Check for updates

Received: 28 May 2021 | Revised: 27 October 2021 | Accepted: 15 November 2021

DOI: 10.1111/ddi.13451

RESEARCH ARTICLE

Diversity and Distributions WILEY

A decade implementing ecosystem approach to fisheries management improves diversity of taxa and traits within a marine protected area in the UK

Bede F. R. Davies[1] | Luke Holmes[1] | Anthony Bicknell[2] | Martin J. Attrill[1] | Emma V. Sheehan[1]

[1]University of Plymouth, Plymouth, UK

[2]University of Exeter, Exeter, Devon, UK

Correspondence
Bede F. R. Davies, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK.
Emails: bede.davies@plymouth.ac.uk; bedeffinian@gmail.com

Funding information
This work was supported by Natural England and The European Commission [EMFF RETURN ENG1388]

Editor: Enrico Pirotta

Abstract

Aim: Ecosystem Approach to Fisheries Management has highlighted the importance of studying ecosystem functions and services, and the biological traits that drive them. Yet, ecosystem services and the associated benefits that they provide are rarely the motive for creating marine protected area (MPA). Therefore, many MPA monitoring projects do not explicitly study these functions and services or the underlying biological traits linked to them.

Location: Lyme Bay MPA, located in the SW of England, was established in 2008 to protect the reef biodiversity across a 206-km^2 area, which includes rocky reef habitats, pebbly sand and soft muddy sediments. Mobile demersal fishing was excluded across the whole site to allow the recovery of the reef habitats.

Methods: Using a combination of towed underwater video and Baited Remote Underwater Video Systems changes in diversity (taxonomic and trait), and traits affected by mobile demersal fishing were assessed in Lyme Bay MPA over 10 years.

Results: There was a consistent increase in the number of taxa and the trait diversity they provide within the MPA as well as an increase in functional redundancy, which may increase community resilience to perturbations. Outside of the MPA there was an increase in the abundance of mobile species, while the MPA showed an increase in filter feeders.

Main conclusions: The MPA showed a trend towards more diverse and potentially resilient rocky reef habitats. This study constitutes a novel MPA assessment using multiple sampling methods to encompass a wide range of taxa. It also reinforces the importance of effective MPA monitoring, which has demonstrated changes in trait diversity and trait composition driven by changes in taxonomic diversity.

KEYWORDS
biodiversity, BRUVs, conservation, functional trait analysis, monitoring, TUVs, whole-site approach

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2021 The Authors. *Diversity and Distributions* published by John Wiley & Sons Ltd.

1 | INTRODUCTION

Coastal areas of the marine environment have historically been overexploited and subjected to high levels of pressure, such as commercial fishing, nutrient loading and noise from shipping (Brown et al., 2001; Letessier et al., 2019; Pine et al., 2016). Arguably one of the most destructive impacts to the marine environment have come from unsustainable commercial practices, such as fisheries trawling and dredging (Solandt et al., 2020), and aggregate and maintenance dredging (Cooper et al., 2008). To negate the impacts of commercial fishing, one widely used management tool is the implementation of marine protected areas s (MPAs; Cleguer et al., 2015; Gallacher et al., 2016; Jones, 2008). There are many different types of MPA varying in level of protection, spatial extent and temporal coverage. The spatial extent of a MPA can range from tens of square metres to thousands of square kilometres, while temporal extent can cover specific months, a season or all-year-round protection (Ferse et al., 2010). MPAs can be designated to protect overall biodiversity, specific species or habitat 'features' (Solandt et al., 2020), with the level of protection ranging from the protection of one single species or 'feature', to the complete exclusion of potentially harmful activity in a whole area (Boonzaier & Pauly, 2016). By excluding the most destructive human activities to protect sensitive biogenic habitats that provide essential feeding and nursery ground for species of commercial importance, MPAs can help to achieve both conservation and fisheries goals. Consequently, MPAs have been advocated within an Ecosystem Approach to Fisheries Management (EAFM) approach (Halpern et al., 2010). To effectively manage the whole ecosystem, appropriate monitoring must be applied which can detect changes in ecosystem function, diversity and health over time-scales that can allow for adaptive management (Maxwell et al., 2015).

To monitor and assess whether ecosystems are recovering under the protection that a MPA has provided, taxonomy-based biodiversity metrics are often used, such as species richness or Shannon's diversity (Ferreira et al., 2017). Higher levels of taxonomy-based biodiversity are often linked to higher ecosystem functioning and increased productivity (Vackár et al., 2012). However, large changes in taxonomic based biodiversity do not necessarily imply equally large changes to ecosystem function (Törnroos & Bonsdorff, 2012; Wong & Kay, 2019), especially when an ecosystem contains high levels of functional redundancy: when many different species share the same trait modalities (such as predator, detritivore or filter feeder for an organisms feeding trait; Guillemot et al., 2011). Ecosystem function is a complex system of interactions, which combine to make up the whole system through multiple different processes (Jax, 2005). Thus, when assessing the change in the trait diversity, the combination of functional richness, functional evenness, functional divergence, functional distinctiveness and functional dispersion (Laliberté & Legendre, 2010; Murgier et al., 2021; Violle et al., 2017) of a system can indicate its functioning in relation to ecosystem-wide processes, such as productivity and regulation of biogeochemical fluxes (Perović et al., 2018; Ricotta et al., 2016). Specific traits, modalities (e.g. filter feeding within the feeding trait) or groups of traits being heavily linked to specific processes and fluxes. For example, feeding habit has been linked to bentho-pelagic coupling and trophic linkage (Beauchard et al., 2017), environmental position (benthic, pelagic, etc.) with sensitivity to destructive fishing and longevity, maturation age and reproductive strategy with recovery from destructive fishing (Rijnsdorp et al., 2016). Functional richness measures the size of the trait space filled by the community, while functional evenness and functional divergence indicate how the abundance is distributed across this trait space (Table 1). Evenness increases as organism abundance is spread more evenly across the trait space, whereas divergence increases as specific extreme traits or combinations of traits become more abundant in relation to others (Laliberté & Legendre, 2010; Mason et al., 2007; Mason et al., 2008). Further, the study of functional redundancy, the similarity of traits within the community, can indicate the resilience of a MPA to perturbations, such as destructive fishing, biological invasions and storm events (McLean et al., 2019; Tillin et al., 2006). Hence, the study of functional traits has been suggested for both monitoring and management (Rijnsdorp et al., 2016; Tillin et al., 2006; Wiedmann et al., 2014).

Initially applied within terrestrial and freshwater environments, the use of biological trait analysis has increased in recent years in the marine environment (Berthelsen et al., 2015; Coleman et al., 2015) and has mostly been used to assess either fish or benthic invertebrate communities (Beauchard et al., 2017). Benthic invertebrates are well known as bio-indicators of ecosystem health, disturbance or biogeochemical processes (Belley & Snelgrove, 2016; De-La-Ossa-Carretero et al., 2012; Munroe et al., 2018; Parmar et al., 2016) and fish assemblages have been used to assess the impacts of fishing and climate change (Benoıt & Swain, 2008; Benoit et al., 2013). Particular groups of organisms can be used as indicators for different elements of ecosystem health, and the assessment of multiple groups of organisms will provide a more comprehensive image of the function of the whole ecosystem and allow for adaptive management, as set out by EAFM (Long et al., 2015).

The most common form of MPAs in Northern Europe follows the 'feature'-based approach, where the whole ecosystem is not

TABLE 1 The definitions of the different functional metrics calculated by Biological Trait Analysis

Metric	Definition
Functional richness	The trait space filled by the community
Functional divergence	The abundance of extreme traits or trait combinations
Functional evenness	How even the spread of abundance is across the trait space
Functional redundancy	The amount of similarity of traits within the community

necessarily considered (Solandt et al., 2020). This management means that the most destructive activities are only excluded in designated areas within MPAs, where specific features of conservation importance have been evidenced (Sheehan, Cousens, et al., 2013), leaving the majority of MPAs effectively open to damage and further degradation (Solandt et al., 2020). These "feature-based" MPAs have been considered ineffective for both fisheries and conservation management (Pikitch et al., 2004), meaning MPAs that provide consistent protection across their whole area, known as whole-site approach, are being advocated (Rees et al., 2020). One example of a MPA managed through a whole-site approach is in Lyme Bay, SW England. Due to high levels of mobile demersal fishing in the bay, which were shown to be damaging the rocky reef system characterized by sessile fauna species, such as pink sea fans *Eunicella verrucosa* and ross corals *Pentapora foliacea*, stakeholders created a voluntary closure agreement (Mangi et al., 2011; Rees et al., 2010). Initially consisting of four, small, reef areas (22 km^2), these voluntary closures were later superseded and enveloped within a larger area designated using a government Statutory Instrument (SI) in 2008; the MPA covers 206 km^2 of the bay. This designation excluded all forms of mobile demersal fishing activity, primarily trawling and scallop dredging, consistently throughout the whole site to protect the reef biodiversity from the effects of these most damaging fishing methods, while still allowing other fishing methods such as pots, static nets and scallop diving. The area was renowned for the high levels of ecologically important rocky reef habitat (Hiscock & Breckels, 2007), which can be severely damaged by the mobile fishing gear that was prevalent throughout the bay. The exclusion of this degradation of reef habitat, which many species rely on, was expected to allow habitat recovery and in doing so increase the associated diversity (taxonomic and trait). To assess whether the reefs could recover, and over what timescale, long-term monitoring research commenced in 2008, shortly after the SI designation.

