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Ecosystem benefits of adopting a whole-site approach to MPA management

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Abstract

Globally, nations are designating marine protected areas to recover and protect habitats and species. With targets to protect 30% of marine areas by 2030, the effectiveness of MPAs to protect designated space is important. In Lyme Bay (south-west UK), two co-located MPAs have each adopted different management styles to exclude mobile demersal fishing: a Special Area of Conservation (SAC) protecting the known extent of sensitive reef habitat and an area including a mosaic of reef and sedimentary habitats where the whole site is protected from mobile demersal fishing under a statutory instrument (SI). Underwater videography, both towed (individuals m^{-2}) and baited (MaxN), was used to enumerate change over time of reef species (number of taxa, total abundance, functional richness and functional redundancy) in the MPAs and nearby control areas (2008–2019). Total abundance and functional redundancy of sessile taxa and functional richness of mobile taxa increased, while the number of sessile or mobile taxa, functional richness of sessile taxa, total abundance of mobile taxa or functional redundancy of mobile taxa did not differ from nearby control sites. Over time, both management styles did result in increases in sessile and sedentary taxa diversity relative to open controls, with increases in total abundance of 15% and 95% in the "feature-based" and whole-site MPAs, respectively, alongside increases in the number of sessile taxa of 44% over time in the "feature-based" MPA. However, the mobile taxa in the whole-site MPA showed levels of functional redundancy 7% higher than the "feature-based" MPA, indicative of a higher community resilience inside the whole-site MPA to perturbations, such as storms or biological invasions. Increases seen in the diversity of sessile taxa were expected only in areas where mobile demersal fishing was excluded (~46.8% of its areas). Therefore, if the whole "feature-based" MPA was consistently protected, we expected to see similar levels of increase in the functional extent of reef. While the "feature-based" MPA showed similar results over time to that of the "whole site," the "whole site" showed higher levels of diversity, both taxonomical and functional.

KEYWORDS
benthic, biodiversity, functional ecology, management, marine protected areas, whole-site approach

1 | INTRODUCTION

The use of marine protected areas (MPAs) as a tool to protect habitats and species is increasing globally (Edgar and Stuart-Smith 2014; Lubchenco and Grorud-Colvert 2015; Sala and Giakoumi 2018). MPAs have been shown to recover benthic ecosystems (Sheehan et al. 2013a), including increased species' biomass, catch per unit effort, diversity, density and community stability (Lester et al. 2009; Sciberras et al. 2013; Sheehan et al. 2013b; Mellin et al. 2016) and predicted benefits for carbon sequestration and climate change mitigation (Sala et al. 2021). MPAs are widely advocated by the Convention of Biological Diversity (CBD), the International Union for the Conservation of Nature (IUCN) and European Union (EU), with a current target set by the Global Ocean Alliance to protect 30% of marine areas by 2030 (O'Leary et al. 2016; Brander et al. 2020; Rees et al. 2020; Waldron et al. 2020). The effectiveness of MPAs at achieving defined objectives such as climate resilience, resource conservation, tourism or fisheries production depends on a combination of being no take, large, old, isolated and well enforced (Carpenter et al. 2001; Lubchenco et al. 2003; Edgar and Stuart-Smith 2014; Roberts et al. 2017; Kerr et al. 2019). MPAs that have been designated but not managed appropriately are ineffective, and sometimes, effects are counter to their objectives (Edgar et al. 2004; Rife et al. 2013; Devillers et al. 2015; Claudet 2018).

In the UK, MPAs are designated as Special Areas of Conservation (SACs: Natura 2000 agreement and EU Habitats Directive), Special Protection Areas (SPAs: Natura 2000 agreement and EU Habitats Directive: European Commission 1992), Marine Conservation Zones (MCZs: Marine and Coastal Access Act) and No Take Zones (NTZ) (Gall and Rodwell 2016; Sheehan et al. 2016; Rees et al. 2020; Solandt et al. 2020; Stewart et al. 2020; Rees et al. 2021). SACs, SPAs and MCZs are all partially protected, where activities deemed to be detrimental to the health of the designated Annex I or II species or habitat are prohibited from areas where such features have been found within the MPA boundary. These types of protection are more acceptable to the public than full NTZs by allowing some level of commercial and recreational fishing. SACs, SPAs and MCZs are "feature-based" by only protecting a feature of interest within the confines of where it has been identified. However, this assumes that species and habitats operate in isolated patches and limits potential for recovery and expansion (Sheehan et al. 2013a). Furthermore, all remaining habitats and species within the confines are at risk of destructive and damaging activities despite that area being defined as "protected" (Rees et al. 2020; Solandt et al. 2020). This lack of protection for all habitats and species within their boundaries has meant that large proportions of MPAs are not protected at all (Solandt et al. 2020) and that "feature-based" management does not effectively protect marine ecosystems, or deliver fisheries and conservation objectives (Costanza et al. 1998; Pikitch et al. 2004). Therefore, MPAs that protect the whole site from damaging practices and activities are being advocated as a more effective management method for both fisheries and conservation targets (Sheehan et al. 2013a; Sheehan et al. 2013b; Sheehan et al. 2016; Rees et al. 2020; Solandt et al. 2020).

Within Lyme Bay, in the south-west of the UK, a statutory instrument was used in 2008 to exclude mobile demersal fishing from 206 km^2 of the bay while allowing other static forms of fishing, such as scallop diving, static potting and netting (Figure 1). In 2011, a Site of Community Importance was also established, which later became a SAC. This SAC similarly excluded mobile demersal fishing and allowed static forms of fishing. However, this was only applied to areas of Annex I reef (Natural-England 2015). This co-location of management approaches provided the rare opportunity to compare the effectiveness of feature vs whole-site management.

Our objectives were to compare: (1) effects of the SAC to open controls (OC), which continued to be open to mobile demersal fishing

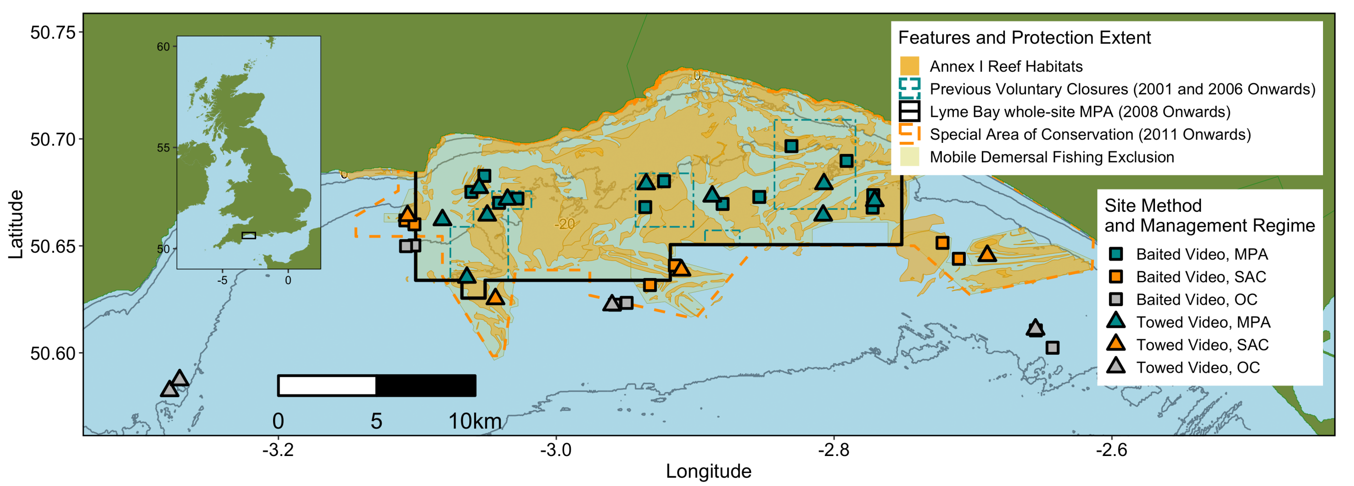

FIGURE 1 Survey locations for towed flying array (triangles) and baited remote underwater video system (squares) in the Special Area of Conservation (orange shapes), whole-site MPA (blue shapes) and open controls (grey shapes), and closure boundaries within Lyme Bay with UK map inlaid. Each location represents three replicates. The Lyme Bay whole-site MPA excluded all forms of Mobile Demersal Fishing from 2008 onwards, while the Special Area of Conservation excluded all forms of mobile demersal fishing from known areas of Annex I Reef Habitats from 2011 onwards

