by UWTV surveys (Bell et al., 2018). This approach expanded on the results of animal density in relation to behavioral rhythms obtained through UWTV surveys in shallower areas of the Atlantic Ocean (Aguzzi et al., 2021). In regard to the day-night activity of Norway lobsters in deep-sea waters, we observed the limited presence of visible individuals during the night, corroborating how the locomotor activity of Norway lobsters that inhabit deep ecosystems below 300 m in depth is predominant during daylight hours (Aguzzi et al., 2003; Vigo et al., 2021). This result confirms that any video-based fishery-independent assessment of species along the continental slope should be carefully centered on daytime hours to better capture visible animals and to perform their count for calibration with counting burrow systems (Aguzzi et al., 2021).

The abundance of Norway lobster was higher in the no-take reserve compared to the control area. However, we only noticed this significant increase during daylight hours, whereas at night the abundance of Norway lobster was similar: very scarce in both the control area and the no-take reserve. This fact can be explained by their burrowing behaviour, which indicates that the demographic indicators of this species should be evaluated

according to their activity patterns which depend on optimum environmental light conditions (Chapman and Rice, 1971). The class-size distribution of the no-take reserve showed a higher mode size with larger sizes absent in the control area. We expect that the ranges of body size distribution and mode will increase in the no-take reserve, proportionally to the years of protection at a relatively fast pace (Babcock et al., 2007; Lester et al., 2009; Moland et al., 2013). It is important to highlight that before the closure, the body size distribution of Norway lobster was similar in both no-take reserve and control area (Fig. 2). However, a long-term monitoring for demographic assessment is crucial to observe these beneficial size shifts in the no-take reserve in comparison to adjacent areas.

Total biomass reflects both size and abundance, resulting in a robust measure for MPA protection (Lester et al., 2009; Soykan and Lewison, 2015). In some cases, MPAs have only a detectable biomass response, and not an abundance response, due to the low pre-MPA harvest of some species or high variability in recruitment (Kaplan et al., 2019). Biomass can increase much more quickly than abundance as a result of the low mortality of older and larger-sized individuals. On the other hand, if biomass is low, but abundance is still high, an increase in recruitment into the area could be indicated (Nalepa et al., 2010). Estimating this demographic variable through mean body size as calculated in the two approaches (i.e., burrow-system and animal counts) indicates how in both cases biomass was higher in the no-take reserve. All the evaluated variables (i.e., abundance, mean body size, and biomass) reflected the positive effects of passive restoration in the no-take reserve. We found the species in the no-take area showed a rapid response to protection from fishing and that it may asymptotically increase until reaching carrying capacity over the years as long as this protection measure lasts. Comparing both counting methods, burrow-system and animal counts, we recommend the second approach as it provides more accurate information.

Table 3

Mean (\pm SD) of the abundance (No.km⁻²) of the megafauna species observed in the control area and the no-take reserve based on ROV surveys. Results of PERMANOVA statistical tests performed are also indicated with the Bonferroni-based adjusted *p*-values. The predators of Norway lobster based on Vigo et al. (2022) are indicated with a (P). The species that showed significant differences in statistical results are in bold.