Sessile and sedentary epifauna were monitored using a towed underwater video system ("towed flying array" henceforth), while mobile species were monitored with Baited Remote Underwater Video systems (BRUVs; Davies et al., 2020; Davies, Holmes, Rees, et al., 2021; Sheehan et al., 2010; Sheehan, Stevens, et al., 2013; Sheehan et al., 2016; Stevens et al., 2014). The combination of these data collection methods, which estimate the abundance of species ranging from sessile branching sponges to highly mobile elasmobranchs, allow the assessment of a large proportion of the benthic ecosystem. In the present study, trait analysis was carried out on this surveyed proportion of the benthic ecosystem, analysing change in trait diversity metrics captured by the combination of the towed video and BRUVs data. As protection of the benthic ecosystem was expected to allow increases in biodiversity as well as prevalence and abundance of regionally rare trait combinations, trait diversity metrics were expected to increase over time in the MPA relative to the nearby areas open to mobile demersal fishing. Furthermore, as mobile demersal fishing gear is known to significantly impact the relative proportion of specific trait modalities present within an ecosystem (Howarth et al., 2018; van Denderen et al., 2015), causing decreases in sessile, filter feeding and long-lived organisms and an increase in mobile and scavenging organisms (Tillin et al., 2006), the relative proportions of trait modalities were assessed over time. Here, a unique assessment ranging across a large portion of the benthic ecosystem is provided, with the intent to best inform adaptive management of Lyme Bay and improve MPA management elsewhere.

To assess how the health and overall ecosystem of the functional reef habitats inside Lyme Bay MPA changed over time, the diversity (taxonomic and trait) and traits of epibenthic and demersal communities were assessed inside the MPA and outside the MPA, in unprotected Open Controls over 10 years.

The following hypotheses were tested:

1. Number of taxa and functional richness increase over time in the MPA, relative to the Open Controls.
2. Functional Divergence and Functional Evenness increase over time in the MPA, relative to the Open Controls.
3. Functional redundancy increases over time in the MPA, relative to the Open Controls.
4. The relative proportion of sessile, filter feeder and long-lived trait modalities increase over time in the MPA, while mobile and scavenger trait modalities decrease, relative to the Open Controls.

2 | MATERIALS AND METHODS

2.1 | Survey design

2.1.1 | Location

Lyme Bay is a moderate energy, south-facing area of the south-west coast of the UK (Figure 1). The Lyme Bay MPA (50.67 N, −2.95 E) is 206 km^2 and was designated by the UK government's Department of Environment, Food and Rural Affairs (Defra) under a statutory instrument (SI) in 2008. Henceforth, the SI is referred to as the MPA unless stated otherwise. The MPA includes rocky reef habitats (bedrock, boulders and cobbles), pebbly sand and soft muddy sediments (Sheehan, Stevens, et al., 2013). Since designation, a 'feature'-based Special Area of Conservation (SAC) has been designated in the surrounding areas of the MPA. However, the focus of the current study is on the whole-site approach designated in 2008, which prohibited mobile demersal fishing across all habitats within the 206 km^2.

2.1.2 | Sample design

To identify suitable sites for monitoring, spatial analyses were conducted combining historical fishing effort, benthic substrate and depth (Sheehan, Stevens, et al., 2013; Stevens et al., 2014). Sites were selected inside and outside the MPA and were located on comparable depths, bathymetry and substrate (Davies, Holmes, Rees, et al., 2021; Sheehan, Cousens, et al., 2013; Sheehan, Stevens, et al., 2013; Stevens et al., 2014). The sites outside are termed Open Controls (OC), as they remained open to

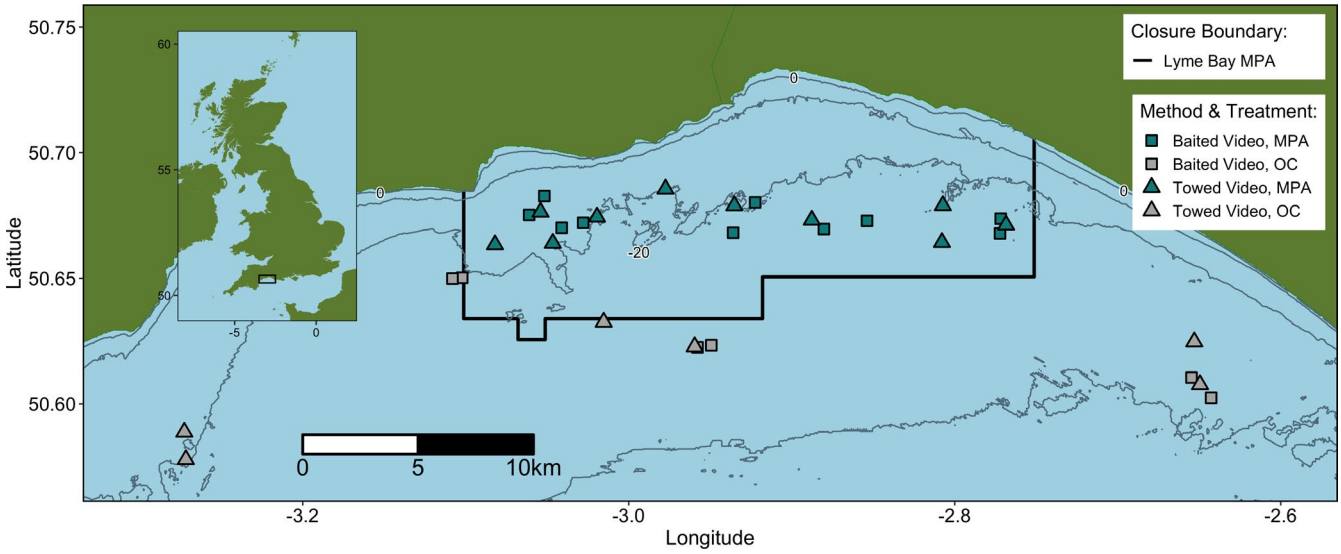

FIGURE 1 Towed video (triangles) and baited remote underwater video system (squares) locations within Lyme Bay MPA (blue) and Open Controls (grey). Each represents an area of three replicate sites

mobile demersal fishing, being within neither the SI nor the SAC. Annual towed video surveys were undertaken at 11 areas in the MPA and 6 OC, with two to five replicate transects conducted at each area. This totalled 46 video transects in 2008 to 2010 (28 MPA and 18 OC) and 51 in 2011 to 2018 (33 MPA and 18 OC). Annual BRUVs surveys were undertaken at 12 areas inside the MPA and 6 OC (Figure 1). Three replicate BRUV deployments were deployed at each area. All BRUVs and towed video surveys were carried out from June to August in all years.

2.2 | Towed flying array

2.2.1 | Video collection

The towed flying array is used to record: 200 m by 0.5-m-wide high definition (HD) video transects over heterogeneous and fragile benthic ecosystems (Sheehan et al., 2010, 2016). The array was a bespoke aluminium frame mounted with: a HD video camera (Surveyor-HD-J12 colour zoom titanium, 720p); LED lights (Bowtech Products limited, LED-1600–13); two green lasers (Z-bolt Scuba-1); and a mini CTD profiler (Valeport Ltd.). The camera was connected to a Bowtech System power supply/control unit by an umbilical cable, which allowed video to be monitored in real time to ensure control of the lights, camera aperture and camera focus. The camera and the parallel lasers were positioned at an oblique angle to the seabed, with the lasers set 300 mm apart, to allow the quantification of the field of view.

2.2.2 | Video analysis

An overall Site x Species matrix ([S]) was created by combining abundance information from two separate video analysis methods (Figure 2). Firstly, all inconspicuous or infrequent fauna were counted from watching the entire video at normal speed, enumerating all individuals that passed through the 'gate' made by the lasers. Secondly, frame grabs were extracted from the video (Cybertronix frame extractor) and a digital 0.25 m^2 quadrate overlaid. Frames were selected and analysed if they met certain criteria of habitat (occurrence of hard substrate), focus of camera (substrate and any taxa within focus) laser placement (lasers are within boundaries of the digital quadrate that make the area of the digital quadrate 0.25 m^2) and visibility (the substrate and any taxa are discernible and identifiable). Thirty frames per transect was shown to give equivalent results to assessing the entire transect, while saving significant amounts of time (Sheehan, Cousens, et al., 2013; Stevens et al., 2014). All species were identified to the highest possible taxonomic resolution. Morphologically similar species were grouped to ensure accurate and consistent identification, following CATAMI grouping system (Althaus et al., 2015).

2.3 | Baited remote underwater video systems

2.3.1 | Video collection

Baited remote underwater video systems (BRUVs) consisted of an aluminium 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, 1 m from the camera, filled with ~100 g of Atlantic mackerel *Scomber scombrus* cut into segments. Fresh bait was replenished for each deployment. Replicate deployments were spaced ~100 m apart to depths ranging from 15 to 32 m, before being recovered after 45 min. Videos from BRUVs were assessed in situ to ensure that the camera had landed and recorded a viable sample (Davies et al., 2020; Davies, Holmes, Rees, et al., 2021). Failed attempts were repeated to ensure that all samples were suitable.