on benthic and demersal fauna, and (2) the recovery trajectory of taxa over 5 years since protection between the SAC ("feature-based" SAC: Year 1 = 2012), the SI MPA (whole-site MPA: Year 1 = 2008) and open controls (areas open to mobile demersal fishing: Year 1 = 2012). To assess changes in biodiversity, assemblage composition, number of taxa and total abundance were measured. To assess changes in ecosystem service provision and resilience of community to perturbations (storms, invasive species and destructive fishing: Tillin et al. 2006), functional richness (the number of different functional traits in a community) and functional redundancy (the overlap of functional traits between different species in the community) were measured. We expected that assemblage composition in the SAC would shift away from the OC from before to after SAC designation, with an increase in number of taxa, total abundance, functional richness and functional redundancy. Secondly, we expected that assemblage composition would shift significantly with age of protection in both the "feature-based" SAC and whole-site MPA relative to the OC, with an increase in number of taxa, total abundance, functional richness and functional redundancy and that the whole-site MPA would increase more rapidly than the "feature-based" SAC. The OC data were sampled to align with the SAC age of protection. Each hypothesis was tested twice, first using sessile and sedentary fauna data collected by the towed flying array (sessile taxa henceforth: Sheehan et al. 2013a; Sheehan et al. 2021; Davies et al. 2022) and second using mobile taxon data sampled by the baited remote underwater video systems (BRUVs) (mobile taxa henceforth: Davies et al. 2020; Davies et al. 2021; Davies et al. 2022).

2 | METHODS

2.1 | Location

Lyme Bay, in the south-west of the UK, contains nationally important Annex I reef habitats that are home to pink sea fans *Eunicella verrucosa*, a sessile species listed under the species protection provision of the Wildlife and Countryside Act (1981). Reefs support many species of conservation and commercial importance, including King Scallop *Pecten maximus*, Dover Sole *Solea solea* and Blonde Ray *Raja brachyura*. Mobile demersal fishing (e.g. scallop dredging and trawling) in Lyme Bay was believed to be severely degrading and damaging biogenic reef species and mudstone reef habitat. For this reason, the area has been the focus of debate between conservationists and fishers since the early 1990s. Subsequently, areas of the reefs have been protected under voluntary agreements (7 km^2 from 2001 and 41 km^2 from 2006, Jones (2012); Figure 1); a statutory instrument (whole-site exclusion of mobile demersal fishing of 206 km^2 from 2008; Figure 1); local byelaws set by Devon IFCA and Southern IFCA; and a "feature-based" SAC that encompassed the SI (a 312 km^2 Site of Community Importance from November 2011, Rees et al. (2012), and then a SAC from 2017; Figure 1).

Originally designated as a Site of Community Importance, the Lyme Bay and Torbay designated Special Area of Conservation (SAC) encompasses a large area of Lyme Bay and Torbay, a portion of the south-west coastline of the UK encompassing an area of 2460 km^2. The Lyme Bay element of the SAC, under study here, encompasses ~270 km^2 of seabed, including a 206-km^2 area, which prohibited mobile demersal fishing from 2008 under a statutory instrument (SI) (Figure 1). The area designated under the SI (whole-site MPA henceforth) ranges in depths from 15 to 35 m and, similar to the SAC, allows less destructive fishing activities, such as recreational angling, potting, netting and scallop diving. The SAC only excludes mobile demersal fishing from areas where Annex I rocky reef habitat (bedrock, boulders and cobbles) was previously found (Natural-England 2015). Consequently, ~33.9 km^2 of other habitats (46.8% of the SAC not inside the SI boundary), including pebbly sand veneers that can be colonised by reef-associated species (Sheehan et al. 2013b), is "protected" but can be legally dredged or trawled.

2.2 | Data collection

A long-term benthic monitoring project in Lyme Bay was established in 2008 to assess the recovery of the Annex I reef habitats using non-extractive and non-destructive underwater video surveys in the form of a towed flying array and baited remote underwater video systems (BRUVs) (Sheehan et al. 2013a; Stevens et al. 2014; Sheehan et al. 2016; Davies et al. 2020; Davies et al. 2021; Davies et al. 2022). These methods allowed the assessment of the change in benthic taxa from before to after designation of the SAC with appropriate control comparisons following a before–after control–impact assessment (BACI: Underwood 1991; Underwood 1992; Underwood 1994). This assessment style is advocated globally, yet the necessary "before" data for MPA assessment are rarely available (Fraschetti et al. 2002; Osio et al. 2007; Solandt et al. 2020).

Annual underwater video was used to survey Lyme Bay (Figure 1) within three management regimes: (1) the feature-based "SAC" but outside the whole-site MPA in areas identified as sensitive areas that are protected from mobile demersal fishing (found Annex I reef habitat) ("SAC" henceforth); (2) inside the whole-site MPA ("whole-site MPA" henceforth); and (3) outside of either protection where mobile demersal fishing is permitted "open controls" ("OC" henceforth). Areas were selected based on historic fishing effort, benthic substrate/biotope, previous voluntary closure boundaries and preliminary ground truthing so that all surveys were on representative sites within the management regimes (Stevens et al. 2014). Areas were sampled annually using a towed flying array from 2008 and baited remote underwater video systems (BRUVs) from 2009. Surveys were carried out during the summer for 4 years prior (before) and 7 years after designation of the SAC (after). All SAC areas were on Annex I reef habitats and therefore protected from mobile demersal fishing. Areas within the SAC that were open to mobile demersal fishing were not surveyed because they were assumed to function the same as OC areas. Unless otherwise stated, "designation of the SAC" refers to the designation in 2011, which created the Site of Community Importance that later became the SAC.

A towed flying array was used to record high-definition (HD) video transects (~200 m × 0.5 m) over heterogeneous mudstone reef and pebbly sand habitats (Sheehan et al. 2010). This method of surveying the seafloor is cost- and time-effective, as well as non-destructive and non-extractive (Sheehan et al. 2016). During 2008–2010, 18 areas, comprising 3 sites each, were surveyed annually (1 × 200 m transect) by the towed flying array across management regimes (10 whole-site MPA and 8 OC). In 2011, when the SAC was designated, 4 OC areas became SAC areas and a new OC area was added. Therefore, during 2011–2018, 19 areas were surveyed across management regimes (10 whole-site MPA, 4 SAC and 5 OC; Figure 1). The array (consisting of camera, lights, lasers and CTD profiler) was connected to a Bowtech System power supply and control unit by an umbilical cable, which allowed video to be monitored in real time to ensure control of lights, camera aperture and camera focus. The camera and parallel lasers were positioned at an oblique angle to the seabed, with lasers set 300 mm apart, to allow quantification of the field of view. To analyse video transects, each transect was viewed at normal speed and all conspicuous taxa that passed through the gap between the lasers were enumerated. Next, to quantify abundance and enumerate remaining visible taxa, each video transect was extracted into frame grabs, separated by 5 s. Blurred or overlapping frames were removed, and 30-frame grabs were randomly selected for analysis. Digital quadrats of known area (0.25 m^2) were overlaid on frames, and all taxa enumerated Davies et al. (2021). The density of each taxon per transect was calculated for video transects by dividing taxa counts by area of the transect (300 mm × Transect length) and for frames by dividing taxa counts by known quadrat area. Each taxon was only recorded by one method, so abundance from both methods was then combined.

