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RESEARCH ARTICLE

Ecosystem Approach to Fisheries Management works—How switching from mobile to static fishing gear improves populations of fished and non-fished species inside a marine-protected area

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Abstract

1. Designated using a Statutory Instrument in 2008, Lyme Bay marine-protected area (MPA) is the UK's first and largest example of an ambitious, whole-site approach to management, to recover and protect reef biodiversity. The whole-site approach applies consistent management, in this case excluding bottom towed fishing, across the full 206 km^2 extent of the MPA, thus protecting a mosaic of reef-associated habitats from regular damage, while still allowing less destructive fishing methods, such as static gear, rod and line, and diving.
2. To assess the effectiveness of this management strategy for mobile taxa and the sustainability for those taxa that continue to be targeted, Exploited and Non-Exploited species' populations were compared inside the MPA, relative to open control sites spanning 11 of the 12 years of designation. baited remote underwater video systems (BRUVs) were deployed annually to assess mobile benthic and demersal fauna.
3. Overall, the number of taxa significantly increased in the MPA relative to the open controls while total abundance increased in both treatments.
4. Exploited fish showed increases in number of taxa (430%) and total abundance (370%) inside the MPA over 11 years.
5. Likewise, but to a lesser degree in the open controls, number of taxa of commercially Exploited fish increased over time, potentially showing 'spillover' effects from the MPA.
6. Non-Exploited fish did not show such changes. Regardless of constituting the majority of the fishery value, highly valuable Exploited invertebrates showed no significant changes over time.
7. *Synthesis and applications*. The Lyme Bay marine-protected area shows importance of protecting a whole site, comprising mosaics of different benthic habitats, through protection of sessile organisms that contribute to essential fish habitats.

This Ecosystem Approach to Fisheries Management can benefit and maintain sustainable fisheries and species of conservation importance.

KEYWORDS
baited remote underwater video systems, biodiversity, conservation, marine management, marine-protected areas, monitoring, whole-site approach

1 | INTRODUCTION

Globally, the implementation of marine-protected areas (MPAs) to conserve and protect marine biodiversity and aid fishery management has increased rapidly over the last 25 years (Da Silva et al., 2015; Halpern et al., 2010). By protecting vulnerable species and habitats, MPA management strategies have successfully increased the abundance and size of fisheries' target species and increased resilience to natural and anthropogenic disturbance (Edgar et al., 2014; Sheehan, Cousens, et al., 2013). Thus, depending on how they are managed and enforced, MPAs have the potential to simultaneously benefit fisheries and conservation (Babcock et al., 2010). However, only 7.9% of the oceans are designated as MPAs (UNEP-WCMC, IUCN and NGS, 2018; ~17,000 MPAs covering 28.6 million km^2), over 2% short of the 10% target for 2020, set by the convention of Biological Diversity's Aichi Target 11 (Lubchenco & Grorud-Colvert, 2015). Furthermore, 'paper parks' (MPAs established without appropriate management and or resources to monitor, maintain or enforce protection) are prevalent despite increased global pressure to protect ecosystems using the MPA approach (Rife et al., 2013).

Permitted activities vary between different MPA designations and are typically zoned within MPAs, whereby only listed features such as specific habitats are afforded protection (Solandt et al., 2020), particularly within European waters. Partial protection can also include seasonal closures, specific species protection and fishing practice restrictions (Dinmore et al., 2003; Hattam et al., 2014; Topor et al., 2019; Williams et al., 2006). This form of management limits recovery potential as the presence, extent and condition of features are required to be evidenced. For example, this 'feature-based' management, which is the most common approach employed within UK waters, means that out of 66,507 km^2 of seabed within UK MPAs only 4,811 km^2 (7.2%) is protected from the most destructive fishing methods (Marine Conservation Society & Marine Mapping Ltd., 2019)—just the habitat or species 'feature' for which the MPA is designated, not the rest of the seabed area. This approach only protects the evidenced extent of a 'feature' at a specific moment in time, potentially limiting any future growth or migration that may occur in other habitats through natural ecological processes (Solandt et al., 2020). A more ambitious approach is the whole-site approach, a method for applying the Ecosystem Approach to Fisheries Management (EAFM: Serpetti et al., 2017) through consistent protection, across the whole seabed, acknowledging that habitats and species can recover beyond their current status when protected (Sheehan, Cousens, et al., 2013). Therefore, this approach protects a range of species and habitats across a larger area than the current evidenced extent of the 'feature' of interest (Solandt et al., 2020), including species or habitats that are highly important to the 'feature' of interest. The most extreme example is no take zones (NTZs) that exclude all extractive or destructive practices (Harasti et al., 2018; Sale et al., 2005). However, partial protection that only excludes the most destructive fishing activities has also been shown to be highly effective at protecting conservation features, yet evidence of benefits to fisheries are rare (Beukers-Stewart et al., 2005; Sheehan, Cousens, et al., 2013; Sheehan, Stevens, et al., 2013). MPAs are often seen as a compromise between conservationists and groups with direct fishing interests (Denny & Babcock, 2004; Sciberras et al., 2015). This compromise can lead to less protection for partial MPAs and decreased spatial extent for NTZs (Hamel et al., 2013), and has led to a debate as to the effectiveness of these areas (Edgar, 2011; Turnbull et al., 2021). The level of protection and enforcement of an MPA, alongside the size, age and isolation, determines how species and habitats recover following designation, with greater protection generally causing a more positive response (Edgar & Stuart-Smith, 2014). Most studies to date considering the effectiveness of 'feature-based' partial MPAs have found them ineffectual at achieving the conservation or fisheries' goals that instigated their designation (Piet & Rijnsdorp, 1998; Shears et al., 2006; Turnbull et al., 2021) and, in some cases, even increased the human threats to the system inside the protected zone (Zupan et al., 2018). Thus, it has been suggested that the whole-site approach can more adequately achieve the goals of both fisheries and conservation management (Rees et al., 2020; Solandt et al., 2020). Yet, due to the rarity of MPAs that have adopted the whole-site approach, few studies have assessed this style of marine management.

The Lyme Bay Statutory Instrument was established in 2008 (Mangi et al., 2011) to recover and protect reef habitats and species. The most destructive fishing activities, trawling and scallop dredging, were excluded from a mosaic of habitats (~206 km^2) while static gear and diving were still permitted. This created both the Lyme Bay MPA and the rare opportunity to study the effect of the whole-site approach for the first time over such a large temporal (11 years) and spatial scale (>200 km^2).

Marine-protected area effectiveness is dependent on appropriate management and enforcement, and requires robust standardised monitoring to evidence ecological effectiveness, socio-economic benefit and justify the inherent costs (Edgar et al., 2014). To evidence the ecological effectiveness and inform adaptive management, methods must be used which can quantify elements of the ecosystem of interest over appropriate temporal and spatial scales. Sessile and sedentary species were monitored in Lyme Bay using a flying towed video array (Sheehan, Cousens, et al., 2013; Sheehan et al., 2010), and recovery of certain benthic species was only detectable 3 years after bottom towed fishing was excluded. Monitoring mobile, often shy, species with highly variably temporal and spatial distributions in the marine environment is challenging and in the past has been limited to destructive trawl surveys (Murphy & Jenkins, 2010) and fisheries' landings (Coleman et al., 2004). Increasingly, less destructive methods are now used, such as underwater visual census (Kough et al., 2017), underwater video survey (Sheehan, Cousens, et al., 2013; Sheehan Stevens & Attrill, 2010) and fisheries' acoustic surveys (Erisman & Rowell, 2017).