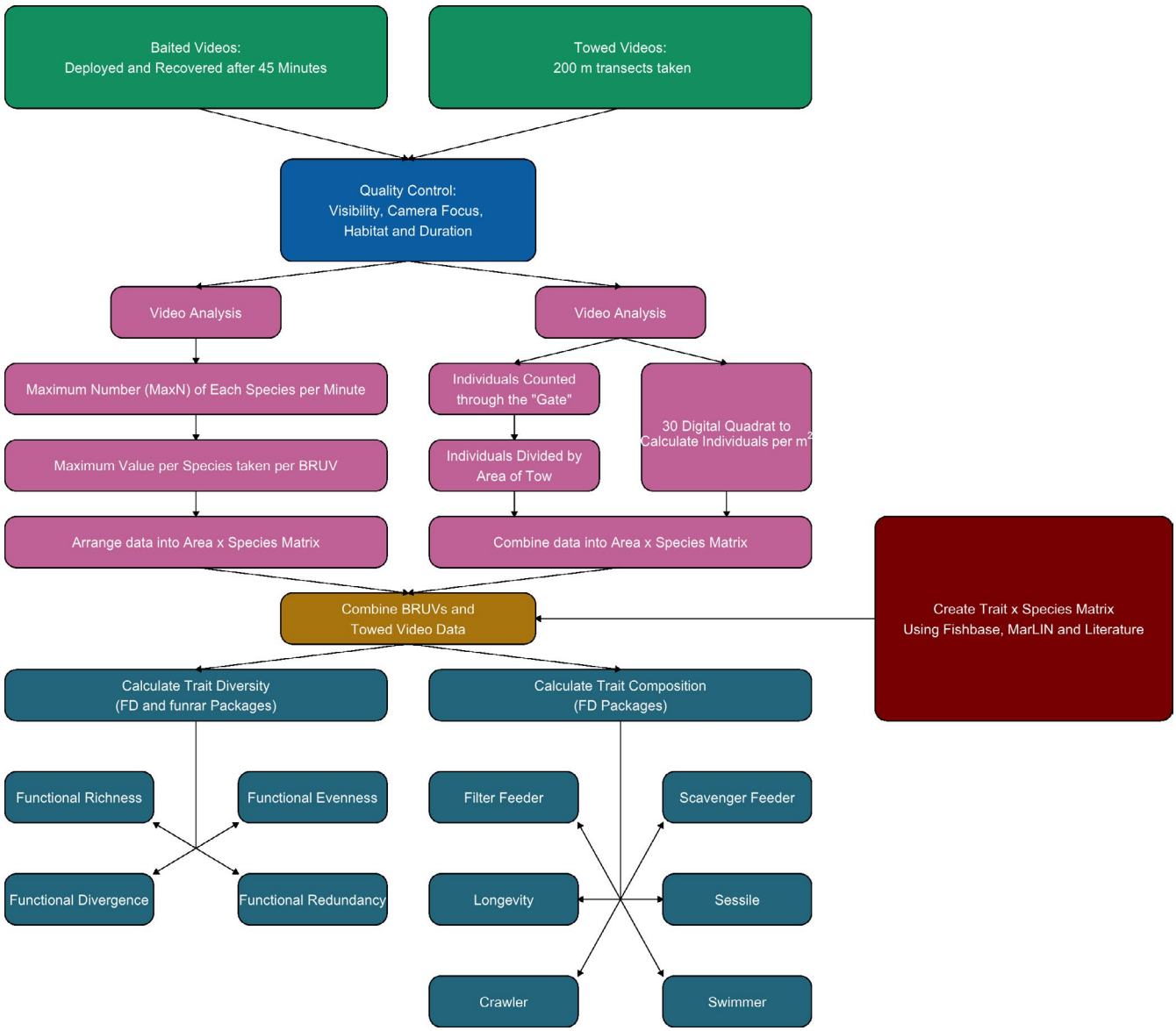

FIGURE 2 Steps taken to collect, combine and convert baited remote underwater video system and towed video data into trait diversity metrics and composition

2.3.2 | Video analysis

Videos were subject to quality control checks according to the following requirements: videos had to be in focus, have adequate visibility to discern the bait box clearly (often impeded by suspended sediment from nearby fishing activity, high levels of plankton or organisms in the foreground: Figure 3a), have no fauna or flora obscuring the view and have the seafloor within view. All criteria had to be maintained for a minimum of 30 min across the recording. Videos that did not meet these requirements were omitted from analysis and resampled. Videos that did meet the requirements were watched at normal speed for 30 min, after a preliminary 5-min settling period when the camera landed on the seabed. For every minute, all mobile fauna were identified to the highest taxonomic resolution possible and counted. Mobile species were categorized 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 scallops (*Pecten maximus* and *Aequipecten opercularis*), which are mostly sedentary, and the brittle star *Ophiothrix fragilis*, which forms aggregations, were not included. For every one-minute segment of the video, the MaxN (maximum number of individuals) for each taxon was recorded. Relative abundance of each taxa was recorded as the greatest MaxN value in any 1 min, within the 30 min analysed. MaxN is considered a conservative estimate of relative abundance, which decreases the chance of an individual being repeatedly recorded (Cappo et al., 2004; Willis et al., 2000).

2.4 | Combining BRUV and Towed data

Baited remote underwater video systems and towed video data were combined by converting all abundance and MaxN values, averaged by area, into relative values using the 'make_relative'

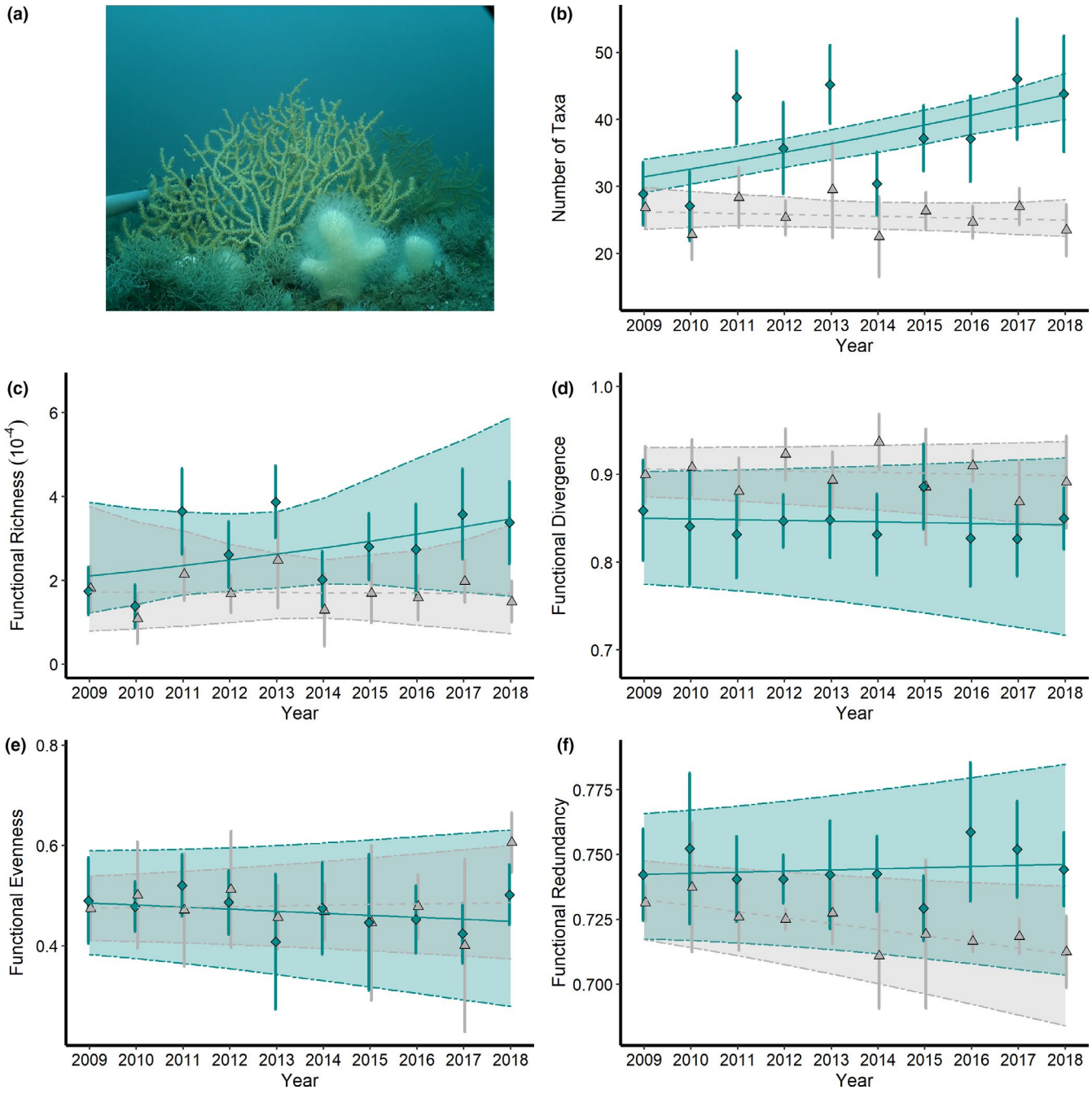

FIGURE 3 Temporal changes in diversity metrics from combined towed underwater video and baited remote underwater video systems data inside the MPA (blue diamonds) and OC (grey triangles). An example screenshot from the baited remote underwater video systems (a), Number of taxa (b), Functional richness (c), Functional divergence (d), Functional evenness (e) and Functional redundancy (f). Lines show model estimates with shading and dotted lines indicating 95% confidence intervals. Symbols with errors bars show raw mean values and 95% confidence intervals

function within the 'funrar' package in R (Grenié et al., 2017; Grenié et al., 2020), as relative values can be used in functional metric creation. Relative data sets were then joined by year, treatment and similar areas (based on habitat, substrate and depth), creating a combined site by species matrix of relative abundances. For all analyses, BRUV and towed video data were combined to assess the trait diversity and how it changes over time inside and outside the MPA.