Baited remote underwater video systems (BRUVs) were used to collect 30-min videos of mobile benthic taxa. During 2009–2010, 19 areas were surveyed annually, comprising 3 BRUVs deployments (12 whole-site MPA and 6 OC). After SAC designation, all OC areas became SAC, to add 6 new OC areas. Therefore, during 2011–2019, 24 areas were surveyed (12 whole-site MPA, 6 OC and 6 SAC; Figure 1). BRUVs consisted of a horizontal front-facing camera inside an underwater housing, connected to a source of bait (~ 100g of *Scomber scombrus*) 1 metre in front of the camera. After an initial post-deployment settling period of 5 min, videos were viewed for 30 min, while recording, the maximum number of individuals of all mobile benthic taxa was viewed every minute. The MaxN or relative abundance of each taxon was calculated as the maximum value recorded in any 1-min segment for that taxon over the 30-min video (see Bicknell et al. (2019), Davies et al. (2020) & Davies et al. (2021) for further details of equipment and analytical methods).

2.3 | Univariate metric calculation

For both towed flying array and BRUVs data, number of taxa and total abundance were calculated. The R packages "FD" and "funrar" were used to calculate functional richness using the Euclidean distance and functional distinctiveness using the Gower distance (Laliberté and Legendre 2010; Laliberté et al. 2014; Grenié et al. 2017; Grenié et al. 2020). Both metrics are unaffected by difference in type of abundance values (e.g. biomass, count, percentage cover or density: Villeger et al. 2008). Functional richness represents the number of different functional trait modalities within a community, and functional distinctiveness represents functional rarity of species per survey. Here, functional redundancy was calculated as the inverse of functional distinctiveness (Equation 1, Ricotta et al. 2016; Biggs et al. 2020). When O is functional redundancy and U is functional distinctiveness:

$$O = 1 - U$$

2.4 | Statistical analysis

2.4.1 | Hypotheses

The hypotheses for the BACI assessment were as follows:

1. Number of taxa, total abundance, functional richness and functional redundancy increase from before to after in the "feature-based" SAC, relative to the open controls.
2. Assemblage composition in the "feature-based" SAC significantly changes from before to after designation, becoming less similar to the OC over time.

The hypotheses for the age of protection assessment were as follows:

1. Number of taxa, total abundance, functional richness and functional redundancy increase with age of protection in the "feature-based" SAC and whole-site MPA, relative to the OC.
2. Rate of increase in number of taxa, total abundance, functional richness and functional redundancy with age of protection is higher in the whole-site MPA than in the "feature-based" SAC.
3. Assemblage composition significantly changes with age of protection in the "feature-based" SAC, becoming more similar to the whole-site MPA and less similar to the OC.

2.4.2 | Diversity

Mixed-effects models were used to test for changes in univariate metrics for taxonomic and functional diversity using "lme4," "lmerTest" and "glmmADMB" packages within R (Fournier et al. 2012; R Core Team 2019; Kuznetsova et al. 2020; Bates et al. 2022). Generalised linear mixed-effects models (GLMMs) were applied using a Poisson distribution for count variables (number of taxa for sessile and mobile taxa, and total abundance for mobile taxa), gamma distribution for continuous positive variables (total abundance for sessile taxa and functional richness for both sessile and mobile taxa) and beta distribution for proportional variables between 0 and 1 (functional redundancy for both sessile and mobile taxa). For the BACI assessment, diversity metrics were modelled as a function of Time Frame

(BA: Before–After) and Management Regime (Tr: SAC and open control) with Year (11 levels for both sessile and mobile taxa) and Site (8 and 12 levels for sessile and mobile taxa, respectively) as random factors. Year was nested within BA, and Site was nested within Tr. The whole-site MPA was protected with no "before" data and so was not included in the BACI assessment. Diversity metrics were modelled as a function of Age of Protection (a continuous integer: 1–7 for sessile taxa and 2–8 for mobile taxa, discrepancy in years was due to BRUVs not being deployed in the first year of survey and towed flying array analysis taking longer timescales to become available for analysis) and Management Regime (three levels: SAC, whole-site MPA and OC) with Year (11 levels for both sessile and mobile taxa) and Site (14 and 18 levels for sessile and mobile taxa, respectively) as random factors. Sample vs. fitted residuals, quartile–quartile and autocorrelation of temporally sequential samples were assessed visually, to evaluate model assumptions. Stated values of change with management regime and/or time (BA or age of protection) were GLMM estimate means per video ± standard error. For BACI analyses, a significant effect of management regime relates to a detectable BAxTr effect.

2.4.3 | Assemblage composition

For both the BACI and age of protection assessment, permutational multivariate analysis of variance (PERMANOVA) was used to test differences in assemblage composition using Primer v7 and PERMANOVA+ (Anderson et al. 2008; Clarke and Gorley 2015). Statistical models used were the same as for univariate analyses above. Statistical significance of variance components was tested using 9999 permutations under a reduced model (Anderson 2001; Anderson and Braak 2002). PERMANOVA is robust to unbalanced designs (Anderson et al. 2008) and was carried out on adjusted Bray–Curtis similarity matrices calculated from fourth-root-transformed abundance data to allow rare taxa to contribute, and further down-weight high-abundance taxa (Clarke et al. 2006). Distance to centroid was calculated for Year and Tr and then ordinated using non-metric multidimensional scaling (MDS).

3 | RESULTS

Across 11 years of towed flying array and baited remote underwater video system (BRUVs) surveying, 147 different sessile taxa were recorded by the towed flying array and 52 different mobile taxa were recorded by the BRUVs. For the towed flying array, 113 of the 147 taxa were recorded in the SAC, 138 in the whole-site MPA and 113 in the OC. For the BRUVs, 36 of the 52 taxa were recorded inside the SAC, 49 in the whole-site MPA and 37 in OC. The most ubiquitous taxa recorded across all management regimes and years were as follows: Hydroids, *Stolonica socialis* and *Cellaria fistulosa* for the towed flying array, and *Pagurus* spp., *Trachurus trachurus* and *Tritia reticulata* for the BRUVs.

3.1 | Before–after control–impact (BACI) assessment

3.1.1 | Diversity

The number of sessile taxa was not significantly related to management regime (Table 1 and Figure 2a). However, numbers of sessile taxa were higher within the SAC than OC and increased from before to after in both the SAC (18.3 ± 1.44 to 22.1 ± 1.21) and OC (16.4 ± 1.25 to 17.7 ± 0.972; Table 1 Figure 2a). Total abundance changed significantly for both management regimes, with an increase in the SAC (51.1 ± 33 to 88.2 ± 48.6) and a marginal decrease in the OC (Table 1 & Figure 2b). Functional richness was not related to management regime from before to after designation (0.000903 ± 0.000375 to 0.00156 ± 0.000472 in the SAC and 0.00104 ± 0.000438 to 0.00121 ± 0.000398 in the OC: Table 1 and Figure 2c), whereas the functional redundancy was significantly affected by both management regimes, with an increase from before (0.747 ± 0.0122) to after (0.758 ± 0.0162) in the SAC and a decrease from before (0.743 ± 0.00792) to after (0.731 ± 0.0116) in the OC (Table 1 & Figure 2d).

Unlike the sessile taxa, there was no detectable effect to mobile taxa from management regime in any of the univariate diversity metrics, except for functional richness (0.0579 ± 0.0186 to 0.0565 ± 0.0118 in the SAC and 0.0691 ± 0.0365 to 0.0581 ± 0.0116 in the OC: Table 1 & Figure 3).