Trawl surveys are destructive and so could compromise the recovery of the MPA that is being monitored (Murphy & Jenkins, 2010) while fisheries' landing assessments are restricted to commercially desirable species (Murphy & Jenkins, 2010). Underwater visual censusing, in the form of diver surveys (Edgar & Stuart-Smith, 2014), is restricted by diver ability (Harvey et al., 2004), depth range and number of dives in a day while acoustic surveys struggle to reliably identify fish species (Gannon, 2008). Underwater video survey is restricted by water clarity, light levels, camera specification and organism behaviour (Cappo et al., 2004). However, it is non-extractive and non-invasive, and is capable of sampling extreme depths for long periods of time while creating a permanent record of the survey, which can allow subsequent reanalysis and quality control (Stevens et al., 2014). Baited remote underwater video systems (BRUVs) sample the mobile fauna of a large area, unconstrained by depth, to provide cost-effective data on fish diversity and relative abundance (Harasti et al., 2018; Whitmarsh et al., 2017). Frequently used to monitor MPAs, BRUVs provide a conservative estimate of relative abundance of predatory species that are attracted to the bait, as well as non-predatory species that pass through the field of view (Cappo et al., 2004; Whitmarsh et al., 2017).

To monitor the recovery of the mobile reef-associated fauna in Lyme Bay MPA, replicate BRUVs were deployed between 2009 and 2019 within the MPA and in areas still open to bottom towed fishing (Stevens et al., 2014). Despite the continued fishing pressure on many mobile species within the MPA, it was considered that the recovery of the biogenic reefs, which are essential fish habitats (Rabaut et al., 2010), would lead to increases in both Exploited and Non-Exploited mobile species (Solandt et al., 2020).

To assess this prediction, the following hypotheses were tested:

1. Over time, assemblage composition of mobile species in the MPA progressively changes relative to areas that remain open to bottom towed fishing.
2. The total number of taxa increase over time in the MPA, relative to areas that remain open to bottom towed fishing.
3. The total abundance increase over time in the MPA, relative to areas that remain open to bottom towed fishing.
4. When considered separately, the number of taxa of Exploited and Non-Exploited species all increase over time in the MPA, relative to areas that remain open to bottom towed fishing.
5. When considered separately, the total abundance of Exploited and Non-Exploited species all increase over time in the MPA, relative to areas that remain open to bottom towed fishing.

2 | MATERIALS AND METHODS

2.1 | Survey location and design

Lyme Bay MPA (Figure 1), located on the southwest coast of England, covers 206 km^2 of nationally important rocky reef habitat (Hiscock & Breckels, 2007). For site selection, suitably comparable rocky reef regions comprising bedrock, boulders and cobbles were identified by utilising fishing effort and habitat data (Stevens et al., 2014). Within these broadly defined regions, sites were spread across each treatment (MPA and open controls: OC) to ensure that sites were spatially interspersed as much as possible (Figure 1). BRUVs were deployed each summer from 2009 to 2019. Sites of three replicate BRUVs, spaced ~100 m apart, were deployed, to depths ranging from 14 to 29 m (see Figure S1), for 45 min before being recovered. In all, 12 sites were inside the MPA (36 BRUVs) and 6 were in the OC (18 BRUVs). Annually, the same latitude and longitude of sites were used as targets, yet each replicate is considered independent as location will be influenced by the prevalent tidal and atmospheric conditions during deployment.

2.2 | Equipment

Baited remote underwater video systems consisted of a metal frame, lead weights (~30 kg), underwater wide-angle camera housing with horizontal facing camera (Panasonic HDC-SD60 and HDC-SD80), LED lights and a fixed bait pole (Bicknell et al., 2019). Metal bait boxes were fixed on the pole one metre from the camera filled with ~100 g of Atlantic mackerel *Scomber scombrus* cut into segments. Fresh bait was replenished for each deployment. Videos from BRUVs were assessed in situ to ensure that the camera had landed and recorded a viable sample. Failed attempts were repeated to ensure that all samples were suitable.

2.3 | Video analysis

Videos were subject to quality control checks according to the following requirements. Videos must: be in focus; have adequate visibility to discern the bait box clearly (caused by suspended sediment from nearby fishing activity or high levels of plankton); have no fauna or flora obscuring the view and have the seafloor within view (Figure 2: Examples of unacceptable (a and b) and acceptable (c–f) videos). All criteria must be maintained for a minimum of 30 min across the recording. Videos which did not meet these requirements were omitted from analysis. Videos which did meet the requirements were watched at normal speed for 30 min, after a preliminary

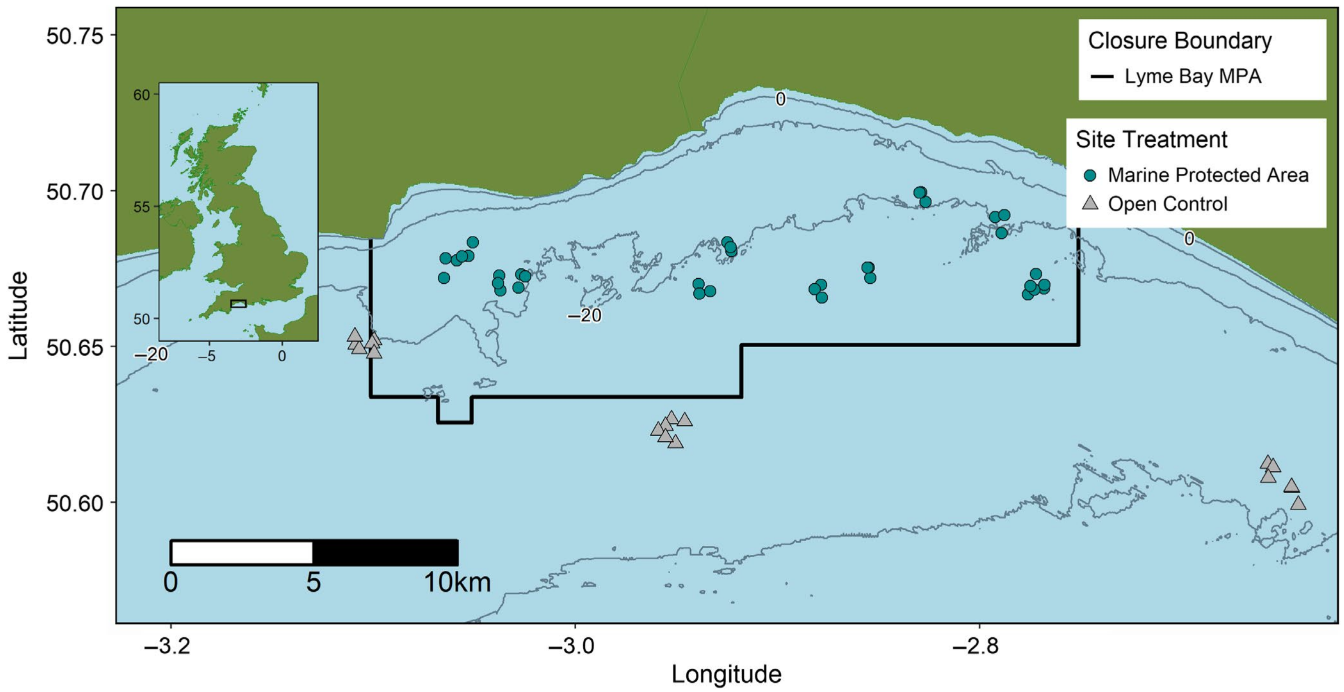

FIGURE 1 Baited Remote Underwater Video system locations within Lyme Bay marine-protected area (blue circles) and open controls (grey triangles)

5 min settling period. For every minute, all mobile fauna were identified to the highest taxonomic resolution possible, and counted. Mobile species were categorised as taxa that were deemed able to continuously move, either in response to the bait or in response to other taxa, which are themselves reacting to the bait. Thus, benthic taxa such as *Pecten maximus*, *Aequipecten opercularis* and *Ophiothrix fragilis* were not included. For every 1-minute segment of the video, the MaxN (maximum number of individuals on screen) for each taxon was recorded. Relative abundance of each taxa was recorded as the greatest MaxN value in any 1 minute, within the 30 min analysed. MaxN is considered a conservative estimate of relative abundance of mobile species attracted to the bait, which decreases the chance of an individual being repeatedly recorded (Cappo et al., 2004).