2.5 | Functional metrics

2.5.1 | Trait acquisition

In total, 11 traits were used with a cumulative 58 modalities (Table 2). They were selected for importance for the benthic environment and its coupling with other components in the ecosystem (e.g. Pelagic/Neritic), as well as availability of information. Trait data were taken

TABLE 2 Traits and their constituent modalities used to assess trait diversity. Bold denotes traits above their constituent modalities

Traits and modalities	
Categorical traits	**Ordinal traits**
Feeding habit	*Age at maturity*
Surface deposit	<1 year
Subsurface deposit	1–2 years
Suspension/Filter	2–4 years
Interface	4–8 years
Predator	8–15 years
Sand Licker	>15 years
Grazer	*Fecundity*
Parasite	0–10 eggs
Predatory scavenger	10–100 eggs
Photosynthesizer	100–1000 eggs
Motility	1000–10,000 eggs
Swimmer	10,000–1,000,000 eggs
Crawler	>1,000,000 eggs
Burrower	*Adult longevity*
Sessile	<1 year
Larval development	1–2 years
Direct	2–10 years
Lecithotrophic	10–15 years
Planktitrophic	15–20 years
Sexual differentiation	>20 years
Gonochoric	*Adult dispersal potential*
Synchronous hermaphrodite	<1 m
Sequential hermaphrodite	1–10 m
Environmental position	10–100 m
Epifauna	100–1000 m
Infauna	1000–10,000 m
Epizoic	>10,000 m
Demersal	*Maximum size*
Pelagic	<1 cm
Diet type	1–10 cm
Carnivore	10–20 cm
Herbivore	20–50 cm
Detritivore	50–100 cm
Photosynthesizer	>100 cm

from multiple sources: MarLIN BIOTIC; Fishbase and Sealifebase (Beauchard et al., 2017; Froese & Pauly, 2019; MarLIN, 2006; Palomares & Pauly, 2019; Shojaei et al., 2015). When appropriate trait information was not available from these three repositories, relevant literature was selected. If trait data for close taxonomic relatives were available (Genus/Family), they were used for species with limited trait information. Fuzzy coding (0–1) was used to quantify categorical traits where individuals may follow multiple modalities for a single trait (Chevenet et al., 1994), all other factors were considered ordinal (Podani, 2005). For categorical traits, all modalities within each individual trait sum to equal 1 so that a trait with more modalities would not be weighted higher than another (Laliberté & Legendre, 2010). This created a Species x Trait matrix ([T]) for the species sampled by the towed flying array and the BRUVs (Appendix S1).

2.5.2 | Metric calculation

The number of taxa was calculated as the total number of different taxa present within each area. Functional richness, functional divergence, functional evenness and functional distinctiveness were calculated for each area from relative abundance using the R package 'FD' and functional distinctiveness from the 'funrar' package (Greni´e et al., 2020; Laliberté & Legendre, 2010). Computation of functional richness and divergence utilized 13 axes out of 68 using the 'Podani' method to deal with ordinal traits, with a quality value of 0.795. Equal weight was given to all columns of [T] to calculate community-level weighted means (CWM). Functional richness represents the trait space filled by the community, functional evenness and functional divergence describe how the abundance is distributed across the trait space filled by the community. The combination of the three diversity indices (functional richness, functional evenness and functional divergence) is thought to be a comprehensive assessment of trait diversity (Mason et al., 2008,2007; Villeger et al., 2008). Functional distinctiveness calculates how functionally rare each species is at each site, returning a value from zero (not rare) to one (fully distinct). Functional redundancy was calculated as one minus the mean functional distinctiveness of the community (Equation 1), meaning values close to one imply high redundancy (Biggs et al., 2020; Ricotta et al., 2016). Where O is functional redundancy and U is mean functional distinctiveness:

$$O = 1 - U \tag{1}$$

It is problematic to distinguish whether traits of organisms in benthic systems are 'response' or 'effect' as the direct links between these specific traits and ecosystem functioning are less well understood (but see: Lam-Gordillo et al., 2020). Therefore, functional redundancy was calculated on all traits, unlike some other definitions of functional redundancy where only traits that are 'effects' rather than 'responses' are included.

2.5.3 | Community-level weighted means

The CWM, which represents the relative proportions of all traits at each site, was calculated from the 'FD' package in R. Specific traits, known to be affected by mobile demersal fishing, were selected a priori for analysis. The traits selected were as follows: longevity; filter and scavenger feeding types; and sessile, crawler and swimmer motility types.

2.6 | Statistical analysis

To assess changes in metrics and CWM (http://www.dassh.ac.uk/doitool/data/1718) of a priori selected traits mixed effect modelling was carried out from the 'glmmADMB', 'lme4' and 'ordinal' packages within R (Bates et al., 2020; Christensen, 2019; Fournier et al., 2012; Skaug et al., 2016). Generalized linear mixed effect models were applied using: a Poisson distribution for the count variable, number of taxa; a gamma distribution for the continuous non-negative variable, functional richness; a beta distributions for the proportional variables between 0 and 1 (functional divergence, functional evenness, functional redundancy and numeric CWM of a priori selected traits); and a logistic regression using a Cumulative link function for the ordinal CWM trait Longevity. Logistic regression using a Cumulative link function allowed the assessment of all present longevity categories (1–2 years, 2–10 years and more than 20 years) to be compared with each other as response variables. All response variables were modelled as a function of Year (continuous: 2009:2018) and Treatment (MPA and OC) as fixed factors and Area (1:16) as a random factor. A marginal transformation (Equation 2) was applied to the numeric CWM data to fit the assumptions of the beta distribution following Smithson & Verkuilen (2006) to account for the presence of zeros and ones in the data. Stated values are model estimate mean values per area ± standard error.

$$y'' = (y'(N-1) + 0.5)/N \quad (2)$$

3 | RESULTS

3.1 | Diversity metrics

The number of taxa changed significantly through time across the two treatments, with a clear increase in the MPA (from 31.5 ± 1.09 in 2009 to 43.7 ± 2.16 in 2018: a 38.9% increase) and a minimal decrease in the OC (from 26.2 ± 1.64 in 2009 to 25 ± 1.59 in 2018: a 4.8% decrease: Table 3 & Figure 3b). Likewise, the functional richness changed significantly through time between treatments, with an increase over time in the MPA (from 0.000211 ± 0.00063 in 2009 to 0.000347 ± 0.00012 in 2018: a 64.6% increase), while the OC showed no substantial change over time (from 0.000172 ± 0.0000725 in 2009 to 0.000169 ± 0.0000808 in 2018: a 1.85% decrease: Table 3 & Figure 3c). Functional divergence did not change significantly through time across treatments but was significantly lower in the MPA compared with the OC (the MPA changed from 0.85 ± 0.0271 in 2009 to 0.842 ± 0.0389 in 2018: a 0.919% decrease, while the OC changed from 0.906 ± 0.0124 in 2009 to 0.899 ± 0.0196 in 2018: a 0.822% decrease: Table 3 & Figure 3d). There was no significant interaction between treatments over time in functional evenness, nor was there a significant main effect of treatment or time (the MPA changed from 0.485 ± 0.053 in 2009 to 0.449 ± 0.093 in 2018: a 7.51% decrease, while the OC changed from 0.474 ± 0.0331 in 2009 to 0.486 ± 0.0579 in 2018: a 2.54% increase: Table 3 & Figure 3e). The functional redundancy showed a significantly different change over time between the two treatments, with the MPA showing a minimal increase and the OC a minimal decrease (the MPA changed from 0.742 ± 0.012 in 2009 to 0.746 ± 0.0196 in 2018: a 0.53% increase, while the OC changed from 0.733 ± 0.00762 in 2009 to 0.712 ± 0.0133 in 2018: a 2.87% decrease: Table 3 & Figure 3f).

TABLE 3 Generalized linear mixed effects model outputs for diversity metrics (number of taxa, functional richness, function divergence, functional evenness and functional redundancy) as a function of Year and Treatment with Area as a random factor

Term	Estimate (SE)	*z*/*t* value	*p* value
Number of taxa			
Intercept	3.28 (0.073)	45.000	**<.0001*** **
Yr	−0.005 (0.009)	−0.617	.54
Tr	0.097 (0.089)	1.090	.27
Yr x Tr	0.042 (0.011)	3.980	**<.0001*** **
Functional richness			
Intercept	−8.66 (0.16)	−54.200	**<.0001*** **
Yr	−0.002 (0.02)	−0.102	.92
Tr	0.087 (0.203)	0.430	.67
Yr x Tr	0.057 (0.026)	2.210	**.027***
Functional divergence			
Intercept	2.29 (0.163)	14.000	**<.0001*** **
Yr	−0.009 (0.019)	−0.490	.62
Tr	−0.536 (0.196)	−2.740	**.0062** **
Yr x Tr	0.003 (0.023)	0.120	.9
Functional evenness			
Intercept	−0.115 (0.128)	−0.900	.37
Yr	0.005 (0.018)	0.300	.76
Tr	0.089 (0.161)	0.550	.58
Yr x Tr	−0.022 (0.023)	−0.956	.34
Functional redundancy			
Intercept	1.03 (0.038)	26.900	**<.0001*** **
Yr	−0.012 (0.005)	−2.340	**.019***
Tr	0.022 (0.049)	0.458	0.65
Yr x Tr	0.014 (0.006)	2.190	**.028***

Note: Year and Treatment are abbreviated throughout to Yr and Tr. Bold values denote significant p values (<0.05) and asterick's define level of significance: p<0.0001 = '<0.0001***'; p< 0.001 = '***'; p < 0.01 = '**' ; p<0.05 = '*'

3.2 | Trait modalities

3.2.1 | Feeding type

The relative proportion of the filter feeding modality, within the feeding type trait, changed significantly through time between the two treatments, with an apparent increase over time in the MPA and a decrease over time in the OC (the MPA changed from 0.613 ± 0.749 in 2009 to 0.7 ± 0.86 in 2018: a 14.1% increase, while the OC

changed from 0.519 ± 0.614 in 2009 to 0.403 ± 0.549 in 2018: a 22.3% decrease: Table 4 & Figure 4a). The scavenger feeding modality showed no significant interaction but a significant increase over time in both treatments (the MPA changed from 0.0443 ± 0.0676 in 2009 to 0.0632 ± 0.105 in 2018: a 42.7% increase, while the OC changed from 0.0792 ± 0.104 in 2009 to 0.111 ± 0.164 in 2018: a 40.5% increase: Table 4 & Figure 4b).

3.2.2 | Longevity

Only longevity ranges 1–2 years, 2–10 years and more than 20 years were the dominant community longevities across all years and treatments. These longevity ranges showed no significant change over time between treatments. 1–2 years had the highest probability (the MPA was 0.818, while the OC was 0.688 throughout: Table 4 & Figure 4c). Similarly, 2–10 years longevity probability did not change over time (0.169 in the MPA and 0.306 in the OC: Table 4 & Figure 4c). There was no difference in the probability of taxa of more than 20 years longevity between treatments or through time (0.0133 in the both treatments: Table 4 & Figure 4c).