3.1.2 | Assemblage composition

Assemblage composition of sessile taxa (surveyed by the towed flying array) was related to management regime (BAxTr; Table 2). Assemblages were similar between SAC and OC management regimes from 2008 until 2012, diverged until 2015, when they became similar again, and finally diverged from 2016 until 2018, with increased correlation with *Ophiura ophiura* during 2014–2015 at OC sites (Figure 4a). Assemblage composition of mobile taxa (surveyed by the BRUVs) was not related to management regime, with only the interaction of random effects being significant (Si(Tr):Yr(BA); Table 2). Assemblage composition was similar between management regimes every year, with no trend from before (2009, 2010 and 2011) to after (2012:2019) designation, and correlation of higher abundance of *Macropodia* spp. in early years (Figure 4b).

3.2 | Age of protection assessment

3.2.1 | Diversity

The number of sessile taxa differed significantly between management regimes (Table 3) and increased with age of protection of the SAC (from 18.3 ± 1.63 at age 1 to 26.3 ± 2.99 at age 8: Table 3 and Figure 5a) towards the higher levels of the whole-site MPA, which did

TABLE 1 Mixed-effects model results for before–after control–impact assessment of SAC vs. OC with number of taxa, total abundance, functional richness and functional distinctiveness as response variables measured from baited and towed videos

			Sessile taxa				Mobile taxa			
Type	Response variable	Term	Estimate	Std. error	t/z value	*p* Value	Estimate	Std. error	t/z value	*p* Value
Taxonomic diversity										
	Number of taxa									
		Intercept	2.8000	0.07370	37.900	**<0.0001*****	1.95000	0.12400	15.8000	**<0.0001*****
		BA	0.0777	0.07390	1.050	0.29	−0.18000	0.13400	−1.3400	0.18
		Tr	0.1110	0.08480	1.300	0.19	−0.11800	0.11700	−1.0100	0.31
		BA*Tr	0.1130	0.07320	1.540	0.12	0.10300	0.12700	0.8150	0.42
	Total abundance									
		Intercept	3.6700	0.00164	2240.000	**<0.0001*****	3.19000	0.32200	9.8900	**<0.0001*****
		BA	−0.0559	0.00164	−34.000	**<0.0001*****	0.05430	0.32400	0.1670	0.87
		Tr	0.2600	0.00164	158.000	**<0.0001*****	−0.09540	0.29300	−0.3260	0.74
		BA*Tr	0.6030	0.00164	367.000	**<0.0001*****	−0.19700	0.23700	−0.8300	0.41
Functional diversity										
	Functional richness									
		Intercept	−6.8700	0.19100	−35.900	**<0.0001*****	−2.67000	0.00197	−1350.0000	**<0.0001*****
		BA	0.1560	0.19200	0.817	0.41	−0.17300	0.00197	−87.7000	**<0.0001*****
		Tr	−0.1370	0.24400	−0.562	0.57	−0.17600	0.00197	−89.3000	**<0.0001*****
		BA*Tr	0.3920	0.23500	1.670	0.094	0.14900	0.00197	75.5000	**<0.0001*****
	Functional redundancy									
		Intercept	1.0600	0.04140	25.600	**<0.0001*****	0.98200	0.05330	18.4000	**<0.0001*****
		BA	−0.0591	0.04050	−1.460	0.14	−0.04450	0.04950	−0.8990	0.37
		Tr	0.0221	0.05130	0.430	0.67	0.00304	0.06270	0.0485	0.96
		BA*Tr	0.1190	0.04540	2.610	**0.009****	−0.01290	0.05490	−0.2350	0.81

Note: Terms are shortened with Year as Yr, Before–After as BA and Control–Impact as Tr. Bold values denote significant *p* values (<0.05), and asterisks define level of significance: $p < 0.0001$ = "<0.0001***"; $p < 0.001$ = "****"; $p < 0.01$ = "**"; and $p < 0.05$ = "*".

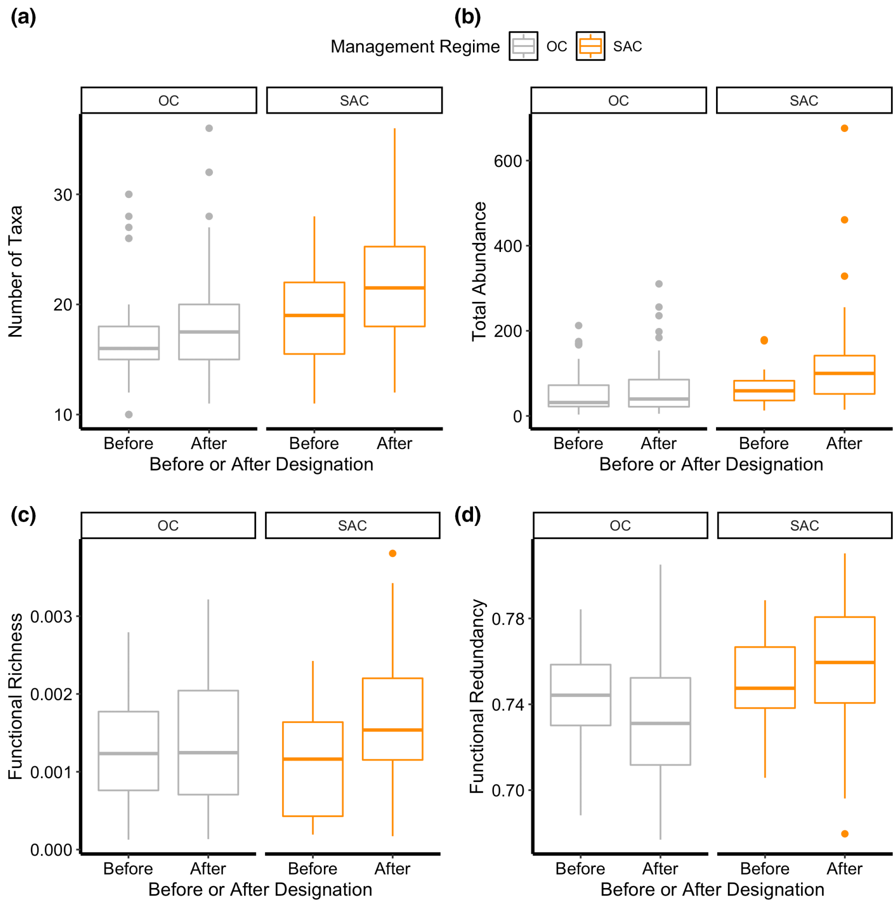

FIGURE 2 Metrics (a: number of taxa, b: total abundance, c: functional richness and d: functional redundancy) of sessile taxa, before and after designation inside (orange) and outside (grey) the SAC