Species	Control	No-take reserve	Statistical results
Teleostei			
<i>Arctozenus risso</i>	442 \pm 202	487 \pm 1	Pseudo-F = 0.54 adjusted- <i>p</i> = 0.59
<i>Coelorinchus caelorhincus</i>	597 \pm 231	397 \pm 236	Pseudo-F = 1.08 adjusted- <i>p</i> = 0.30
<i>Conger conger</i> (P)	837 \pm 453	927 \pm 425	Pseudo-F = 1.19 adjusted- <i>p</i> = 0.28
<i>Gadiculus argenteus</i>	456 \pm 200	718 \pm 520	Pseudo-F = 0.06 adjusted- <i>p</i> = 0.81
<i>Helicolenus dactylopterus</i>	280 \pm 1	2157 \pm 2954	Pseudo-F = 23.36 adjusted-<i>p</i> = 0.002
<i>Lepidopus caudatus</i>	407 \pm 121	995 \pm 834	Pseudo-F = 1.49 adjusted- <i>p</i> = 0.28
<i>Lepidorhombus boscii</i>	4059 \pm 4040	4277 \pm 1763	Pseudo-F = 1.102 adjusted- <i>p</i> = 0.31
<i>Lophius</i> spp. (P)	346 \pm 148	241 \pm 120	Pseudo-F = 2.20 adjusted- <i>p</i> = 0.16
<i>Merluccius merluccius</i> (P)	496 \pm 628	281 \pm 192	Pseudo-F = 0.22 adjusted- <i>p</i> = 0.86
<i>Micromesistius poutassou</i>	177 \pm 56	0	Pseudo-F = 2.66 adjusted- <i>p</i> = 0.22
<i>Molva macrophthalma</i>	252 \pm 80	199 \pm 69	Pseudo-F = 2.26 adjusted- <i>p</i> = 0.17
Family Myctophidae	964 \pm 776	538 \pm 668	Pseudo-F = 1.27 adjusted- <i>p</i> = 0.19
<i>Ophichthus rufus</i>	0	138 \pm 1	Pseudo-F = 1.40 adjusted- <i>p</i> = 0.42
<i>Ophisurus serpens</i>	0	166 \pm 59	Pseudo-F = 3.25 adjusted- <i>p</i> = 0.17
<i>Phycis blennoides</i>	2183 \pm 4144	1786 \pm 929	Pseudo-F = 1.25 adjusted- <i>p</i> = 0.26
<i>Symphurus nigrescens</i>	272 \pm 148	142 \pm 4	Pseudo-F = 0.12 adjusted- <i>p</i> = 0.85
<i>Trigla lyra</i>	212 \pm 78	772 \pm 427	Pseudo-F = 5.65 adjusted-<i>p</i> = 0.017
<i>Trisopterus capelanus</i>	388 \pm 290	255 \pm 155	Pseudo-F = 0.02 adjusted- <i>p</i> = 0.83
Unclassified	705 \pm 244	386 \pm 285	Pseudo-F = 0.67 adjusted- <i>p</i> = 0.38
Echinodermata			
<i>Astropecten</i> sp.	410 \pm 228	363 \pm 154	Pseudo-F = 0.31 adjusted- <i>p</i> = 0.60
<i>Brissopsis lyrifera</i>	391 \pm 1	253 \pm 166	Pseudo-F = 4.31 adjusted- <i>p</i> = 0.10
<i>Holothuroidea</i> spp.	1683 \pm 3097	440 \pm 252	Pseudo-F = 0.57 adjusted- <i>p</i> = 0.54
Elasmobranchs			
<i>Raja</i> spp.	251 \pm 1	138 \pm 1	Pseudo-F = 0.05 adjusted- <i>p</i> = 1.00
<i>Scyliorhinus canicula</i> (P)	4901 \pm 3069	5678 \pm 2408	Pseudo-F = 1.57 adjusted- <i>p</i> = 0.23
Cephalopods			
Decapodiformes (P)	342 \pm 217	226 \pm 165	Pseudo-F = 0.92 adjusted- <i>p</i> = 0.93
Octopoda (P)	1496 \pm 2811	365 \pm 256	Pseudo-F = 0.08 adjusted- <i>p</i> = 0.90
Sepiidae (P)	475 \pm 435	249 \pm 106	Pseudo-F = 0.81 adjusted- <i>p</i> = 0.52
Cnidaria			
<i>Arachnanthus oligopodus</i>	16,294 \pm 14,046	14,391 \pm 10,927	Pseudo-F = 1.62 adjusted- <i>p</i> = 0.21
Family Cerianthidae	34,982 \pm 23,279	63,745 \pm 30,532	Pseudo-F = 4.30 adjusted-<i>p</i> = 0.02
<i>Funiculina quadrangularis</i>	933 \pm 874	1059 \pm 884	Pseudo-F = 1.27 adjusted- <i>p</i> = 0.22
Crustacea			
<i>Dardanus arrosor</i>	666 \pm 163	1034 \pm 755	Pseudo-F = 0.05 adjusted- <i>p</i> = 0.76
<i>Goneplax rhomboides</i>	731 \pm 342	377 \pm 247	Pseudo-F = 0.39 adjusted- <i>p</i> = 0.66
<i>Brachyura</i>	15,206 \pm 13,986	12,155 \pm 13,639	Pseudo-F = 1.01 adjusted- <i>p</i> = 0.36
<i>Monodaeus couchii</i>	21,471 \pm 18,809	13,065 \pm 10,831	Pseudo-F = 0.72 adjusted- <i>p</i> = 0.44
<i>Munida</i> sp.	1036 \pm 754	647 \pm 248	Pseudo-F = 0.63 adjusted- <i>p</i> = 0.38
Family Pandalidae	4025 \pm 3924	2921 \pm 2525	Pseudo-F = 0.89 adjusted- <i>p</i> = 0.91
<i>Parapenaeus longirostris</i>	238 \pm 1	317 \pm 229	Pseudo-F = 4.27 adjusted- <i>p</i> = 0.0
<i>Plesionika heterocarpus</i>	2279 \pm 2047	3824 \pm 2642	Pseudo-F = 1.51 adjusted- <i>p</i> = 0.16
<i>Processa</i> sp.	2642 \pm 1961	2424 \pm 2079	Pseudo-F = 0.07 adjusted- <i>p</i> = 0.89
<i>Solenocera membranacea</i>	1797 \pm 2037	1023 \pm 1076	Pseudo-F = 0.43 adjusted- <i>p</i> = 0.65
Porifera			
<i>Polymastia</i> spp.	2023 \pm 2177	2287 \pm 1838	Pseudo-F = 1.59 adjusted- <i>p</i> = 0.23