3.2.3 | Motility

The relative proportion of the sessile modality, within the motility trait, changed significantly across the treatments over time. Within the MPA, the relative proportion of the sessile modality stayed consistent while decreasing in the OC over time (the MPA changed from 0.762 ± 0.881 in 2009 to 0.779 ± 0.933 in 2018: a 2.19% increase, while the OC changed from 0.723 ± 0.813 in 2009 to 0.434 ± 0.634 in 2018: a 40% decrease: Table 4 & Figure 4d). Between the two treatments, the relative proportion of the crawler modality changed differently, with an increase over time in the OC (the MPA changed from 0.076 ± 0.154 in 2009 to 0.0883 ± 0.268 in 2018: a 16.2% increase, while the OC changed from 0.141 ± 0.206 in 2009 to 0.307 ± 0.477 in 2018: a 118% increase: Table 4 & Figure 4e). Similar to the crawler modality, the relative proportion of the swimmer modality changed significantly differently between treatments, with an increase in the OC over time and a slight decrease over time in the MPA (the MPA changed from 0.142 ± 0.261 in 2009 to 0.109 ± 0.313 in 2018: a 23.1% decrease, while the OC changed from 0.118 ± 0.176 in 2009 to 0.203 ± 0.359 in 2018: a 72% increase: Table 4 & Figure 4f).

TABLE 4 Generalized linear mixed effect model outputs for the cumulative weighted means of a priori selected trait modalities (filter feeder, scavenger feeder, longevity, sessile motility, crawler motility and swimmer motility) as functions of Year and Treatment with Area as a random factor

Term	Estimate (SE)	*z*/*t* value	*p* value
Filter feeder			
Intercept	0.129 (0.196)	0.656	.51
Yr	−0.052 (0.023)	−2.300	**.021***
Tr	0.29 (0.25)	1.160	.25
Yr x Tr	0.095 (0.029)	3.290	**.001****
Scavenger			
Intercept	−2.63 (0.195)	−13.500	**<.0001*****
Yr	0.065 (0.027)	2.450	**.014***
Tr	−0.369 (0.257)	−1.440	.15
Yr x Tr	−0.044 (0.036)	−1.200	.23
Longevity			
1–2 vs. 2–10 years	1.76 (0.727)	2.420	**.016***
1–2 vs. >20 years	4.2 (1)	4.180	**<.0001*****
Yr	−0.163 (0.104)	−1.570	.12
Tr	0.042 (0.932)	0.045	.96
Yr x Tr	0.128 (0.136)	0.940	.35
Sessile motility			
Intercept	1.09 (0.258)	4.230	**<.0001*****
Yr	−0.136 (0.033)	−4.080	**<.0001*****
Tr	0.06 (0.327)	0.183	.85
Yr x Tr	0.147 (0.043)	3.400	**<.0001*****
Crawler motility			
Intercept	−1.92 (0.233)	−8.240	**<.0001*****
Yr	0.11 (0.03)	3.620	**<.0001*****
Tr	−0.6 (0.302)	−1.990	**.047***
Yr x Tr	−0.092 (0.041)	−2.230	**.026***
Swimmer motility			
Intercept	−2.08 (0.234)	−8.870	**<.0001*****
Yr	0.072 (0.032)	2.220	**.027***
Tr	0.313 (0.294)	1.060	.29
Yr x Tr	−0.105 (0.042)	−2.520	**.012***

Note: Year and Treatment are abbreviated throughout to Yr and Tr. Bold values denote significant p values (<0.05) and asterick's define level of significance: p<0.0001 = '<0.0001***'; p< 0.001 = '***'; p < 0.01 = '**' ; p<0.05 = '*'

4 | DISCUSSION

The taxonomic and trait changes in the Lyme Bay MPA were assessed over 10 years since protection and compared to unprotected (open) areas, using a combination of video survey methods (towed flying array and Baited Remote Underwater Video Systems). As predicted, both the number of taxa and functional richness increased over time by 38.9% and 64.6%, respectively, in the MPA, while in the unprotected areas they decreased by 4.8% and 1.85%. In contrast, the functional divergence showed decreases of 0.919% and 0.822% over time in the MPA and unprotected areas, respectively, but was consistently lower in the MPA. Functional evenness showed no change over time or difference between areas, partly contradicting our prediction. Functional redundancy, like functional richness,

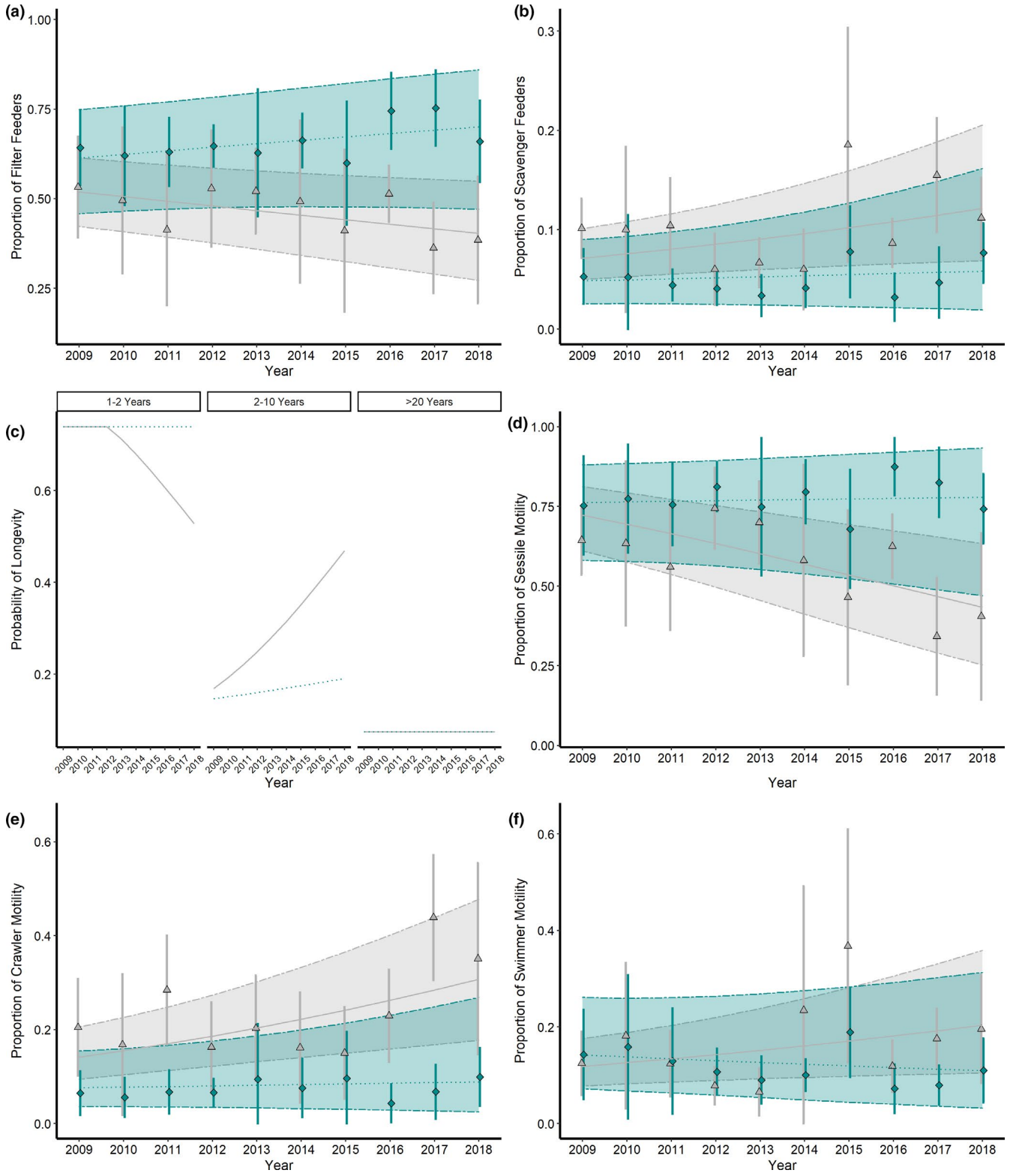

FIGURE 4 Temporal change in trait modalities from combined towed underwater video and baited remote underwater video systems data inside the MPA (blue diamonds) and OC (grey triangles). Filter feeder (a), Scavenger feeder (b), Longevity (c), Sessile motility (d), Crawler motility (e) and Swimmer motility (f). Lines show model estimates with shading and dotted lines indicating 95% confidence intervals. Symbols with errors bars show raw mean values and 95% confidence intervals

was highest in the MPA and remained stable over time, whereas it decreased over time in the unprotected areas, as predicted. Filter feeders increased by 14.1% in the protected area compared to the unprotected areas, where swimmers and crawlers increased. There was a marginal (2.19%) increase in the MPA and a 40% decrease in the unprotected areas in the proportion of sessile modality. Across

the whole bay, there was an increase in the proportion of scavenger modality and no change in the proportion of the longevity modality.

Although it has had many definitions, functional richness has consistently been shown to be an important driver for ecosystem stability, resilience and services (Canning-Clode et al., 2010; Törnroos et al., 2015; Wahl et al., 2011). Functional and taxonomic richnesses are closely related, regardless of how functional richness is defined: the trait space filled by a community, used here (Boyé, et al., 2019; Villeger et al., 2008); the species richness within functional groupings (Canning-Clode et al., 2010; Wahl et al., 2011); the species richness of functionally unique species (Canning-Clode et al., 2009; McLean et al., 2021); or the number of functional traits (de Juan et al., 2015). Here, the exclusion of mobile demersal fishing inside the MPA has allowed the increase in both the number of taxa and the trait space. It is likely the increase will have altered ecosystem-wide processes, with positive effects to productivity and regulation of biogeochemical fluxes (Perović et al., 2018; Ricotta et al., 2016; Vackár et al., 2012). However, further research is required to explicitly assess how changes in trait diversity and composition can alter or influence the functioning of ecosystems, especially when the identity and traits of dominant species can be more influential than overall diversity (Gammal et al., 2020; Strong et al., 2015).