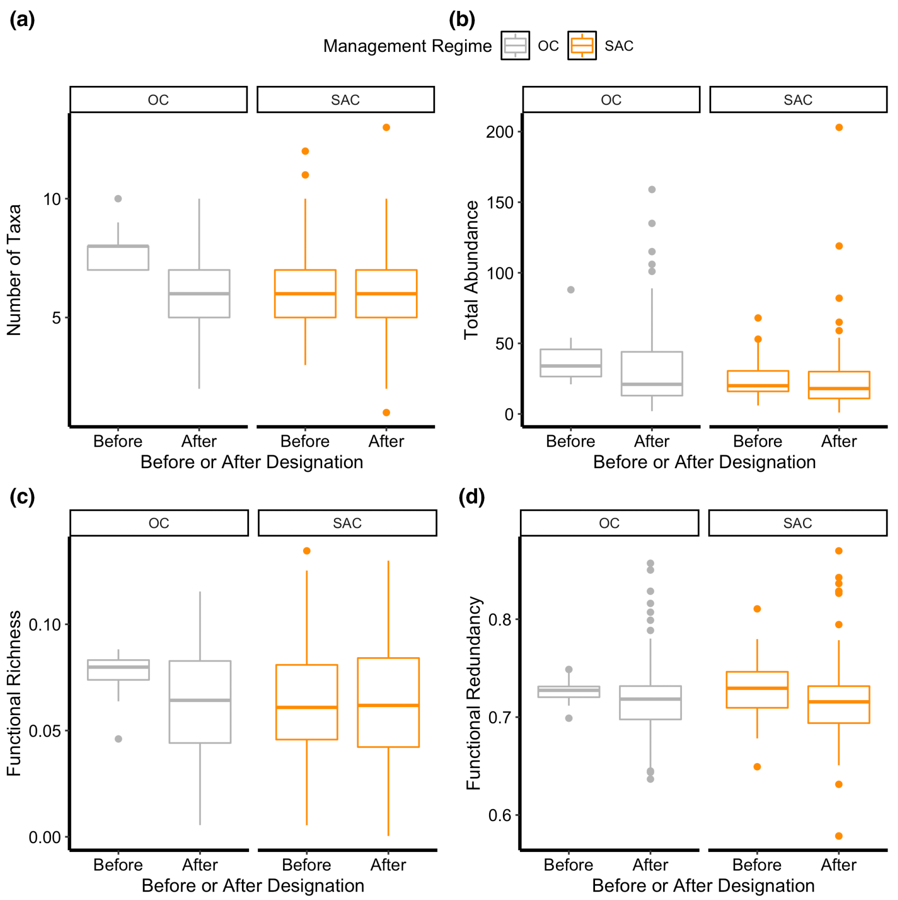

FIGURE 3 Metrics (a: number of taxa, b: total abundance, c: functional richness and d: functional redundancy) of mobile taxa, before and after designation inside (orange) and outside (grey) the SAC

TABLE 2 PERMANOVA model results for before–after control–impact assessment of SAC vs. OC with assemblage composition as response variables measured from baited and towed videos. Terms are shortened with Year as Yr, Site as Si, Before–After as BA and Control–Impact as Tr

Source	Sessile taxa: Numerator df	Denominator df	SS	Pseudo-F	*p* value	Mobile taxa: Numerator df	Denominator df	SS	Pseudo-F	*p* value
BA	1	12	19,000	4	**<0.0001*** **	1	15	7700	1.5	0.16
Tr	1	8.3	8200	1.6	0.06	1	17	2900	0.73	0.77
Yr(BA)	9	49	55,000	5.9	**<0.0001*** **	9	78	81,000	6.8	**<0.0001*** **
Si(Tr)	6	49	36,000	5.9	**<0.0001*** **	10	78	51,000	3.8	**<0.0001*** **
BAxTr	1	15	3400	2.2	**0.0033** **	1	15	1100	0.6	0.89
BAxSi(Tr)	6	49	6600	1.1	0.32	10	78	22,000	1.6	**0.0048** **
TrxYr(BA)	9	49	12,000	1.3	**0.037***	7	78	13,000	1.4	**0.041***
Si(Tr)xYr(BA)	48	180	50,000	2.1	**<0.0001*** **	78	230	100,000	2.1	**<0.0001*** **
Res	180	-	89,000	-	-	232	-	150,000	-	-

Note: Bold values denote significant *p* values (<0.05), and asterisks define level of significance: $p < 0.0001$ = "<0.0001***"; $p < 0.001$ = "***"; $p < 0.01$ = "**"; and $p < 0.05$ = "*".

not change with age of protection (24.4 ± 2.14 at age 1 to 24.8 ± 1.77 at age 8: Table 3 and Figure 5a). The change in total abundance with age of protection differed significantly between the whole-site MPA and OC and between the SAC and whole-site MPA (Table 3 and Figure 5b). Total abundance in the MPA and SAC increased with age of protection (from 85 ± 54.1 at age 1 to 97.9 ± 57.3 at age 8 in the SAC and 72.8 ± 34.1 at age 1 to 142 ± 58.9 at age 8 in the whole-site MPA; Figure 5b), whereas the OC decreased (63.4 ± 38.5 at age 1 to 23.9 ± 18.6; Table 3 and Figure 5b). Functional richness did not change with protection age or differ between management regimes (Table 3 and Figure 5c). Functional redundancy did not change with age of protection in the whole-site MPA (0.768 ± 0.00737 at age 1 to 0.777 ± 0.012 at age 7; Table 3 & Figure 5d), but increased with age of protection in the SAC (from 0.752 ± 0.0152 at age 1 to 0.764 ± 0.0245 at age 7; Table 3 and Figure 5d) and decreased with age of protection in the OC (0.754 ± 0.0151 at age 1 to 0.708 ± 0.0275 at age 7; Table 3 and Figure 5d).

The number of mobile taxa did not change with age of protection or management regimes (Table 3). Total abundance of mobile taxa was marginally lower inside the whole-site MPA (15.6 ± 2.88: Table 3 and Figure 6a) than in the OC, but did not change with age of protection (13.6 ± 3.24 in the SAC and 18.9 ± 4.06 in the OC; Table 3 and Figure 6b). Like number of taxa, functional richness of mobile taxa did not change with age of protection or differ between management regimes (Table 3). Likewise, functional redundancy did not differ between management regimes or change with age of protection on functional redundancy of mobile taxa, but there was marginally higher functional redundancy in the whole-site MPA (0.756 ± 0.0181) than in the SAC and OC (0.711 ± 0.0396 in the SAC and 0.719 ± 0.0391 in the OC; Table 3 and Figure 6d).

3.2.2 | Assemblage composition

Assemblage composition of sessile and mobile taxa was significantly related to management regime and changed with age of protection (Table 4). Assemblages differed between the whole-site MPA and the other two management regimes (Figure 7a,b). With age of protection, sessile and mobile taxon assemblages within the SAC became more similar to the whole-site MPA and less similar to the OC, and the difference was more pronounced for sessile taxa (Figure 7a,b). *Cellopora pumicosa*, *Phallusia mammiliata*, Turf, *Eunicella verucosa*, *Scyliorhinus stellaris*, *Ctenolabrus rupestris*, *Labrus mixtus* and *Necora puber* were more prominent in whole-site MPA sites, while burrowing anemones, *Luidia ciliaris* and *Macropodia* spp. were more prominent in early years of SAC and OC sites, and *Pagurus spp.* were more prominent in OC sites (Figure 7a,b).

4 | DISCUSSION

Once protected, the SAC in Lyme Bay became more similar to the older and successful whole-site MPA already within the bay (Rees et al. 2010; see, for example, Sheehan et al. 2013a; Davies et al. 2021;