2.4 | Statistical analysis

The univariate metrics, number of taxa and total abundance, were calculated in 'DPLYR' and 'VEGAN' in R using BRUVs MaxN values (Oksanen et al., 2019; Wickham et al., 2019b). Unless stated otherwise, total abundances were fourth root transformed to meet assumptions of normality. Exploited taxa were defined as taxa which are either landed by fishers or caught and used as bait to catch other species in Lyme Bay (*Personal Communication with Lyme Bay fishers*, Table 1). As the BRUVs enumerated a wide range of species (Table 1), from sharks (*Mustelus mustelus*) and wrasse (*Labrus bergylta*, *Ctenolabrus rupestris*, etc.) to echinoderms (*Asteria rubens*) and hermit crabs (*Pagurus* spp.), Exploited and Non-Exploited species were assessed as either fish (Actinopterygii and Elasmobranchii) or invertebrates (Asteroidea, Cephalopoda, Echinoidea, Gastropoda, Holothuroidea, Malacostraca and Ophiuroidea). Thus, taxa were grouped as Exploited or Non-Exploited fish, or Exploited or Non-Exploited invertebrates.

Permutational multivariate analysis of variance (PERMANOVA; Anderson et al., 2008; Clarke & Gorley, 2015) was used to test differences between years and treatments for both multivariate (Assemblage composition) and univariate (number of taxa and total abundance) response variables for all taxa, then just univariate response variables for Exploited and Non-Exploited fish and Non-Exploited invertebrates. Year and Treatment were fixed factors (Year, 11 levels: 2009–2019; Treatment, 2 levels: MPA and open control). Multivariate analyses were carried out on the basis of a Bray–Curtis dissimilarity matrix, calculated from dispersion weighted fourth root transformed abundance data. Univariate analyses were carried out based on Euclidean distances. The statistical significance of the variance components was tested using 9,999 permutations under a reduced model (Anderson, 2001). PERMANOVA was selected as it is robust to unbalanced designs (Sheehan, Stevens, et al., 2013). Visualisation of multivariate data was carried out by a non-metric multidimensional scaling (MDS) ordination. Percentage contribution of taxa to dissimilarity between sites was assessed using the SIMPER (similarity percentages) method within each year and treatment (Clarke & Gorley, 2015).

Due to a high proportion (~60%) of zero values when the data were split into Exploited invertebrates, zero-inflated Poisson (ZIP) regression models were used from the 'PSCL' package in R to assess the data (Zeileis et al., 2008; Zuur & Ieno, 2016). Model selection utilised Akaike information criteria (AIC) for both the Poisson 'count' and binomial (Bernoulli) 'zero' portions of the model.

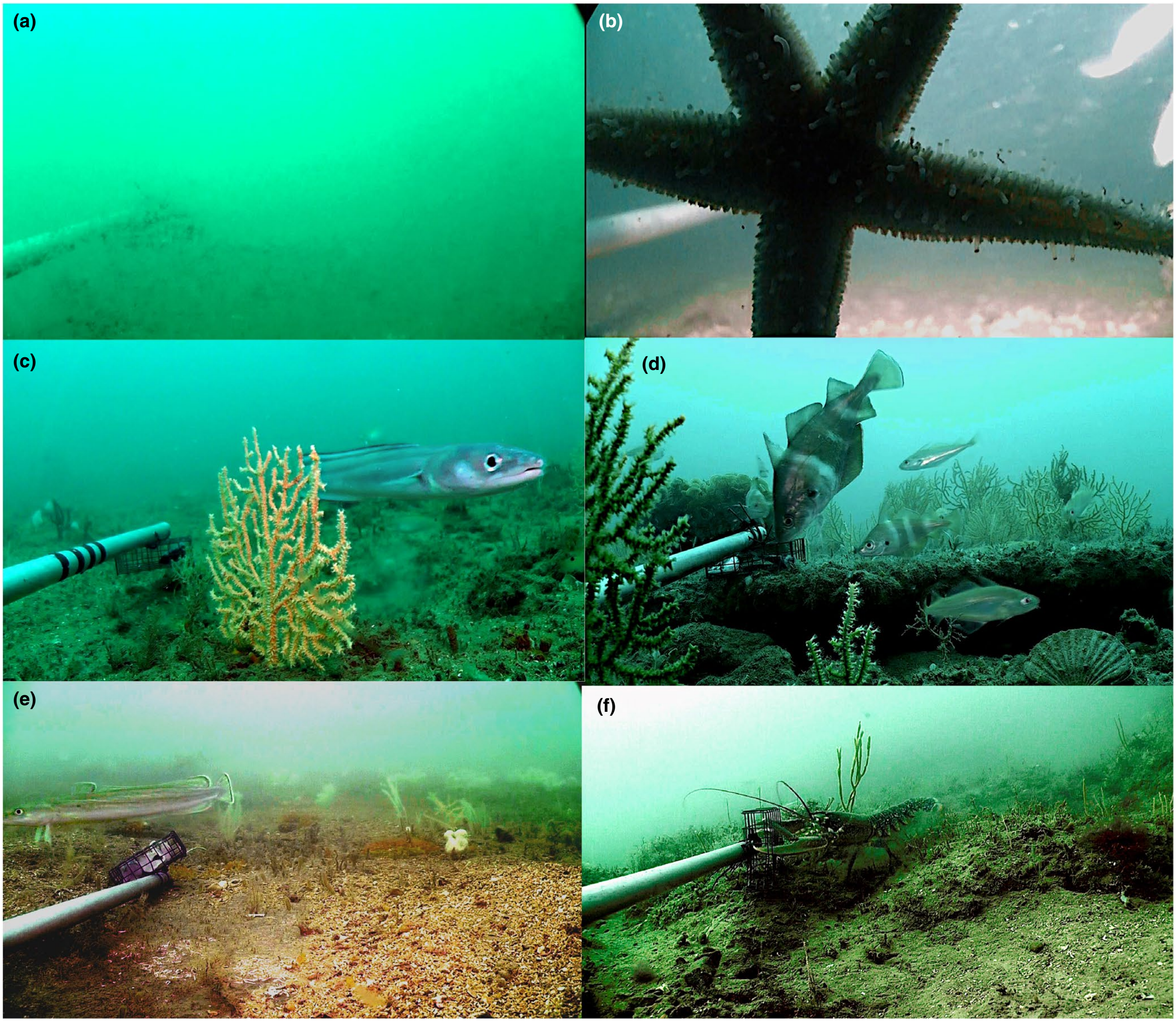

FIGURE 2 Example screen grabs from BRUVs: poor visibility (a: unacceptable), a seastar *Asterias rubens* obscuring the field of view (b: unacceptable), a Conger Eel *Conger conger* infront of a Pink Seafan *Eunicella verrucosa* (c: acceptable), multiple fish, *Trisopterus luscus* and *Trisopterus minutus*, among Pink Seafans *Eunicella verrucosa* and a King Scallop *Pecten maximus* (d: acceptable), a Common Ling *Molva molva* (e: acceptable) and a European Lobster *Homarus gammarus* (f: acceptable)

To assess long-term linear trends in univariate metrics, significant ($p < 0.05$) temporal terms (Year and Year × Treatment) were further analysed and visualised, using linear regression analyses. Linear regression analyses were carried out utilising the 'TIDYVERSE' and 'STATS' packages within R (R Core Team, 2019; Wickham, Averick, et al., 2019). Sample versus fitted residuals, quartile–quartile and autocorrelation of temporally sequential samples were assessed visually, to fit assumptions of the models used.