4.2. Community megafauna taxa recovery

The number of megafauna taxa detected showed similar values in both areas, with a total of 43 and 40 taxa in the no-take reserve and control area, respectively. The ROV video-surveys may not have been able to detect all species of the benthic community, as many different behavioral reactions to ROV presence occur, from stillness to active avoidance (see behavioral classifications in Ayma et al., 2016; Lorange and Trenkel, 2006). We found that two Teleostei species, *H. dactylopterus* and *T. lyra*, showed higher abundance in the no-take reserve than in the control area. These species are commercialized by Norway lobster fishers and therefore may also benefit Norway lobster fisheries outside the reserve. The anemones from the family Cerianthidae that can retract when the gear of bottom trawl fisheries approaches (Hall-Spencer, 1999) may still be vulnerable to trawling impacts (Kenchington et al., 2006). In our study, these species were abundant in

both areas although they also showed a higher abundance in the no-take reserve than in the control area.

Sessile species increase the roughness of mud plains and thus can accelerate the restoration of seabed quality by trapping drifting sediment (Buhl-Mortensen et al., 2010; Grinyó et al., 2020). The anemones from the Cerianthidae family may act as a refuge for other species, such as demersal fishes and crustaceans (Shepard et al., 1986). In fact, we observed the co-presence of *H. dactylopterus* and *Munida* spp. with these anemones, indicating higher abundances of both species within the family Cerianthidae patches as previously reported in other areas (Auster et al., 2003; Uzmann et al., 1977; Valentine et al., 1980). The greater abundance of anemones in the no-take reserve could offer more refuges against predation to other fish and decapod crustacean species, resulting in their increased abundance, as reported here for *H. dactylopterus* and also by Grinyó et al. (2020) in the Alboran Sea. Thus, *H. dactylopterus* and *T. lyra* could be