Pressures imposed by high levels of demersal towed fishing can impact communities in varying ways (Fragkopoulou et al., 2021; Olsgard et al., 2008; Wang et al., 2021). One example, strong disturbance regimes, will continually reset communities to small initial successional stage assemblages (Song & Saavedra, 2018). This may introduce high levels of competitive interactions and, as such, will increase the functional divergence and decrease trait redundancy (Perronne et al., 2017). Cumulatively, this will restrict the increase in abundance of novel traits into the community and can lead to dominance of a few species with unique traits, such as high fecundity and short life span that allow them to persist (Boyé, et al., 2019). This was likely the driver for the observed minor decrease over time in functional divergence across both treatments and decrease in functional redundancy seen in the unprotected areas (Table 3). Furthermore, trawling and other destructive fishing practices can significantly alter the proportion of traits present within a benthic community (Howarth et al., 2018). Specifically, chronic trawling can cause a decrease in sessile filter feeding organisms and an increase in mobile scavenger species (Tillin et al., 2006). This effect of chronic impact can produce a shift in the baseline to measure change or recovery from in heavily trawled systems (Brown & Trebilco, 2014; Ulman & Pauly, 2016). As shown here, the area protected from demersal mobile fishing showed increases in filter feeding organisms, with the unprotected areas showing decreases in the proportion of sessile organisms and increases in the proportion of swimmers and crawlers. The Lyme Bay MPA was designated to protect the rocky reef habitat, which in turn is characterized by sessile fauna species, such as pink sea fans *Eunicella verrucosa* and ross corals *Pentapora foliacea* (Sheehan, Stevens, et al., 2013). Yet in 2008, the first surveys of the MPA showed limited sessile life growing on the boulders and cobbles (Sheehan, Stevens, et al., 2013). Thus, the marginal increase in the MPA in the proportion of sessile modality alongside the strong decrease in the unprotected areas show the protection is being effective and is protecting the sessile rocky reef species, while the unprotected areas continue to be dispossessed of species with these trait.

In this study, functional evenness remained the same. Assuming that resource availability, such as substrate, prey or mate availability, was even across the system, this implies that as the trait space (functional richness) increased, the dominance pattern within this trait space stayed the same. Hence, the community was maintaining its effectiveness at utilizing the available resources (Mason et al., 2005). This lack of change in evenness in the MPA, even though the functional richness (trait space) increased over time, may be due to increases in abundance of species with locally rarer combinations of traits. Yet, these abundances stay minimal in comparison with the traits of the more dominant species. This continued dominance of common combinations of traits across both treatments may have led to the observed functional divergence (Figure 3d).

Communities containing high levels of trait overlap (functional redundancy) have been found to provide a higher resilience to environmental impacts, such as fishing, storms or biological invasions (Mason et al., 2005; McLean et al., 2019; Tillin et al., 2006). When a species becomes regionally extinct, its suite of traits is less likely to become lost when there is high trait overlap. The higher levels of functional redundancy witnessed in the MPA compared to the unprotected areas show potential higher resilience to perturbations (Rincón-Díaz et al., 2018), and the effect increased over time. However, the resilience provided by redundancy will be heavily linked to the traits used (Boyé, et al., 2019). When seen alongside the increases in taxa and the functional richness inside the MPA, the increase in redundancy would imply that the increases in richness are across and within a wide range of niches and trophic levels (Rincón-Díaz et al., 2018). Many studies focusing on fish assemblages have found an opposing pattern, with an increase in richness simultaneous to a decrease in redundancy (Rincón-Díaz et al., 2018; Stuart-Smith et al., 2013). This may be due to the probability of overlap in traits decreasing when there is an increase in functional richness, and the concomitant growth in trait space. The relationship between diversity and the buffer created by trait redundancy is of high importance to managers and conservationists for setting goals and priorities (Micheli et al., 2014), and as such needs to be fully understood at both regional and global scales. With perturbations likely to continue to increase through direct and indirect anthropogenic impacts, so the importance of community resilience increases. Severe storms in early 2014 across the south-west of the UK have been shown to impact the marine benthos in Lyme Bay (Sheehan et al., 2021). The effects can be seen in a reduction in taxa and functional richness and an increase in the scavenging 2014 in both the MPA and unprotected areas. There was also a reduction in the functional redundancy and an increase in the functional divergence in the OC, but the only discernible reduction in the MPA was a year later in 2015, potentially showing a buffering effect in the MPA from

the higher levels of functional redundancy. Here, the Lyme Bay MPA has shown increases in not only diversity but also its potential resilience, displaying the possible functional benefits provided by the whole-site approach to MPA management, which has been employed at the site.

The two survey methods (towed flying array and BRUVs) used were originally conducted to perform taxonomic-based assessments, evaluating the change in the species or taxa, and communities present (Davies et al., 2020; Davies, Holmes, Rees, et al., 2021; Sheehan, Cousens, et al., 2013; Sheehan et al., 2010). Combining the two survey methods data into a single analysis allows an assessment of a broader range of the benthic ecosystem, with benefits of providing more comprehensive understanding of how the monitored ecosystem is changing in relation to anthropogenic and natural perturbations. Functional assessment is already being advocated to inform management (Rijnsdorp et al., 2016; Tillin et al., 2006; Wiedmann et al., 2014), and enabling the assessment of functional change across a large proportion of the benthic ecosystem could aid adaptive management of MPAs, yet caution is needed when comparing between different systems or locations. As mobile demersal fishing impacts specific traits, so other fishing methods will effect other specific traits or trait combinations (Tillin et al., 2006). Therefore, utilizing trait diversity and trait composition to detect effects of different management strategies must be targeted to the expected consequence of the management (Trindade-Santos et al., 2020). For example, the current work is specific to Lyme Bay, where a comparatively rare management regime, especially in Europe, has been in place. This management has protected the whole-site, covering a mosaic of different habitats, from mobile demersal fishing (Sheehan, Cousens, et al., 2013). However, the vast majority of marine protection in Europe utilizes what has been termed 'feature'-based protection (Solandt et al., 2020). Therefore, the effects seen here in this "whole-site" MPA, increases in trait diversity and specific traits, will be specific to this management approach, as well as the assessed spatial and temporal scales. Magnitudes of functional metric values are linked to the number of different traits, these need to be kept consistent to allow comparison (Villeger et al., 2008). Furthermore, the maximum number of potential species assessed requires consistency, as this will heavily influence the potential number of different traits found within a community. Therefore, increases in repositories of trait information for a wide range of species and the standard reporting practices are highly important to allow comparison between locations, nationally and internationally.

Diversity metrics (taxonomic and trait) showed significant trends of increase over the 10 years surveyed, yet without data from pre-fishing, defining recovery is problematic (Ulman & Pauly, 2016). It is expected that a recovering system will eventually reach a plateau of diversity. However, the time-scales for this to occur can be large, more than 75 years in some instances (Anderson et al., 2014). The current work shows diversity increases over 10 years with no clear sign of plateau, indicating the potential for continued recovery. Yet, climate change will inevitably impact marine systems over the coming decades. Thus, emphasizing the need for long-term monitoring to fully appreciate trajectories of recovery both in this specific system and others globally, especially as climate change impacts intensify.

In conclusion, the ecosystem function of the benthic community in Lyme Bay has significantly changed over 10 years following the exclusion of mobile demersal fishing, with increases in number of taxa, the functional richness and the functional redundancy in the MPA. The MPA in comparison with unprotected areas has become more diverse both taxonomically and functionally, which will likely have lead to greater levels of ecosystem service. Sessile organisms, fundamental to the health and development of rocky reef habitats, decreased outside the protected area over time, showing that this MPA is protecting the rocky reefs in areas that were previously damaged by destructive fishing practices. It is difficult to suggest whether the trends of increasing number of taxa, functional richness, functional redundancy and filter feeding traits are a recovery to a pre-fishing state, due to the unknown level of shifting baselines, which before-fishing data could reveal. However, it does show a trend towards a more diverse and potentially resilient rocky reef habitat, providing further evidence of the benefits of employing the whole-site approach to MPA management.

ACKNOWLEDGEMENTS

To carry out fieldwork, thanks are given to Lyme Bay Fishers John Walker, Robert King and Keiran Perree and University of Plymouth staff and student volunteers.

CONFLICT OF INTERESTS

The authors declare that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available via the Archive for Marine Secies and Habitats Data (DASSH) http://www.dassh.ac.uk/doitool/data/1718 (Davies, Holmes, Bicknell et al., 2021).

ORCID

Bede F. R. Davies https://orcid.org/0000-0001-6462-4347

REFERENCES

Althaus, F., Hill, N., Ferrari, R., Edwards, L., Przeslawski, R., Schönberg, C. H. L., Stuart-Smith, R., Barrett, N., Edgar, G., Colquhoun, J., Tran, M., Jordan, A., Rees, T., & Gowlett-Holmes, K. (2015). A standardised vocabulary for identifying benthic biota and substrata from underwater imagery: The Catami Classification Scheme. *PLoS One*, *10*(10), e0141039. https://doi.org/10.1371/journal.pone.0141039

Anderson, A. B., Bonaldo, R. M., Barneche, D. R., Hackradt, C. W., Félix-Hackradt, F. C., García-Charton, J. A., & Floeter, S. R. (2014). Recovery of grouper assemblages indicates effectiveness of a marine protected area in Southern Brazil. *Marine Ecology Progress Series*, *514*, 207–215. https://doi.org/10.3354/meps11032

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2020). *lme4: Linear mixed effects models using eigen and s4* [Computer software manual]. https://github.com/lme4/lme4/ (R package version 1.1-25).