3 | RESULTS

A total of 13,175 individuals from 39 families were recorded during the study with 25 species (15 families) from the class Actinopterygii, 4 species (3 families) from the class Elasmobranchii, 12 species (10 families) from the class Malacostraca and 4 species (4 families) from the class Gastropoda. Hermit crabs *Pagurus* spp. were the most abundant taxa (2,820 individuals), followed by Pouting *Trisopterus minutus* (1,595 individuals) and Netted Dogwhelk *Tritia reticulata* (1,120 individuals). Across both treatments, the most ubiquitous taxa was *Scyliorhinus canicula* with 869 individuals across 71% of sites, followed by *Pagurus* spp. and Gobiidae spp. (2,820 and 1,012 individuals: both across 58% of sites). Inside the MPA, the most common taxa were *Trisopterus minutus* (1,135 individuals), *Tritia reticulata* (1,043 individuals) then Gobiidae spp. (1,012 individuals). For the OC, the most common taxas were *Pagurus* spp. (2,267 individuals), *Trachurus trachurus* (634 individuals) and then *Merlangius merlangus* (589 individuals).

TABLE 1 Exploited and Non-Exploited Fish and Invertebrates. Information based on use and landings of fishers in Lyme Bay. Symbols denote species which were exclusively recorded in the marine-protected area (^{m}) and open controls (°)

Fish		Invertebrates	
Exploited	**Non-Exploited**	**Exploited**	**Non-Exploited**
Chelidonichthys cuculus	Blenniidae spp.$^{(m)}$	*Buccinum undatum*	*Asterias rubens*
Chelidonichthys lucerna	*Callionymus lyra*	*Cancer pagurus*	*Calliostoma zizyphinum*$^{(m)}$
Conger conger	*Centrolabrus exoletus*$^{(m)}$	*Homarus gammarus*	*Goneplax rhomboides*
Eutrigla gurnardus	*Ctenolabrus rupestris*	*Maja squinado*	*Hyas coarctatus*$^{(o)}$
Labrus bergylta$^{(m)}$	*Gaidropsarus* spp.$^{(m)}$	*Sepia officinalis*$^{(m)}$	*Inachus* spp.
Limanda limanda	Gobiidae spp.		*Liocarcinus depurator*
Mullus surmuletus	*Labrus mixtus*$^{(m)}$		*Loligo* spp.$^{(m)}$
Pollachius pollachius	*Lepadogaster* spp.		*Luidia ciliaris*
Raja clavata	*Merlangius merlangus*		*Macropodia* spp.
Scyliorhinus canicula	*Molva molva*$^{(m)}$		*Necora puber*
Scyliorhinus stellaris$^{(m)}$	*Symphodus melops*$^{(m)}$		*Neopentadactyla mixta*$^{(m)}$
Solea solea$^{(o)}$	Triakidae spp.		Ophiuroidea spp.
Spondyliosoma cantharus	*Trisopterus minutus*		*Pagurus* spp.
Trachurus trachurus			*Porcellana platycheles*
Trisopterus luscus			*Psammechinus miliaris*
Zeus faber$^{(m)}$			*Tritia reticulata*
			Tritonia nilsodhneri$^{(m)}$
			Xantho hydrophilus

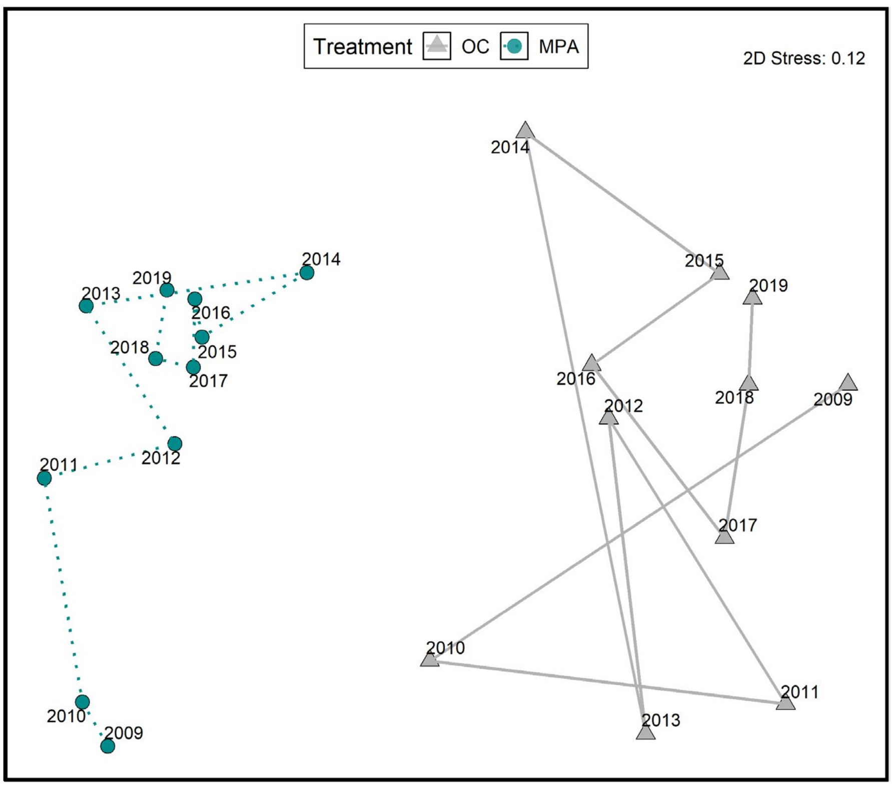

FIGURE 3 Multidimensional scaling ordination showing the differences of assemblage composition over 11 years between the two treatments (marine-protected area [MPA] shown by blue circles and open controls [OC] shown by grey triangles). Lines show yearly progression from 2009 to 2019

TABLE 2 PERMANOVA results for all species (Assemblage, Number of taxa and Total abundance); Exploited and Non-Exploited Fish (Number of taxa and Total abundance) and Non-Exploited Invertebrates (Number of taxa and Total abundance), as well as zero-inflated Poisson generalised linear mixed-effect model results for Exploited Invertebrates (Number of taxa and Total abundance). Year, Treatment, Site and Residual are abbreviated throughout to Yr, Tr, Si(Tr) and Res.

		Assemblage			Number of taxa			Total abundance		
Source	*df*	SS	Pseudo-*F*	*p* value	SS	Pseudo *F*	*p* value	SS	Pseudo *F*	*p* value
All species										
Yr	10	117,000	6.56	<0.0001***	487	9.57	<0.0001***	21.4	11.5	<0.0001***
Tr	1	88,900	12.80	<0.0001***	18.3	0.808	0.38	6.35	7.64	0.013*
Si(Tr)	17	157,000	11.10	<0.0001***	509	10.8	<0.0001***	18.7	10.2	<0.0001***
Yr × Tr	10	32,200	1.81	<0.0001***	74.6	1.47	0.16	2.6	1.4	0.18
Yr × Si(Tr)	156	278,000	2.15	<0.0001***	794	1.84	<0.0001***	29	1.73	<0.0001***
Res	387	320,000			1,070			41.5		
Fish										
Exploited										
Yr	10				93.8	8.35	<0.0001***	53	15.8	<0.0001***
Tr	1				24.1	14.5	0.0015**	0.825	2.42	0.14
Si(Tr)	17				35.2	3.73	<0.0001***	6.91	2.51	0.0011**
Yr × Tr	10				16.8	1.49	0.14	4.67	1.4	0.19
Yr × Si(Tr)	156				175	2.02	<0.0001***	52.3	2.07	<0.0001***
Res	387				215			62.8		
Non-Exploited										
Yr					51.8	3.2	<0.0001***	27	6.83	<0.0001***
Tr					106	28.9	<0.0001***	3.52	6.89	0.021*
Si(Tr)					79.6	4.95	<0.0001***	10.5	2.73	<0.0001***
Yr × Tr					23.8	1.48	0.15	13.3	3.35	0.0012**
Yr × Si(Tr)					252	1.71	<0.0001***	61.8	1.75	<0.0001***
Res					366			87.4		
Invertebrates										
Non-Exploited										
Yr	10				6.1	1.68	0.088	7	2.28	0.016*
Tr	1				0.197	0.1	0.75	0.215	0.149	0.7
Si(Tr)	17				44	8.96	<0.0001***	32.3	8.7	<0.0001***
Yr × Tr	10				8.37	2.3	0.015*	7.26	2.37	0.015*
Yr × Si(Tr)	156				56.7	1.26	0.04*	47.9	1.41	0.0039**