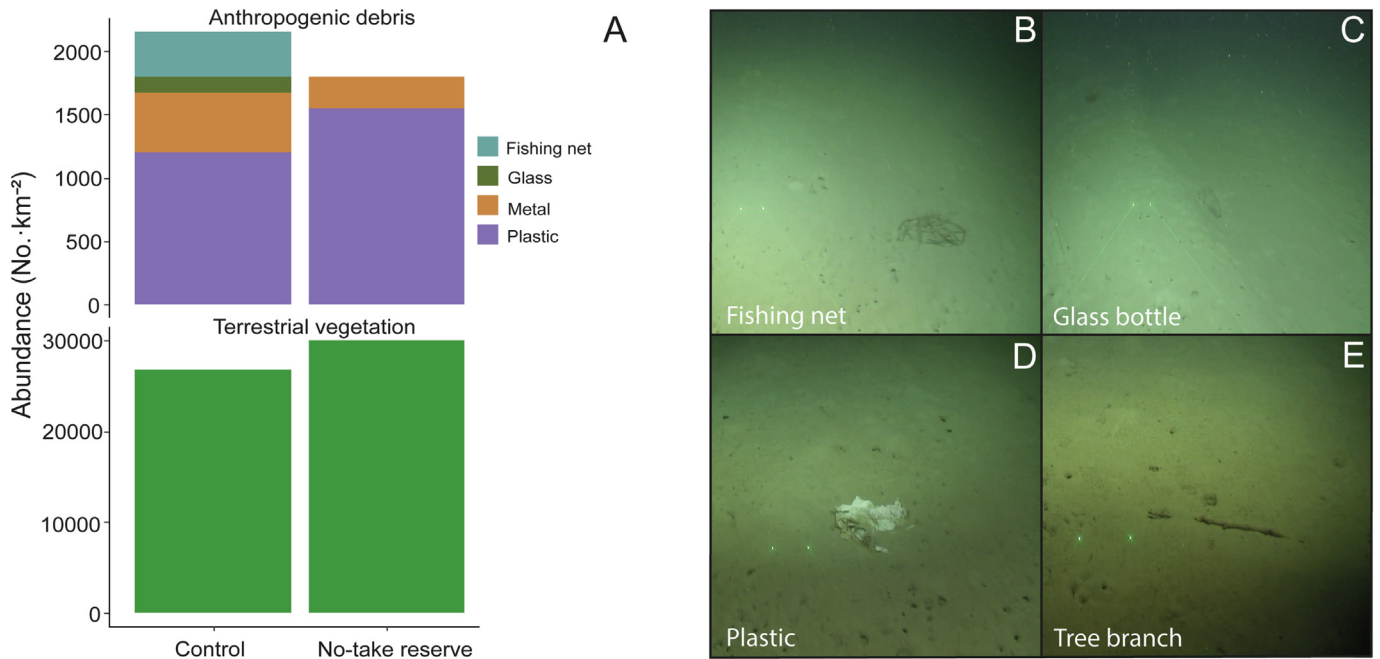


Fig. 7. A) Anthropogenic litter classified as fishing net, glass, plastic, or metal and quantified in both the no-take reserve and the control area; terrestrial vegetation quantified in the control area and the no-take reserve; the plot shows the density of debris from terrestrial vegetation, plastic, and other debris (metal and undefined); examples of B) fishing net, C) glass bottle, D) soft white plastic, and E) tree branch.

defined as key indicators of the effectiveness of a no-take habitat established in Norway lobster grounds, as they are very sensitive to trawling, presenting significant increases in only a short time due to the protection of the no-take reserve. For the remaining species with depleted stocks due to fishing activity, we may likely observe benefits with additional protection (e.g., for species with low fecundity rates and high maturity ages) (Nickols et al., 2019). However, other species may not exhibit benefits because of the small size of the reserve that was designed for the Norway lobster, a crustacean that uses a reduced spatial area (Vigo et al., 2021).

Some MPA assessments consider the species interactions involved, such as predator-prey interactions, evaluating predator densities and biomasses. This approach is crucial even in small MPAs as an incremental shift in predator densities could halt the recovery of an overexploited species and even undermine it (Clements and Hay, 2017), while a lack of predators could

also lead to permanent habitat regime shifts (Daskalov et al., 2007). The predators of Norway lobster (Vigo et al., 2022) observed in this study did not present an increase in abundance in the no-take reserve, apparently not influencing the dynamics of their prey, at least during these first years of protection. This result re-enforces the use of reserves as a tool to preserve Norway lobsters compared to the European spiny lobster (*Palinurus elephas*), where juveniles were highly predated by fishes in the MPA (Díaz et al., 2005). One of the success in recovery on Norway lobsters versus the European spiny lobster could be the different habitat, muddy versus rocky substrates. Establishing a network of small no-take reserves should be considered as an effective management tool for fishery conservation of Norway lobster stocks.