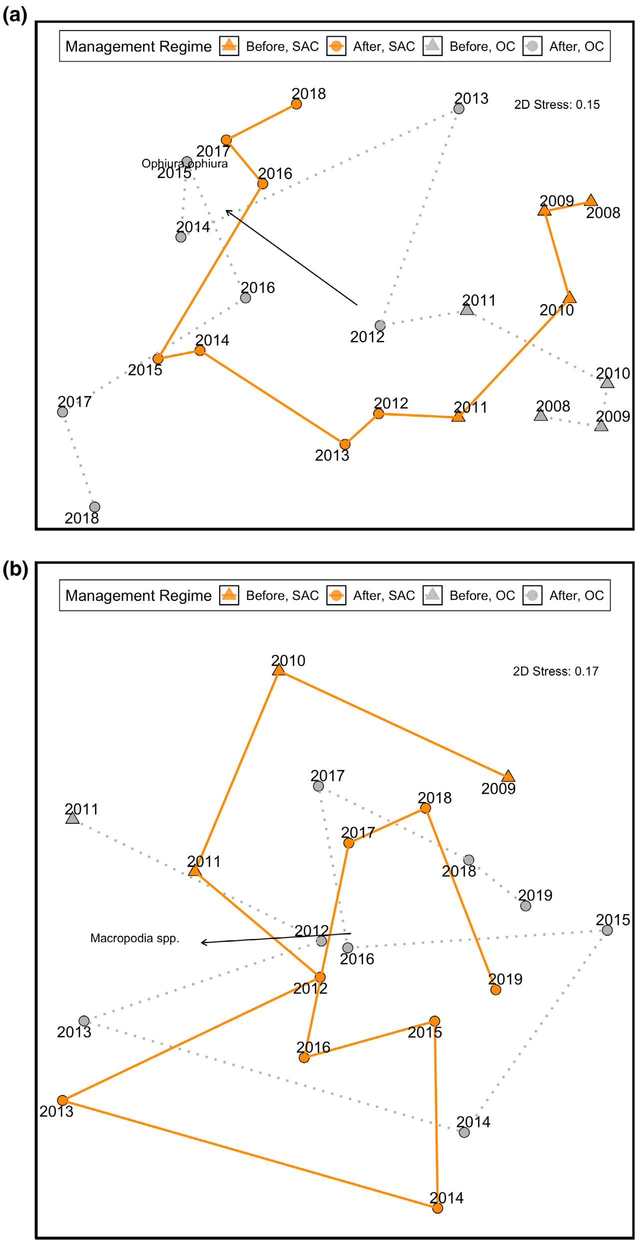

FIGURE 4 Assemblage change over time before (triangles) and after (circles) for inside the SAC (orange) and outside controls (grey) for sessile (a) and mobile (b) taxa. Derived from distance to centroid values based on the Bray–Curtis similarity of fourth-root-transformed abundance. Arrows show species with 0.75 Pearson's correlation or above

Sheehan et al. 2021). Functional redundancy and assemblage composition measured within the SAC in Lyme Bay became more similar over time to the whole-site MPA in comparison with the OC, almost exclusively within sessile taxa surveyed by the towed flying array. Protections in both the whole-site MPA and SAC were aimed at protecting Annex I reef habitats, so we expected that sessile taxa would respond to these protections, as was found after 3 years of protection in the whole-site MPA (Sheehan et al. 2013a). Yet, recovery of reef-associated mobile taxa, due to increased area and availability of reef habitat, is likely over much longer timescales (Kaplan et al. 2019). However, over 12 years of exclusion of mobile demersal fishing, exploited fish taxa responded positively to protection in the whole-site MPA (Davies et al. 2021). Furthermore, the functional extent of reef habitats inside the whole-site MPA increased over time, with growth of reef-associated species in previously defined non-reef protected areas (Sheehan et al. 2013a). The novel occurrence of reef-associated sessile species in areas of protected non-reef habitat is becoming more common as more protected areas include mosaics of reef and non-reef habitats (Pikesley et al. 2021). The protection of areas defined as non-reef and reef habitats allowed this increase. The ecological response in the SAC will likely only extend to the areas of protected features, not the SAC boundary. Currently, only half of the SAC, outside of the whole-site MPA, is protected, but if non-reef features in the SAC were also protected from mobile demersal fishing, we expect similar increases in functional reef habitat extent.

This increased protection of a range of habitats is more likely to support multiple life stages of species (Blampied et al. 2022). The increased connectivity of seascapes is expected to be highly important for reef fish (Endo et al. 2019). This has been shown with increased abundance and diversity of fish in habitats adjacent to reefs (Rees et al. 2018). Yet, connectivity in Europe's network of MPAs is considered weak (Assis et al. 2021). Therefore, future management measures should include connectivity of both MPAs and habitats within MPAs to maximise their potential benefits to biodiversity.

Simultaneous increases in the number and functional redundancy of sessile taxa, along with no detectable change in functional richness, suggest that the traits of the novel species in the SAC protected area were not novel to the community. This increase in novel species with locally non-novel traits increases the level of overlap of functional traits in these protected sites. Therefore, mobile demersal fishing may be removing benthic species with a wide variety of functional traits through non-selective extraction across the community. High functional redundancy in a community will promote resilience to perturbations, such as biological invasions and storm events (Tillin et al. 2006; McLean et al. 2019). Biological invasions, storm events and other perturbations to benthic ecosystems are expected to increase in magnitude and frequency with climate change (Diez et al. 2012; Hettiarachchi et al. 2018), so continuation of mobile demersal fishing across large areas of the marine environment will severely reduce the ability of these ecosystems to recover and continue providing ecosystem services, which humans rely on so heavily (Tillin et al. 2006). A combination of multiple functional and taxonomic univariate metrics better describes the complex suite of ecosystem interactions that drive ecosystem function and health than a single univariate metric (Ricotta et al. 2016; Perović et al. 2018). Therefore, effects of mobile demersal fishing on the community can be assessed by monitoring the changes in a suite of univariate metrics (Tillin et al. 2006; Howarth et al. 2018; Mouchet et al. 2019). However, inter-site comparison by functional metrics used here, calculated with biological trait analysis, will require consistent numbers of traits and modalities (Villeger et al. 2008; Davies et al. 2022), and equivalent coverage of the ecosystem being assessed for values

TABLE 3 Mixed-effects model results for age of protection of SAC, MPA and OC with number of taxa, total abundance, functional richness and functional distinctiveness as response variables measured from baited and towed videos. Terms are shortened with Year as Yr, Site as Si, age of protection as Age and Control–Impact as Tr

			Sessile taxa				Mobile taxa			
Type	Response variable	Term	Estimate	Std. Error	t/z value	*p* Value	Estimate	Std. Error	t/z Value	*p* Value
Taxonomic diversity										
	Number of taxa									
		Intercept	3.19000	0.11500	27.8000	**<0.0001*****	1.71000	0.1620	10.500	**<0.0001*****
		Age	0.00217	0.02250	0.0964	0.92	0.02020	0.0277	0.727	0.47
		MPA-OC	−0.38200	0.16300	−2.3400	**0.019***	0.11300	0.2390	0.472	0.64
		MPA-SAC	−0.34700	0.16400	−2.1200	**0.034***	−0.06780	0.2400	−0.282	0.78
		AgexMPA-OC	0.01160	0.03550	0.3280	0.74	−0.02870	0.0442	−0.649	0.52
		AgexMPA-SAC	0.05810	0.03560	1.6300	0.1	0.00725	0.0443	0.164	0.87
	Total Abundance									
		Intercept	4.18000	0.00133	3140.0000	**<0.0001*****	2.81000	0.3640	7.730	**<0.0001*****
		Age	0.11200	0.00133	84.1000	**<0.0001*****	−0.03240	0.0617	−0.525	0.6
		MPA-OC	0.13600	0.00133	103.0000	**<0.0001*****	−0.10400	0.5430	−0.192	0.85
		MPA-SAC	0.24300	0.00133	183.0000	**<0.0001*****	−0.42500	0.5440	−0.781	0.43
		AgexMPA-OC	−0.27400	0.00133	−206.0000	**<0.0001*****	0.14700	0.0993	1.480	0.14
		AgexMPA-SAC	−0.08820	0.00133	−66.3000	**<0.0001*****	0.14400	0.0995	1.440	0.15
Functional diversity										
	Functional richness									
		Intercept	−6.80000	0.19700	−34.4000	**<0.0001*****	−3.29000	0.2920	−11.300	**<0.0001*****
		Age	0.04040	0.04020	1.0000	0.32	0.02620	0.0487	0.537	0.59
		MPA-OC	0.06240	0.33400	0.1870	0.85	0.45900	0.4440	1.030	0.3
		MPA-SAC	0.17200	0.33400	0.5150	0.61	0.46000	0.4440	1.030	0.3
		AgexMPA-OC	−0.03840	0.07010	−0.5480	0.58	−0.02550	0.0794	−0.322	0.75
		AgexMPA-SAC	−0.00170	0.07020	−0.0243	0.98	−0.02670	0.0793	−0.337	0.74
	Functional redundancy									
		Intercept	1.19000	0.04050	29.3000	**<0.0001*****	1.09000	0.0930	11.700	**<0.0001*****
		Age	0.00836	0.00795	1.0500	0.29	0.02160	0.0157	1.380	0.17
		MPA-OC	−0.03080	0.06610	−0.4660	0.64	−0.14900	0.1590	−0.938	0.35
		MPA-SAC	−0.08960	0.06690	−1.3400	0.18	−0.20800	0.1580	−1.310	0.19
		AgexMPA-OC	−0.04680	0.01310	−3.5600	**<0.0001*****	−0.02180	0.0267	−0.818	0.41
		AgexMPA-SAC	0.00300	0.01340	0.2240	0.82	−0.01150	0.0266	−0.431	0.67