(Continues)

TABLE 2 (Continued)

Source	df	Assemblage SS	Assemblage Pseudo-F	Assemblage p value	Number of taxa SS	Number of taxa Pseudo F	Number of taxa p value	Total abundance SS	Total abundance Pseudo F	Total abundance p value
Res	387				112			84.5		
Exploited										
					Estimate (*SE*)	z value	*p* value	Estimate (*SE*)	z value	*p* value
Zero Model (Bernoulli)										
Intercept					−0.725 (0.0596)	−12.2	**<0.0001*** **	0.656 (0.0898)	7.31	**<0.0001*** **
Tr								−0.744 (0.136)	−5.47	**<0.0001*** **
Count model (Poisson)										
Intercept					−11.6 (59.3)	−0.195	0.84	0.163 (0.302)	0.541	0.59
Yr								−0.0284 (0.0404)	−0.704	0.48
Tr								−0.754 (0.326)	−2.31	**0.021***

Bold values denote significant terms ($p < 0.05$), whilst asteriks denote level of significance (*$p < 0.05$; **$p < 0.01$; ***$p < 0.0001$).

3.1 | All species

3.1.1 | Assemblage composition

Assemblages at MPA sites were always different from those in open controls (Figure 3; Table 2), but over time the assemblage composition of the two treatments also shifted in discordant ways, shown by a significant year:treatment interaction (Table 2). The MPA showed large shifts in assemblage in the first years, then after 5 years proceeded to become consistent over time, unlike the OC, which showed random annual assemblage shifts with little to no consistency over time (Figure 3). Assemblage similarities, within sites across years and treatments, were driven primarily by the Small-Spotted catshark *Scyliorhinus canicula* and Gobiidae spp (Figure 4). Most of the remainder of the similarity within the MPA sites was driven by reef-associated wrasse species (dark blues, Figure 4), whereas in the OC this was driven by scavenging crustaceans, echinoderms and gastropods (yellows, oranges and dark browns, Figure 4). Excluding *Scyliorhinus canicula*, the vast majority of the similarity within the OC sites was driven by the scavenging crustacean, *Pagurus* spp. (Figure 4).

3.1.2 | Number of taxa and total abundance

In the MPA, the mean number of taxa and mean total abundance, derived from MaxN, changed from 4.44 ± 0.397 and 1.66 ± 0.0891 in 2009 to 6.97 ± 0.481 and 2.13 ± 0.0866 in 2019 (56.9% and 28.9% increase in the number of taxa and total abundance, respectively). In the OC, the mean number of taxa and mean total abundance changed from 5.28 ± 0.331 and 1.98 ± 0.0415 in 2009 to 6.11 ± 0.301 and 2.44 ± 0.0958 in 2019 (15.8% and 23.4% increase in the number of taxa and total abundance, respectively).

This change over time was significant in both the number of taxa and total abundance, yet neither metric showed a significant year:treatment interaction (Table 2). However, the total abundance was significantly different between treatments (Table 2). The number of taxa showed a significant linear increase over time inside the MPA (Figure 5a) while the total abundance showed a significant linear increase in both treatments over time (Figure 5b).

3.2 | Fish

3.2.1 | Number of taxa and total abundance

In the MPA, the mean number of taxa and mean total abundance of Exploited fish changed from 0.417 ± 0.122 and 0.311 ± 0.0856 in 2009 to 2.23 ± 0.184 and 1.45 ± 0.0486 in 2019 (430% and 370% increase in the number of taxa and total abundance, respectively). For the Non-Exploited fish, in the MPA, the mean number of taxa and mean total abundance changed from 2.33 ± 0.211 and 1.46 ± 0.0916 in 2009 to 2.23 ± 0.225 and 1.41 ± 0.103 in 2019 (4.5% and 3.3%

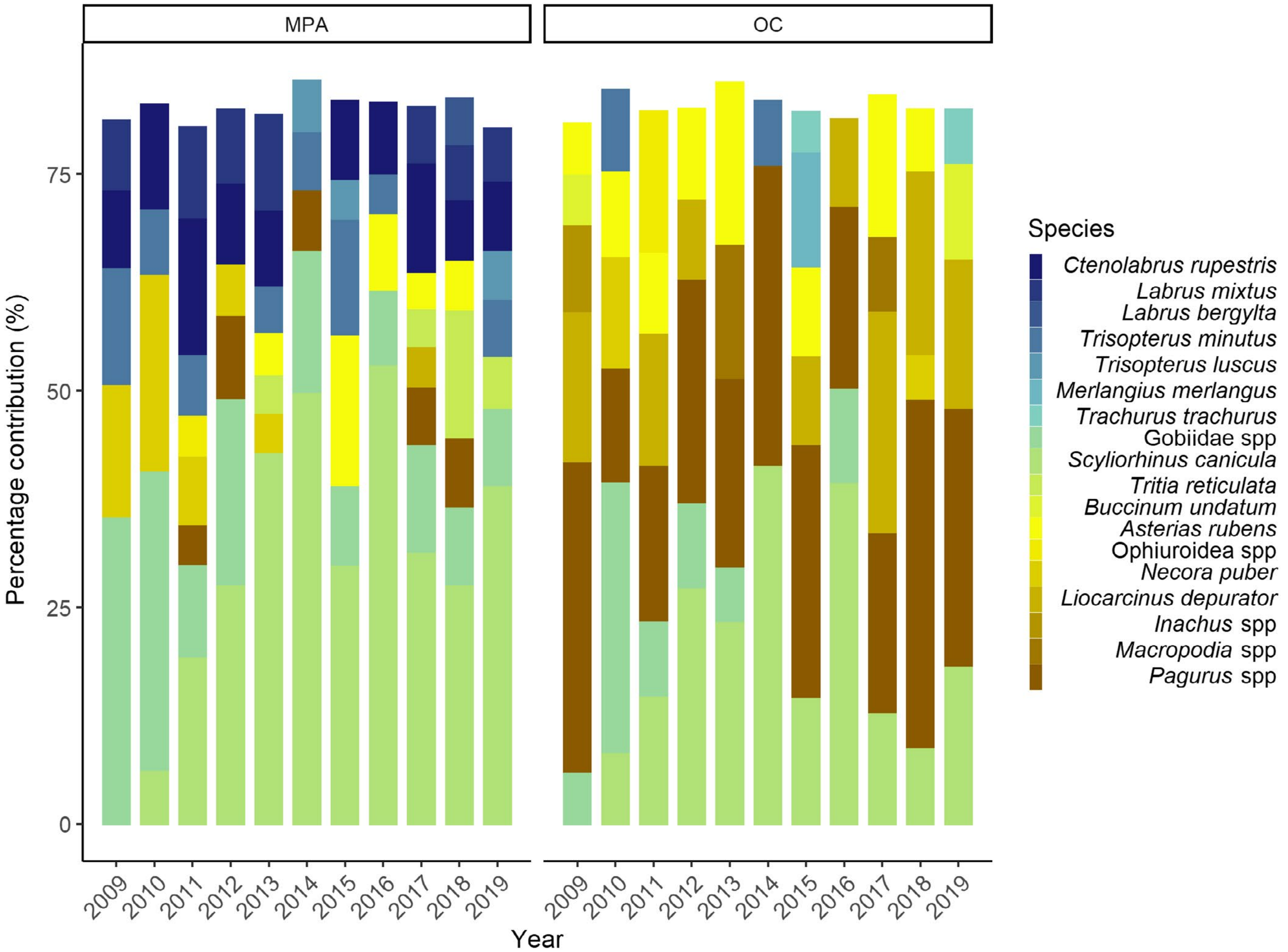

FIGURE 4 Similarity percentages results for the top 80% contributions of species driving the similarities of assemblage compositions of sites within year and treatment