Beauchard, O., Veríssimo, H., Queirós, A. M., & Herman, P. M. J. (2017). The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. *Ecological Indicators*, *76*, 81–96. https://doi.org/10.1016/j.ecolind.2017.01.011

Belley, R., & Snelgrove, P. V. R. (2016). Relative contributions of biodiversity and environment to benthic ecosystem functioning. *Frontiers in Marine Science*, *3*, 1–15. https://doi.org/10.3389/fmars.2016.00242

Benoit, H. P., Plante, S., Kroiz, M., & Hurlbut, T. (2013). A comparative analysis of marine fish species susceptibilities to discard mortality: Effects of environmental factors, individual traits, and phylogeny. *ICES Journal of Marine Science*, *70*(1), 99–113. https://doi.org/10.1093/icesjms/fss132

Benoıt, H. P., & Swain, D. P. (2008). Impacts of environmental change and direct and indirect harvesting effects on the dynamics of a marine fish community. *Canadian Journal of Fisheries and Aquatic Sciences*, *65*(10), 2088–2104. https://doi.org/10.1139/F08-112

Berthelsen, A. K., Hewitt, J. E., & Taylor, R. B. (2015). Biological traits and taxonomic composition of invertebrate assemblages associated with coralline turf along an environmental gradient. *Marine Ecology Progress Series*, *530*, 15–27. https://doi.org/10.3354/meps11337

Bicknell, A. W., Sheehan, E. V., Godley, B. J., Doherty, P. D., & Witt, M. J. (2019). Assessing the impact of introduced infrastructure at sea with cameras: A case study for spatial scale, time and statistical power. *Marine Environmental Research*, *147*, 126–137. https://doi.org/10.1016/j.marenvres.2019.04.007

Biggs, C. R., Yeager, L. A., Bolser, D. G., Bonsell, C., Dichiera, A. M., Hou, Z., Keyser, S. R., Khursigara, A. J., Lu, K., Muth, A. F., Negrete, B., & Erisman, B. E. (2020). Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. *Ecosphere*, *11*(7), e03184. https://doi.org/10.1002/ecs2.3184

Boonzaier, L., & Pauly, D. (2016). Marine protection targets: An updated assessment of global progress. *Oryx*, *50*(1), 27–35. https://doi.org/10.1017/S0030605315000848

Boyé, A., Thiébaut, É., Grall, J., Legendre, P., Broudin, C., Houbin, C., Le Garrec, V., Maguer, M., Droual, G., & Gauthier, O. (2019). Trait-based approach to monitoring marine benthic data along 500 km of coastline. *Diversity and Distributions*, *25*, 1879–1896.

Brown, C. J., & Trebilco, R. (2014). Unintended cultivation, shifting baselines, and conflict between objectives for fisheries and conservation. *Conservation Biology*, *28*(3), 677–688. https://doi.org/10.1111/cobi.12267

Brown, K., Adger, W. N., Tompkins, E., Bacon, P., Shim, D., & Young, K. (2001). Trade-off analysis for marine protected area management. *Ecological Economics*, *37*(3), 417–434. https://doi.org/10.1016/S0921-8009(00)00293-7

Canning-Clode, J., Bellou, N., Kaufmann, M. J., & Wahl, M. (2009). Local-regional richness relationship in fouling assemblages – Effects of succession. *Basic and Applied Ecology*, *10*(8), 745–753. https://doi.org/10.1016/j.baae.2009.05.005

Canning-Clode, J., Maloney, K. O., McMahon, S. M., & Wahl, M. (2010). Expanded view of the local-regional richness relationship by incorporating functional richness and time: A large-scale perspective. *Global Ecology and Biogeography*, *19*(6), 875–885. https://doi.org/10.1111/j.1466-8238.2010.00560.x

Cappo, M., Speare, P., & De'ath, G. (2004). Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. *Journal of Experimental Marine Biology and Ecology*, *302*(2), 123–152. https://doi.org/10.1016/j.jembe.2003.10.006

Chevene, F., Doleadec, S., & Chessel, D. (1994). A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology*, *31*, 295–309. https://doi.org/10.1111/j.1365-2427.1994.tb01742.x

Christensen, R. H. B. (2019). *Ordinal—regression models for ordinal data*. (R package version 2019.12-10). https://CRAN.Rproject.org/package=ordinal

Cleguer, C., Grech, A., Garrigue, C., & Marsh, H. (2015). Spatial mismatch between marine protected areas and dugongs in New Caledonia. *Biological Conservation*, *184*, 154–162. https://doi.org/10.1016/j.biocon.2015.01.007

Coleman, M. A., Bates, A. E., Stuart-Smith, R. D., Malcolm, H. A., Harasti, D., Jordan, A., Knott, N. A., Edgar, G. J., & Kelaher, B. P. (2015). Functional traits reveal early responses in marine reserves following protection from fishing. *Diversity and Distributions*, *21*(8), 876–887. https://doi.org/10.1111/ddi.12309

Cooper, K. M., Barrio Froján, C. R. S., Defew, E., Curtis, M., Fleddum, A., Brooks, L., & Paterson, D. M. (2008). Assessment of ecosystem function following marine aggregate dredging. *Journal of Experimental Marine Biology and Ecology*, *366*(1-2), 82–91. https://doi.org/10.1016/j.jembe.2008.07.011

Davies, B. F. R., Attrill, M. J., Holmes, L., Rees, A., Witt, M. J., & Sheehan, E. V. (2020). Acoustic Complexity Index to assess benthic biodiversity of a partially protected area in the southwest of the UK. *Ecological Indicators*, *111*, 106019. https://doi.org/10.1016/j.ecolind.2019.106019

Davies, B. F. R., Holmes, L., Bicknell, A., Attrill, M., & Sheehan, E. V. (2021). *2009-2018 University of Plymouth Lyme Bay Benthic Video Survey metrics*. http://www.dassh.ac.uk/doitool/data/1718 https://doi.org/10.17031/1718

Davies, B. F. R., Holmes, L., Rees, A., Attrill, M. J., Cartwright, A. Y., & Sheehan, E. V. (2021). 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. *Journal of Applied Ecology*, *58*(11), 2463–2478. https://doi.org/10.1111/1365-2664.13986

de Juan, S., Hewitt, J. E., Thrush, S. F., & Freeman, D. (2015). Standardising the assessment of Functional Integrity in benthic ecosystems. *Journal of Sea Research*, *98*, 33–41. https://doi.org/10.1016/j.seares.2014.06.001

De-La-Ossa-Carretero, J. A., Del-Pilar-Ruso, Y., Giménez-Casalduero, F., Sánchez-Lizaso, J. L., & Dauvin, J.-C. (2012). Sensitivity of amphipods to sewage pollution. *Estuarine, Coastal and Shelf Science*, *96*(1), 129–138. https://doi.org/10.1016/j.ecss.2011.10.020

Ferreira, A., Alves, A. S., Marques, J. C., & Seixas, S. (2017). Ecosystem response to different management options in Marine Protected Areas (MPA): A case study of intertidal rocky shore communities. *Ecological Indicators*, *81*(1830), 471–480. https://doi.org/10.1016/j.ecolind.2017.06.028

Ferse, S. C. A., Costa, M. M., Manez Schwerdtner, K., Adhuri, D. S., & Glaser, M. (2010). Allies, not aliens: Increasing the role of local communities in marine protected area implementation. *Environmental Conservation*, *37*(1), 23–34. https://doi.org/10.1017/S0376892910000172

Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M. N., Nielsen, A., & Sibert, J. (2012). AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, *27*(2), 233–249. https://doi.org/10.1080/10556788.2011.597854

Fragkopoulou, E., Serrão, E. A., Horta, P. A., Koerich, G., & Assis, J. (2021). Bottom trawling threatens future climate refugia of rhodoliths globally. *Frontiers in Marine Science*, *7*, 1–11. https://doi.org/10.3389/fmars.2020.594537

Froese, R., & Pauly, D. (2019). *Fishbase*. www.fishbase.org

Gallacher, J., Simmonds, N., Fellowes, H., Brown, N., Gill, N., Clark, W., Biggs, C., & Rodwell, L. D. (2016). Evaluating the success of a marine protected area: A systematic review approach. *Journal of Environmental Management*, *183*, 280–293. https://doi.org/10.1016/j.jenvman.2016.08.029

Gammal, J., Hewitt, J., Norkko, J., Norkko, A., & Thrush, S. (2020). Does the use of biological traits predict a smooth landscape of ecosystem functioning? *Ecology and Evolution*, *10*(19), 10395–10407. https://doi.org/10.1002/ece3.6696

Grenié, M., Denelle, P., & Tucker, C. (2020). *funrar: Functional rarity indices computation* [Computer software manual]. https://rekyt.github.io/funrar/ (R package version 141)

Grenié, M., Denelle, P., Tucker, C. M., Munoz, F., & Violle, C. (2017). funrar: An R package to characterize functional rarity. *Diversity and Distributions*, *23*(12), 1365–1371. https://doi.org/10.1111/ddi.12629

Guillemot, N., Kulbicki, M., Chabanet, P., & Vigliola, L. (2011). Functional redundancy patterns reveal non-random assembly rules in a species-rich marine assemblage.*PLoS One*, *6*(10), 26735. https://doi.org/10.1371/journal.pone.0026735

Halpern, B. S., Lester, S. E., Mcleod, K. L., & Gaines, S. D. (2010). Placing marine protected areas onto the ecosystem-based management seascape. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(43), 18312–18317. https://doi.org/10.1073/pnas.0908503107

Hiscock, K., & Breckels, M. (2007). *Marine Biodiversity Hotspots in the UK A report identifying and protecting areas for marine biodiversity Marine Biodiversity Hotspots in the UK: their identification and protection*. WWF: http://assets.wwf.org.uk/downloads/marinehotspots.pdf

Howarth, L. M., Waggitt, J. J., Bolam, S. G., Eggleton, J., Somerfield, P. J., & Hiddink, J. G. (2018). Effects of bottom trawling and primary production on the composition of biological traits in benthic assemblages. *Marine Ecology Progress Series*, *602*, 31–48. https://doi.org/10.3354/meps12690