Note: Bold values denote significant *p* values (<0.05), and asterisks define level of significance: $p < 0.0001$ = "<0.0001***"; $p < 0.001$ = "***"; $p < 0.01$ = "**"; and $p < 0.05$ = "*".

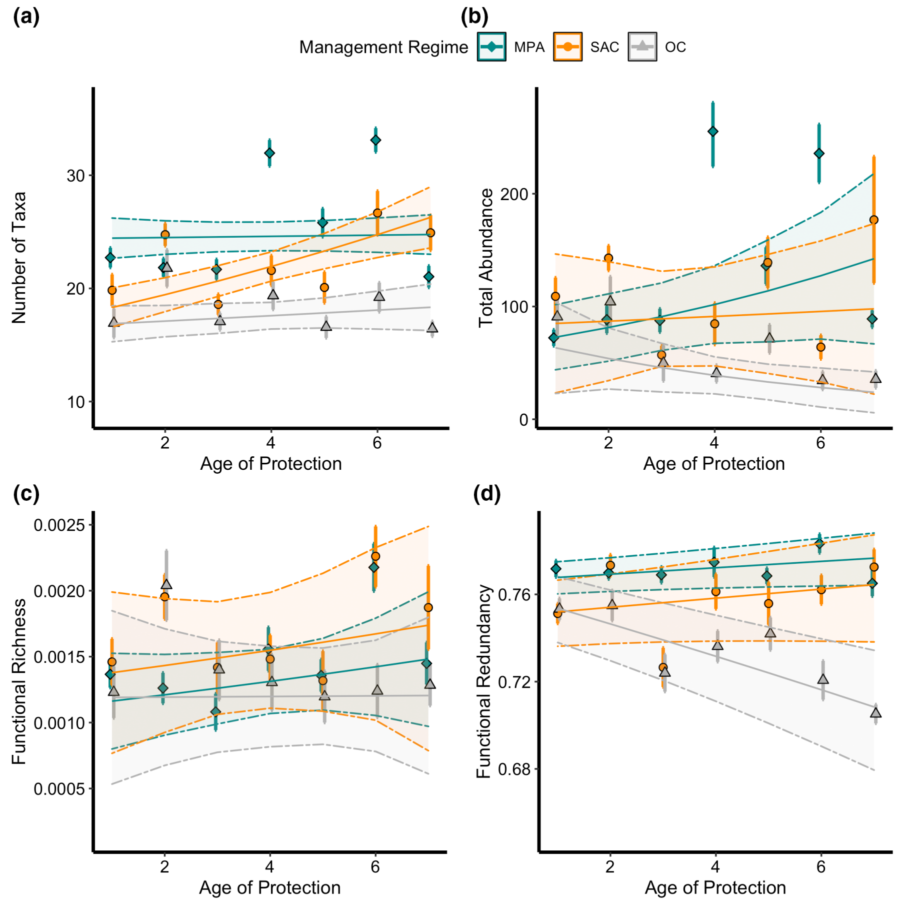

FIGURE 5 Change in metrics (a: number of taxa, b: total abundance, c: functional richness and d: functional redundancy) of sessile taxa, with age of protection of the whole-site MPA (blue), SAC (orange) and OC (grey; age of protection based off of SAC age). Lines with shading show GLMM estimates and standard errors. Points with error bars show mean values and standard errors

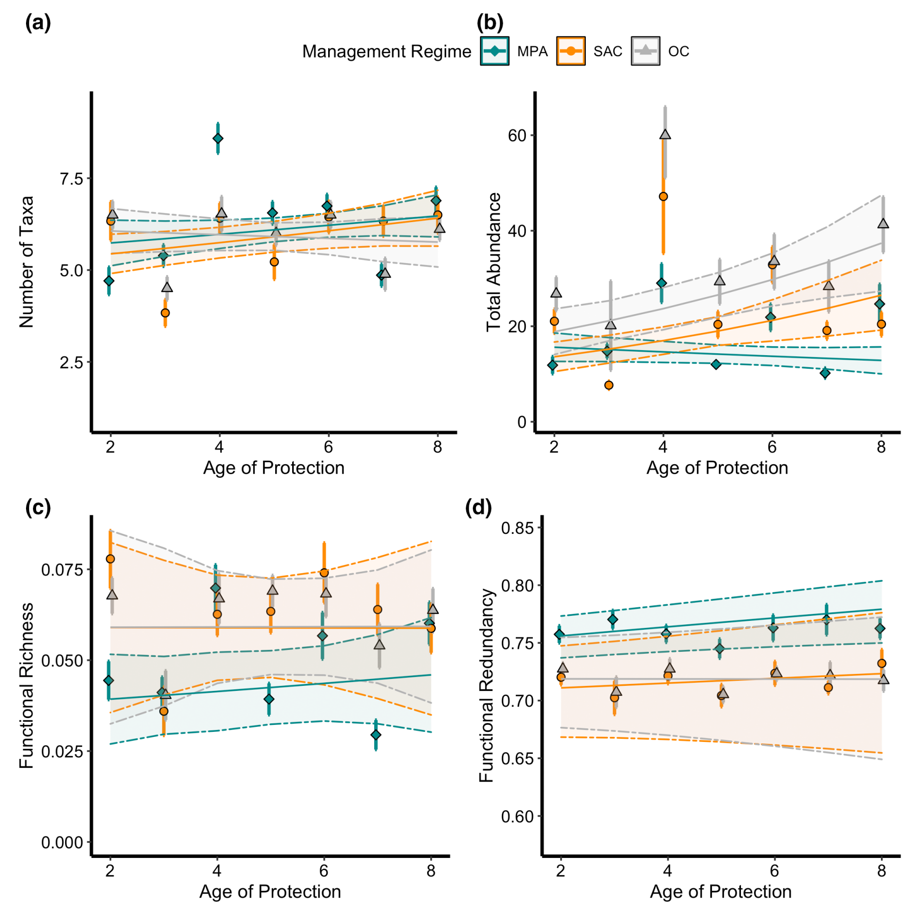

FIGURE 6 Change in metrics (number of taxa (a), total abundance (b), functional richness (c) and functional redundancy (d)) of mobile taxa, with age of protection of the whole-site MPA (blue), SAC (orange) and OC (grey; age based off of SAC age). Lines with shading show GLMM estimates and standard errors. Points with error bars show mean values and standard errors

TABLE 4 PERMANOVA model results for age of protection assessment of SAC, MPA and OC with assemblage composition as response variables measured from baited and towed videos