decrease in the number of taxa and total abundance, respectively). In the OC, the mean number of taxa and mean total abundance of Exploited fish changed from 0.278 ± 0.109 and 0.316 ± 0.125 in 2009 to 1.61 ± 0.216 and 1.63 ± 0.165 in 2019 (480% and 420% increase in the number of taxa and total abundance, respectively). In the OC, the mean number of taxa and mean total abundance of Non-Exploited fish changed from 1.28 ± 0.24 and 1.14 ± 0.156 in 2009 to 1.28 ± 0.195 and 1.56 ± 0.175 in 2019 (0% and 37% increase in the number of taxa and total abundance, respectively). This change over time in the number of taxa of Exploited fish in both treatments was significant (Table 2). The MPA showed a much greater increase over time (gradient of 0.14: Figure 6a) than that of the OC (gradient of 0.062: Figure 6a). The number of taxa of Non-Exploited fish was significantly different across years and treatments but, like the Exploited fish, showed no year:treatment interaction. However, the change over time inside the MPA, unlike that of the Exploited fish, was expressed as a significant linear decrease (Figure 6b). The total abundance of Exploited fish showed a significant difference between years but not between treatments (Table 2). Both treatments showed significant linear increases over time (Figure 6c). There was a significant year:treatment interaction for the total abundance of Non-Exploited fish (Table 2), which was expressed as a significant linear decrease over time inside the MPA (Figure 6d).

3.3 | Invertebrates

3.3.1 | Number of taxa and total abundance

In the MPA, the mean number of taxa and mean total abundance of Exploited invertebrates changed from 0.333 ± 0.0797 and 0.333 ± 0.0797 in 2009 to 0.543 ± 0.118 and 0.686 ± 0.182 in 2019 (63% and 110% increase in the number of taxa and total abundance, respectively). For the Non-Exploited invertebrates, in the MPA, the mean number of taxa and mean total abundance changed from 1.36 ± 0.196 and 0.985 ± 0.104 in 2009 to 1.97 ± 0.297 and 1.35 ± 0.16 in 2019 (45% and 37% increase in the number of taxa and total abundance, respectively). In the OC, the mean number of taxa and mean total abundance of Exploited invertebrates changed from 0.5 ± 0.121 and 0.722 ± 0.24 in 2009 to 0.667 ± 0.14 and

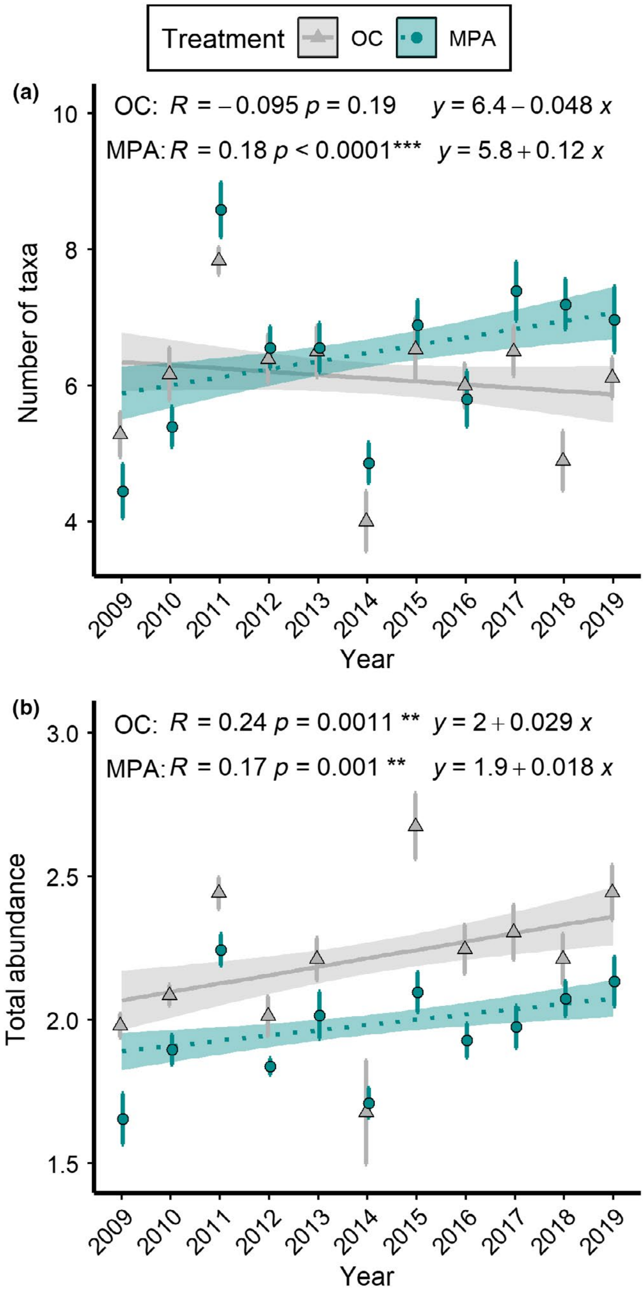

FIGURE 5 Number of taxa (a) and total abundance (fourth root transformed: b) by year across treatments (marine-protected area [MPA]: blue circles, open controls [OC]: grey triangles). Lines and equations show linear regression equation coefficients. Points with errors bars show mean values and standard errors

1.33 ± 0.362 in 2019 (33% and 85% increase in the number of taxa and total abundance, respectively). For the Non-Exploited invertebrates in the OC, the mean number of taxa and mean total abundance changed from 3.22 ± 0.25 and 1.76 ± 0.0588 in 2009 to 2.56 ± 0.294 and 1.77 ± 0.123 in 2019 (21% decrease and 0.47% increase in the number of taxa and total abundance, respectively). Neither year nor treatment could be fitted to model the number of Exploited invertebrate taxa, with the 'best' ZIP model utlising only the intercept for both the count and zero parts of the model (Table 2). However, there was a significant year:treatment interaction for the number of taxa for Non-Exploited invertebrates (Table 2), with a significant linear decrease with time in the OC (Figure 7b). The total abundance of Exploited invertebrates was significantly lower in the MPA compared to the OC (Table 2; Figure 7c). The total abundance of Non-Exploited invertebrates did show a significant year:treatment interaction (Table 2) but there was no significant linear trend over time (Figure 7d).

4 | DISCUSSION

Over the course of the 11-year study, the exclusion of bottom towed fishing inside the MPA significantly altered the assemblage composition and increased the diversity (number of taxa) of mobile taxa, relative to areas that remained open to these fishing practices (open controls: Table 2; Figure 5a). The total abundance of these mobile taxa significantly increased over time in both treatments (Table 2; Figure 5b). When specifically assessing Exploited fish, which continue to be exploited and fished within the protected area, there was a significant increase over time in the number of taxa and total abundance across both treatments (MPA and open controls). Non-Exploited fish significantly decreased over time in the MPA (Table 2; Figure 6). Exploited invertebrates had lower total abundance inside the MPA compared to the OC, but neither treatment showed any change over time in the number of taxa or total abundance (Table 2; Figure 7a,c). Non-Exploited invertebrates showed a lower number of taxa and total abundance in the MPA but with a decreasing number of taxa in the open controls (Table 2; Figure 7b,d).