Accumulation curves indicate the effectiveness of the monitoring effort, here in terms of hours of video observation. To avoid taxa underrepresentation

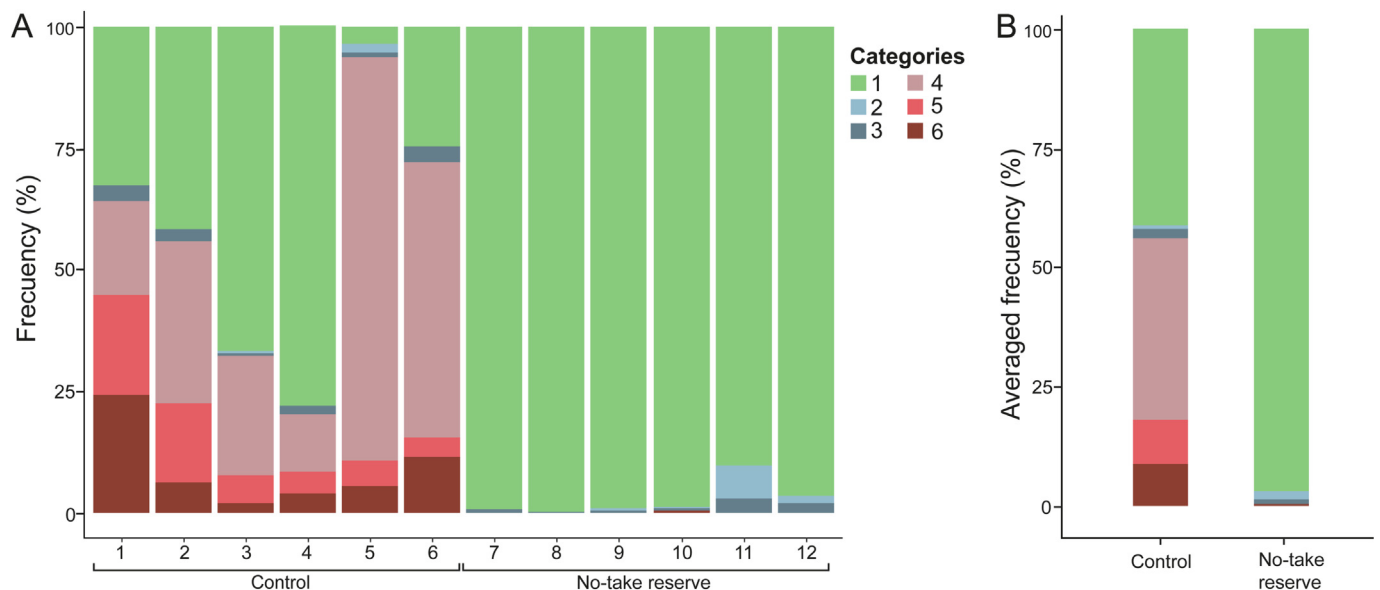


Fig. 8. A) Percentage of trawl mark categories observed via ROV video-survey; B) averaged frequency (%) of trawl mark categories in the control area and the no-take reserve.

in video-based monitoring in NW Mediterranean, we suggest that the minimum ROV video recording time for continental slope, muddy bottom Norway lobster grounds should be 20 h, as indicated by the taxa accumulation curves in the present study. This monitoring indicator, estimated along with data collection during both the daytime and nighttime, could facilitate the monitoring of sessile and motile megafauna in MPAs under restoration.