Source	Sessile taxa					Mobile taxa				
	Numerator df	Denominator df	SS	Pseudo-F	p value	Numerator df	Denominator df	SS	Pseudo-F	p value
Age	1	12	13,000	2	**0.0086****	1	13	20,000	2.2	**0.026***
Tr	2	29	110,000	5.3	**<0.0001*****	2	35	120,000	4.6	**<0.0001*****
Yr(Age)	10	75	72,000	7.2	**<0.0001*****	10	100	110,000	6.3	**<0.0001*****
Si(Tr)	15	85	86,000	6.1	**<0.0001*****	21	100	160,000	4.4	**<0.0001*****
AgexTr	2	5.3	5800	2.4	**0.004****	2	5.1	10,000	2.4	**0.033***
AgexSi(Tr)	15	75	16,000	1	0.42	21	100	47,000	1.1	0.18
Yr(Age)xTr	5	75	5500	1.2	0.15	5	100	9400	1.2	0.22
Yr(Age)xSi(Tr)	75	240	63,000	1.7	**<0.0001*****	104	330	170,000	2	**<0.0001*****
Res	238	-	120,000	-	-	327	-	270,000	-	-

Note: Terms are shortened with Year as Yr, Site as Si, age of protection as Age and Control–Impact as Tr. Bold values denote significant *p* values (<0.05), and asterisks define level of significance: *p* <0.0001 = "<0.0001***"; *p* <0.001 = "***"; *p* <0.01 = "**"; and *p* <0.05 = "*"

to be comparable. As biological trait information increases and becomes more accessible, this approach becomes more widely applicable and could provide a useful tool for MPA management.

The ability to confidently assess effects of a MPA and effectively adapt management based on this assessment is very important for both fisheries and conservation (Claudet et al. 2020). Effective MPA assessment can be highly challenging to achieve, especially when the area is subject to multiple pressures and protections. Thus, the application of spatially and temporally appropriate monitoring programs alongside rigorous statistical assessment is critical, to protect the specific area and to assess the value of MPAs and how they can be optimally applied in the future for resource management (Pelletier et al. 2005; Fox et al. 2014; Kerr et al. 2019). Globally, decisions leading to many MPA designations that were politically driven or altered led to the MPA being unable to attain its objectives (Rife et al. 2013; Devillers et al. 2015). Often, this compromise between political will and conservation objectives may undermine the success of MPAs. Other protections may have attainable objectives but struggle to succeed due to the level of protection offered by management policies (feature vs "whole site"; Solandt et al. 2020). Hence, to appropriately plan and designate future MPAs, assessment of MPA impacts, both positive and negative, need to be analysed. Here, the feature-based MPA showed signs of achieving conservation goals, while still allowing certain extractive activities. This form of management is more widely supported by stakeholders than NTZs, even though the latter are often more successful at achieving conservation objectives (Edgar and Stuart-Smith 2014). With international targets looking to protect 30% of marine areas by 2030 (Brander et al. 2020), partially protected MPAs such as this SAC will become more common. Therefore, understanding differences between management strategies, such as "whole-site" vs. "feature-based," and timescales of expected outcomes will be essential in global cooperative efforts to mitigate climate change and its effects (Solandt et al. 2020).

In conclusion, the designation of the feature-based SAC led to increased diversity (both taxonomic and functional) of sessile taxa in Lyme Bay, specifically in areas within the SAC and outside of the whole-site MPA, where Annex I reef habitats are found (46.8% of the SAC area outside of the whole-site MPA). Therefore, results only pertain to areas where mobile demersal fishing was excluded. The rest of the SAC that lies outside the whole-site MPA (53.2%) cannot be considered protected and rather would be expected to resemble OC sites. The protected feature, Annex I reef habitats, within the SAC are increasing in the potential to provide ecosystem services and resilience to perturbations from storms, destructive fishing, or biological invasions. With age of protection, areas that were protected are increasingly resembling areas within the whole-site MPA with number of exploited mobile species increasing in the SAC. As with other metrics, if more than the extent of the visible reef was protected within the SAC, like the whole-site MPA, the extent of biogenic reef habitats would potentially increase. Therefore, to fully ensure protection of Annex I reef habitats, their functional extent should be protected. Increased creation of MPAs, which is likely to happen globally to hit "'30-by-30" goals, should take the whole site into consideration. This

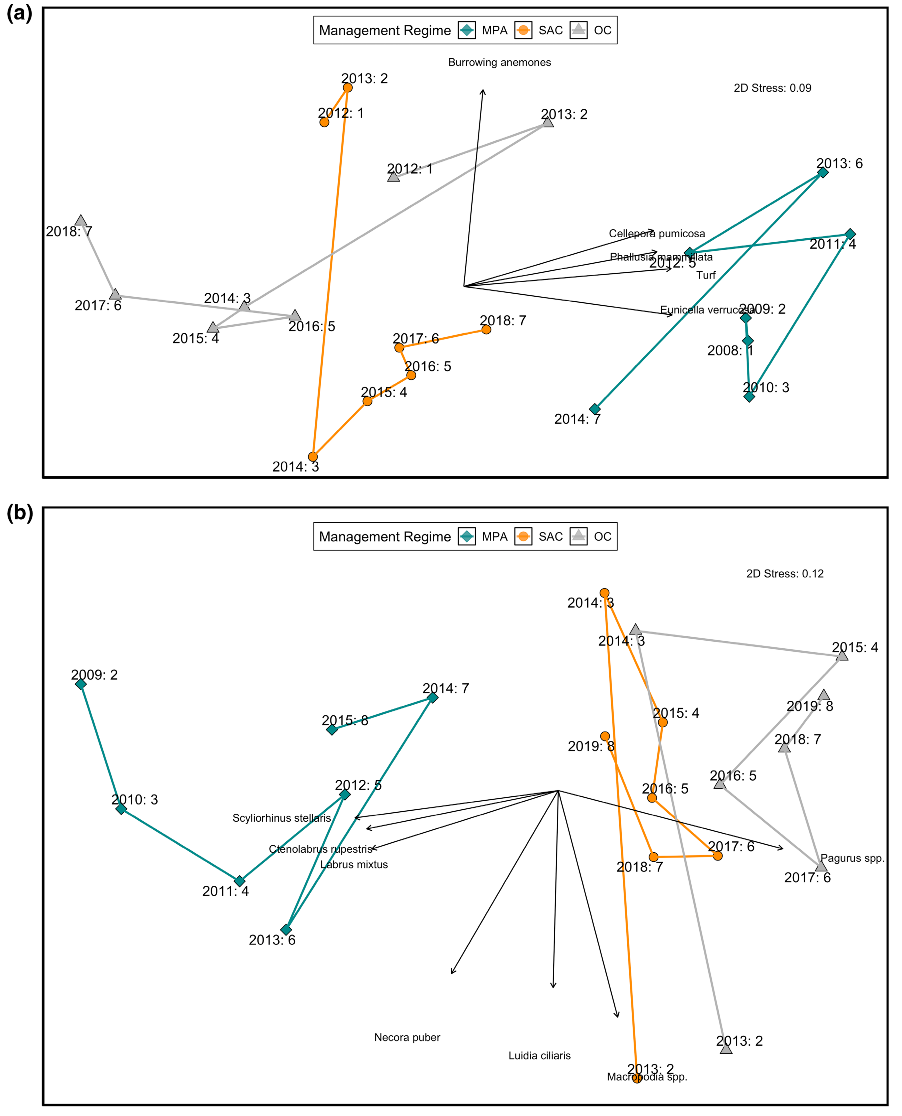

FIGURE 7 Assemblage change with age of protection for inside the SAC (orange), inside the whole-site MPA (blue) and OC sites (grey; age based off of SAC age) for sessile (a) and mobile (b) taxa. Derived from distance to centroid values based on the Bray–Curtis similarity of fourth-root-transformed abundance. Arrows show species with 0.75 Pearson's correlation or above

form of holistic management is more likely to lead to increases in biodiversity as many species rely heavily on a range of habitat types and the protected connectivity between these habitats.

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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