The Lyme Bay Statutory Instrument was designated to allow recovery and protect the biodiversity of fragile sessile reef fauna across 206 km^2 from further damage by bottom towed fishing gear. The protection has shown to positively benefit sessile reef fauna (Sheehan, Cousens, et al., 2013; Sheehan, Stevens, et al., 2013) and the effects of this protection have now led to positive increases to the mobile fauna over time, with increases in the number of taxa in the MPA. This is likely to be due to a combination of direct displacement of species, from areas subject to bottom towed fishing to areas not subject to bottom towed fishing (Dinmore et al., 2003), and through indirect protection and proliferation of the sessile reef habitat, which, in turn, increases survivorship of mobile taxa (Howarth et al., 2015; Sheehan, Cousens, et al., 2013; Wilson et al., 2010).

Fish assemblages are dependent on depth, habitat complexity and availability, competition/predation and larval/recruitment variability (Harasti et al., 2018; Meekan et al., 2018), and, as such, can be highly variable (Stige et al., 2019). However, in this case, over time the number of taxa and total abundance of Exploited fish increased across both treatments. The whole-site approach employed in Lyme Bay has led to the increase in the functional reef area within the bay (Sheehan, Cousens, et al., 2013; Sheehan,

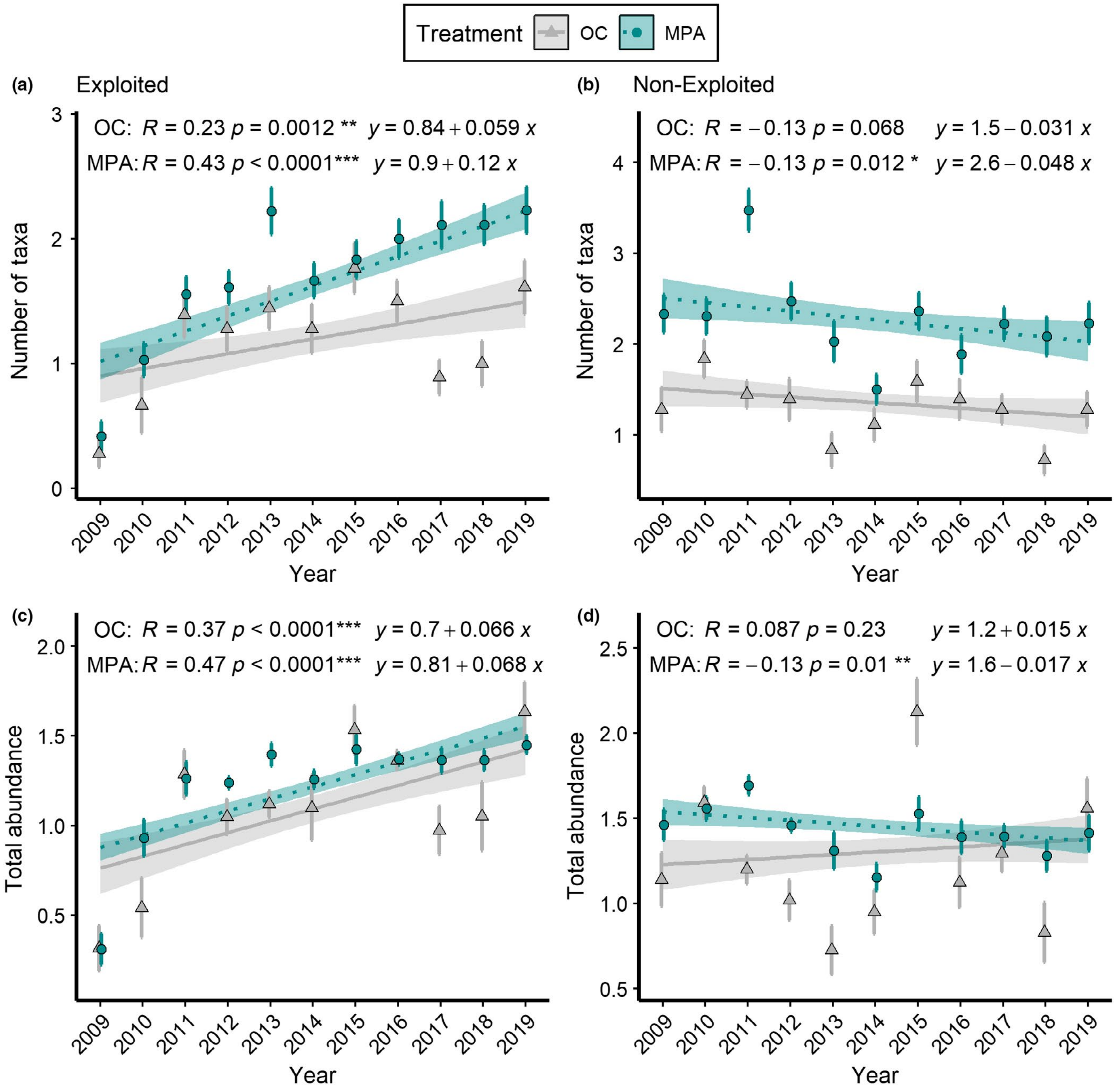

FIGURE 6 Number of taxa (a) and total abundance (c) of Exploited fish by year and treatments, and number of taxa (b) and total abundance (fourth root transformed: d) of Non-Exploited fish by year and treatments (marine-protected area [MPA]: blue circles, open controls [OC]: grey triangles). Lines and equations show linear regression equation coefficients. Points with errors bars show mean values and standard errors

Stevens, et al., 2013). The increase in Exploited fish will likely have been driven by this increase in functional reef area, which is known to be an Essential Fish Habitat (Rabaut et al., 2010). The increase seen in the OC was found to a be at a slower rate than the MPA and may have been due to 'spillover' effects, likely driven by a combination of increased larval export and direct adult movement from the MPA to the surrounding area (Berkeley et al., 2004; Garcá-Rubies et al., 2013). Thus, the simultaneous increase in EFH and reduction in collateral damage to habitat complexity associated with seabed dredging and trawling may have contributed to this general increase in taxa and abundance of around 400%. This co-occurred with a decrease in the number of taxa and total abundance of Non-Exploited fish over time, potentially indicating competitive exclusion by the commercially Exploited fish, which are more likely to be larger higher trophic predators (Baudron et al., 2019). For example, the Exploited shark and ray species *Scyliorhinus canicula*, *Scyliorhinus stellaris* and *Raja clavata* are known to predate on small bony fish (Ellis et al., 1996), such as *Trisopterus minutus* and *Callionymus* spp., which were categorised as Non-Exploited fish here. The increase in abundance of