4.3. Marine litter, terrestrial vegetation, and seafloor recovery

Marine litter and terrestrial vegetation are present in all marine habitats, even in the most remote habitats of the ocean (Pham et al., 2014). We found similar densities between the control area and the no-take reserve in both marine litter and terrestrial vegetation. Most of the marine litter found was plastic, the most abundant form of marine debris, rising globally and with documented impacts on marine ecosystems (Mecho et al., 2021; Sheavly and Register, 2007). In the control area, we also observed fishing nets likely due to recent fishing activities (Galgani et al., 2000; Vieira et al., 2015), which also constitute a major problem as they can cause high fish mortality as a result of “ghost fishing” (Brown and Macfadyen, 2007). Even if trawl fisheries contribute to the removal or displacement of marine litter and terrestrial vegetation, they continuously enter from terrestrial habitats, ships, and other installations at sea. Enclosed areas such as the Mediterranean Sea exhibit some of the highest densities of marine litter (Galgani et al., 2015). The absence of trawling in the no-take reserve did not lead to more accumulation of marine litter nor terrestrial vegetation, as all this debris is continuously distributed, due to hydrography and geomorphological factors of the ocean (Barnes et al., 2009; Galgani et al., 2000), to hotspots of litter accumulation that include shores and the deepest areas in submarine canyons (Corcoran et al., 2009; Pham et al., 2014).

Trawling exerted above the maximum sustainable yield (i.e., overfishing) not only causes stock depletion, but also generates seafloor morphological changes, nutrient cycle alterations, sediment resuspension, and increased bottom-water turbidity (Puig et al., 2012; Pusceddu et al., 2014; Tillin et al., 2006). Here, we reported how the establishment of a no-take reserve helped to recover nearly the full extent of the area from trawling marks in a relatively short time following the termination of this activity. All surveys performed in the no-take reserve indicated only 5 % of the seafloor was altered by trawling marks, with smoother marks already in the process of recovery. In contrast, the control area exhibited >60 % of the seafloor impacted, presenting all categories of trawl marks. The muddy grounds of Norway lobster seem to rapidly recover when trawling fishery activity is stopped. The high density of Norway lobster and other burrowing species such as *Munida* spp. and *Goneplax rhomboides* can produce high bioturbation activity that could also be responsible for surface sediment mixing (to 5–20 cm sediment depth), thereby contributing to the rapid erasure of trawl marks in the no-take reserve (Mengual et al., 2016; Mérillet et al., 2018; Schwinghamer et al., 1998). Nevertheless, although they were not measured in the present study, we believe that the main factors that may be involved in the fast recovery from trawling marks in this area are hydrodynamic parameters such as tidal currents, natural sedimentation, and the deposition of suspended sediments (Friedlander et al., 1999; Linnane et al., 2000). The seafloor state, as we defined it, is a good indicator for measuring the passive restoration of a habitat from trawling. Intermediate approaches to fish stock recovery such as seasonal closure areas may represent too short a time span for the recovery of seafloor habitats (Demestre et al., 2008; Smith et al., 2000).

5. Conclusions

The recovery of overexploited Norway lobster populations and habitats may benefit from applying a passive habitat restoration approach based on total closure of areas for fishing activities. No-take deep-sea reserves require prolonged monitoring that may help to identify potential density-dependent effects on Norway lobster populations in the long-term, inducing

an increase in the competition for space. On the basis of our results, we propose establishing a network of small no-take reserves focused on recovering Norway lobster stocks as an effective management tool for fishery conservation, obtaining relatively rapid gains over the cost of closing fished areas. We also suggest the use of ROVs for monitoring marine reserves as an innovative and non-invasive method for evaluating the ecology and seafloor status. Focusing on target species of commercial interest could make the present monitoring procedure feasible in other deep-sea no-take areas worldwide.

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CRediT authorship contribution statement

Maria Vigo- data collection, methodology, formal analysis, investigation, writing.

Joan Navarro- conceptualization, data collection, investigation, validation, writing.

Jacopo Aguzzi- data collection, investigation, validation, writing.

Nixon Bahamón- data collection, formal analysis, review & editing.

José Antonio García- data collection, programming, review & editing.

Guimar Rotllant- data collection, review & editing.

Laura Recasens- data collection, review & editing.

Joan B. Company- conceptualization, data collection, investigation, validation, writing.

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Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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