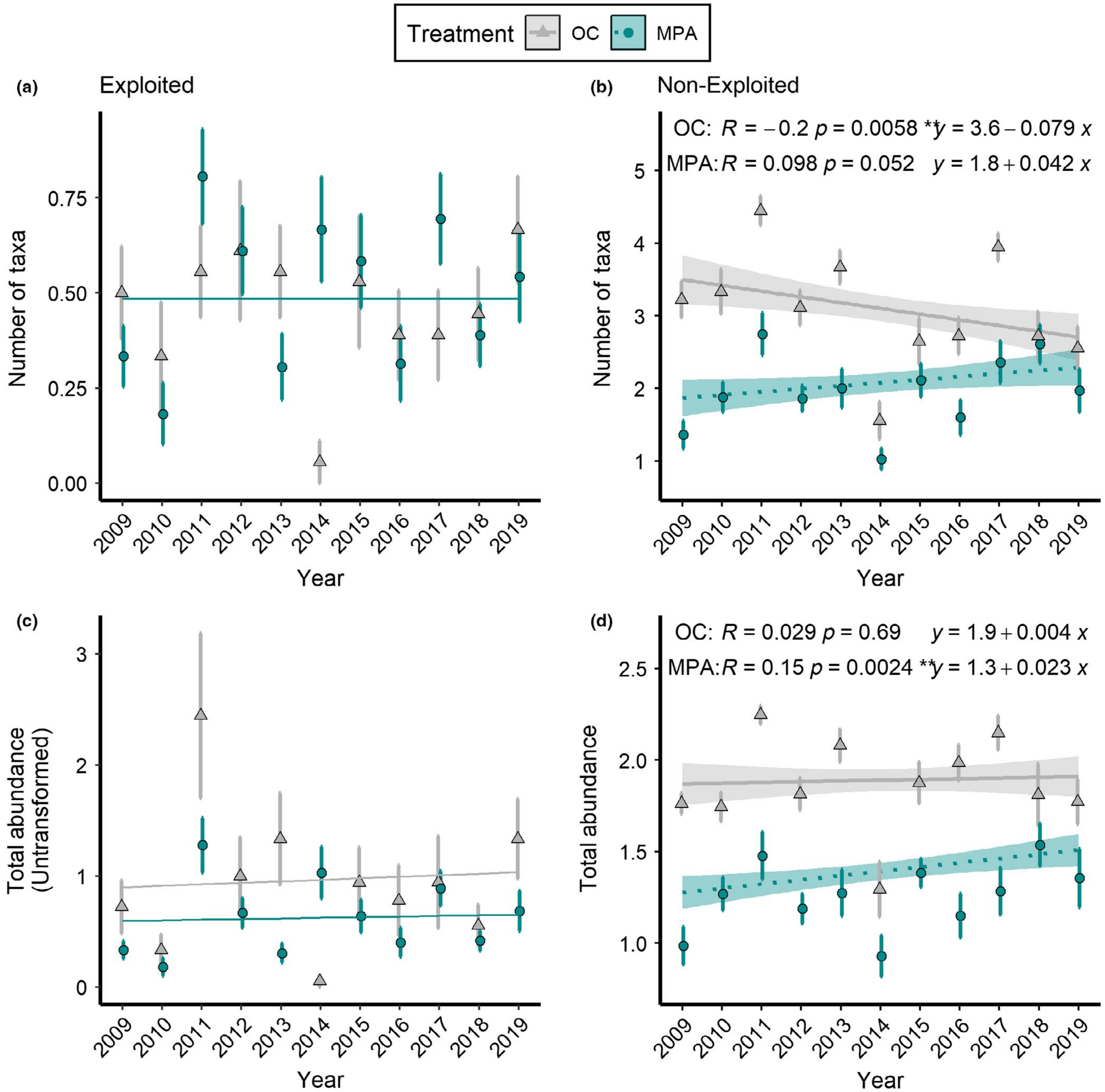

FIGURE 7 Predicted versus observed number of taxa (a) and total abundance (c) of Exploited invertebrates over time for ZIP models and observed number of taxa (b) and total abundance (fourth root transformed: d) of Non-Exploited invertebrates across year and treatment (marine-protected area [MPA]: blue circles, open controls [OC]: grey triangles). Lines show linear and zero-inflated Poisson regressions. Points with errors bars showing mean values and standard errors

these Exploited fish may have led to increased predation on Non-Exploited fish species.

As an indirect effect of exclusion of towed bottom fishing within Lyme Bay, decreases in conflict between towed fishers and potters led to increases in potting levels within the MPA (Mangi et al., 2011). Although less destructive than bottom towed fishing, potting at high densities can have impacts to sensitive habitats (Gall et al., 2020) and target species have harvest-associated selection applied to them, which could lead to alterations in population size and behavioural selection (Madin et al., 2010; Meekan et al., 2018). The three main fisheries in Lyme Bay, which continue to be carried out within the MPA, utilise pots and target whelks *Buccinum undatum*, brown crab *Cancer pagurus* and European lobster *Homarus gammarus*, which constitute three of the five taxa classed as Exploited invertebrates in this study. Yet, regardless of potentially higher fishing levels, Exploited invertebrates showed no significant temporal trends over the 11 years of study, although there was significantly greater total abundance in the OC.

Temporal trends of Non-Exploited groups showed decreases in number of taxa and total abundance of fish inside the MPA and total abundance of invertebrates in the OC. As mentioned, fish population dynamics are highly linked to the available habitats, as well as predation and competition (Harasti et al., 2018; Meekan et al., 2018). Thus, as the functional reef extent has increased, this may have simultaneously increased predation and competition, and decreased the area of the favourable habitat to Non-Exploited fish within the MPA. The decrease in the number of Non-Exploited invertebrates outside of the MPA may be linked to displacement, either of species (Dinmore et al., 2003) or fishing effort (Agardy et al., 2011).

Previous studies of the ecological response to MPAs with partial protection have had varying results (Sciberras et al., 2013), with some, like the current study, finding increases in Exploited taxa (Beukers-Stewart et al., 2005; Pipitone et al., 2000), and others finding no difference between MPAs with partial protection and control sites (Denny & Babcock, 2004; Piet & Rijnsdorp, 1998). This variability in effects of MPAs with partial protection could be attributed to many factors, such as pre designation fishing pressure, enforcement/adherence level, age of protection, size of protected area, the level of protection, as well as the sensitivity/appropriateness of the monitoring effort to detect protection effects (Babcock et al., 2010; Claudet et al., 2008; Edgar et al., 2014). Utilising a whole-site approach, such as in Lyme Bay, is being advocated to better protect the whole ecosystem and, by extension, lead to fisheries' increases (Solandt et al., 2020), particularly for larger (>100 km^2) MPAs (Edgar et al., 2014).

The number of sites assessed inside and outside the MPA here was not fully balanced with 36 BRUV deployments inside the MPA and 18 outside, so potentially this could be seen as a weakness in terms of the comparability of data in and out of the MPA. However, methods that are robust to uneven survey design (PERMANOVA) were used to assess difference between treatments while temporal trends were assessed by regression analyses separately for each treatment, minimising any effects of uneven survey design. This gives high confidence in the reported results.

As many taxa are used as bait by fishers, often extensively, and thus not landed (Davies et al., 2009), the separation between Exploited and target taxa is difficult to define. This creates difficulties in assessing fishing pressure on taxa that are not locally targeted or landed but are used within the fishery. Exploited taxa were defined by landings data, expert commentary and local fisher knowledge. However, the majority of the Exploited invertebrate taxa were the main target taxa of the fishers in Lyme Bay and showed lower total abundance inside the MPA as a result. Yet, long-term increases and decreases in abundances of target species, which were only found for the Exploited fish and not the invertebrates, will be highly dependent on temporal fishing pressures (Mumby et al., 2012). Thus, to fully assess the effects of the protection to the local fishery, comparison of landings alongside abundance data could more adequately quantify any benefits or losses.

In conclusion, after 11 years of BRUVs monitoring and 12 years of protection, Lyme Bay MPA is showing a positive response in the number and total abundance of Exploited fish taxa. Increases in the number of taxa and total abundance of Exploited fish (~400% increase over 11 years) inside the MPA, which happened at the same time as an increase in static fishing, show that the protection and enforcement of the area provide benefits to both conservation and fisheries alike. Yet, inconclusive results regarding the main targeted taxa by value, namely Whelks, Brown Crab and Lobster, require further assessment, alongside fisheries landings data, to fully quantify any benefits the protection has granted the local fishery. Regardless, this study provides further evidence of the capabilities of well enforced and monitored partial protection, which follow an Ecosystem Approach to Fisheries Management, and how the compromise between conservation and fisheries management can benefit benthic ecosystems when the whole-site approach is employed, as opposed to individual feature protection. Furthermore, it illustrates the importance and necessity of monitoring MPAs over appropriate temporal and spatial scales to aid management.

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

AUTHORS' CONTRIBUTIONS

E.V.S. and M.J.A. conceived the ideas and monitoring design; E.V.S., L.H., A.R., A.Y.C. and B.F.R.D. collected the data; A.Y.C., L.H. and B.F.R.D. organised and analysed the data; B.F.R.D., A.R., E.V.S. and L.H. led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Archive for Marine Secies and Habitats Data (DASSH) https://doi.org/10.17031/1741 (Davies et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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