Jax, K. (2005). Function and "functioning" in ecology: What does it mean? *Oikos*, *111*(3), 641–648. https://doi.org/10.1111/j.1600-0706.2005.13851.x

Jones, P. J. (2008). Fishing industry and related perspectives on the issues raised by no-take marine protected area proposals. *Marine Policy*, *32*(4), 749–758. https://doi.org/10.1016/j.marpol.2007.12.009

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*, 299–305. https://doi.org/10.1890/08-2244.1

Lam-Gordillo, O., Baring, R., & Dittmann, S. (2020). Ecosystem functioning and functional approaches on marine macrobenthic fauna: A research synthesis towards a global consensus. *Ecological Indicators*, *115*, 106379. https://doi.org/10.1016/j.ecolind.2020.106379

Letessier, T. B., Mouillot, D., Bouchet, P. J., Vigliola, L., Fernandes, M. C., Thompson, C., Boussarie, G., Turner, J., Juhel, J.-B., Maire, E., Caley, M. J., Koldewey, H. J., Friedlander, A., Sala, E., & Meeuwig, J. J. (2019). Remote reefs and seamounts are the last refuges for marine predators across the Indo-Pacific. *PLOS Biology*, *17*(8), e3000366. https://doi.org/10.1371/journal.pbio.3000366

Long, R. D., Charles, A., & Stephenson, R. L. (2015). Key principles of marine ecosystem-based management. *Marine Policy*, *57*, 53–60. https://doi.org/10.1016/j.marpol.2015.01.013

Mangi, S. C., Rodwell, L. D., & Hattam, C. E. (2011). Assessing the impacts of establishing MPAs on fishermen and fish merchants: The case of Lyme Bay, UK. *Ambio*, *40*, 457–468. https://doi.org/10.1007/s13280-011-0154-4

MarLIN (2006). *BIOTIC: Biological Traits Information Catalogue*. Marine Life Information Network: www.marlin.ac.uk/biotic

Mason, N. W. H., Irz, P., Lanoiselée, C., Mouillot, D., & Argillier, C. (2008). Evidence that niche specialization explains species-energy relationships in lake fish communities. *Journal of Animal Ecology*, *77*(2), 285–296. https://doi.org/10.1111/j.1365-2656.2007.01350.x

Mason, N. W. H., Lanoiselée, C., Mouillot, D., Irz, P., & Argillier, C. (2007). Functional characters combined with null models reveal inconsistency in mechanisms of species turnover in lacustrine fish communities. *Oecologia*, *153*(2), 441–452. https://doi.org/10.1007/s00442-007-0727-x

Mason, N. W., Mouillot, D., Lee, W. G., & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos*, *111*(1), 112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x

Maxwell, S. M., Hazen, E. L., Lewison, R. L., Dunn, D. C., Bailey, H., Bograd, S. J., Briscoe, D. K., Fossette, S., Hobday, A. J., Bennett, M., Benson, S., Caldwell, M. R., Costa, D. P., Dewar, H., Eguchi, T., Hazen, L., Kohin, S., Sippel, T., & Crowder, L. B. (2015). Dynamic ocean management: Defining and conceptualizing real-time management of the ocean. *Marine Policy*, *58*, 42–50. https://doi.org/10.1016/j.marpol.2015.03.014

McLean, M., Auber, A., Graham, N. A. J., Houk, P., Villéger, S., Violle, C., Thuiller, W., Wilson, S. K., & Mouillot, D. (2019). Trait structure and redundancy determine sensitivity to disturbance in marine fish communities. *Global Change Biology*, *25*(10), 3424–3437. https://doi.org/10.1111/gcb.14662

McLean, M., Stuart-Smith, R. D., Villéger, S., Auber, A., Edgar, G. J., MacNeil, M. A., Loiseau, N., Leprieur, F., & Mouillot, D. (2021). Trait similarity in reef fish faunas across the world's oceans. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(12), e2012318118. https://doi.org/10.1073/pnas.2012318118

Micheli, F., Mumby, P. J., Brumbaugh, D. R., Broad, K., Dahlgren, C. P., Harborne, A. R., Holmes, K. E., Kappel, C. V., Litvin, S. Y., & Sanchirico, J. N. (2014). High vulnerability of ecosystem function and services to diversity loss in Caribbean coral reefs. *Biological Conservation*, *171*, 186–194. https://doi.org/10.1016/j.biocon.2013.12.029

Munroe, S. E. M., Coates-Marnane, J., Burford, M. A., & Fry, B. (2018). A benthic bioindicator reveals distinct land and ocean-Based influences in an urbanized coastal embayment. *PLoS One*, *13*(10), e02050408. https://doi.org/10.1371/journal.pone.0205408

Murgier, J., McLean, M., Maire, A., Mouillot, D., Loiseau, N., Munoz, F., Violle, C., & Auber, A. (2021). Rebound in functional distinctiveness following warming and reduced fishing in the north sea. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1942), 20201600. https://doi.org/10.1098/rspb.2020.1600

Olsgard, F., Schaanning, M. T., Widdicombe, S., Kendall, M. A., & Austen, M. C. (2008). Effects of bottom trawling on ecosystem functioning. *Journal of Experimental Marine Biology and Ecology*, *366*(1-2), 123–133. https://doi.org/10.1016/j.jembe.2008.07.036

Palomares, M. L. D., & Pauly, D. (2019). *SealifeBase*. www.sealifebase.org

Parmar, T. K., Rawtani, D., & Agrawal, Y. K. (2016). Bioindicators: the natural indicator of environmental pollution. *Frontiers in Life Science*, *9*(2), 110–118. https://doi.org/10.1080/21553769.2016.1162753

Perović, D. J., Gámez-Virués, S., Landis, D. A., Wäckers, F., Gurr, G. M., Wratten, S. D., You, M.-S., & Desneux, N. (2018). Managing biological control services through multi-trophic trait interactions: review and guidelines for implementation at local and landscape scales. *Biological Reviews*, *93*(1), 306–321. https://doi.org/10.1111/brv.12346

Perronne, R., Munoz, F., Borgy, B., Reboud, X., & Gaba, S. (2017). How to design trait-based analyses of community assembly mechanisms: Insights and guidelines from a literature review. *Perspectives in Plant Ecology, Evolution and Systematics*, *25*, 29–44. https://doi.org/10.1016/j.ppees.2017.01.004

Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., & Sainsbury, K. J. (2004). Ecosystem-based fishery management. *Science*, *305*, 346–347.

Pine, M. K., Jeffs, A. G., Wang, D., & Radford, C. A. (2016). The potential for vessel noise to mask biologically important sounds within ecologically significant embayments. *Ocean & Coastal Management*, *127*, 63–73. https://doi.org/10.1016/j.ocecoaman.2016.04.007

Podani, J. (2005). Multivariate exploratory analysis of ordinal data in ecology: Pitfalls, problems and solutions. *Journal of Vegetation Science*, *16*(5), 497–510. https://doi.org/10.1111/j.1654-1103.2005.tb02390.x

Rees, S. E., Rodwell, L. D., Attrill, M. J., Austen, M. C., & Mangi, S. C. (2010). The value of marine biodiversity to the leisure and recreation industry and its application to marine spatial planning. *Marine Policy*, *34*(5), 868–875. https://doi.org/10.1016/j.marpol.2010.01.009

Rees, S. E., Sheehan, E. V., Stewart, B. D., Clark, R., Appleby, T., Attrill, M. J., Jones, P. J. S., Johnson, D., Bradshaw, N., Pittman, S., Oates, J., & Solandt, J.-L. (2020). Emerging themes to support ambitious UK marine biodiversity conservation. *Marine Policy*, *117*, 103864. https://doi.org/10.1016/j.marpol.2020.103864

Ricotta, C., de Bello, F., Moretti, M., Caccianiga, M., Cerabolini, B. E., & Pavoine, S. (2016). Measuring the functional redundancy of biological communities: A quantitative guide. *Methods in Ecology and Evolution*, *7*(11), 1386–1395. https://doi.org/10.1111/2041-210X.12604

Rijnsdorp, A. D., Bastardie, F., Bolam, S. G., Buhl-Mortensen, L., Eigaard, O. R., Hamon, K. G., Hiddink, J. G., Hintzen, N. T., Ivanović, A., Kenny, A., Laffargue, P., Nielsen, J. R., O'Neill, F. G., Piet, G. J., Polet, H., Sala, A., Smith, C., van Denderen, P. D., van Kooten, T., & Zengin, M. (2016). Towards a framework for the quantitative assessment of trawling impact on the seabed and benthic ecosystem. *ICES Journal of Marine Science*, *73*(suppl_1), i127–i138. https://doi.org/10.1093/icesjms/fsv207

Rincón-Díaz, M. P., Pittman, S. J., Arismendi, I., & Heppell, S. S. (2018). Functional diversity metrics detect spatio-temporal changes in the fish communities of a Caribbean marine protected area. *Ecosphere*, *9*(10), e02433. https://doi.org/10.1002/ecs2.2433

Sheehan, E. V., Cousens, S. L., Nancollas, S. J., Stauss, C., Royle, J., & Attrill, M. J. (2013). Drawing lines at the sand: Evidence for functional vs. visual reef boundaries in temperate Marine Protected Areas. *Marine Pollution Bulletin*, *76*, 194–202. https://doi.org/10.1016/j.marpolbul.2013.09.004

Sheehan, E. V., Holmes, L. A., Davies, B. F. R., Cartwright, A., Rees, A., & Attrill, M. J. (2021). Rewilding of protected areas enhances resilience of marine ecosystems to extreme climatic events. *Frontiers in Marine Science*, *8*, 671427. https://doi.org/10.3389/fmars.2021.671427

Sheehan, E. V., Stevens, T. F., & Attrill, M. J. (2010). A quantitative, non-destructive methodology for habitat characterisation and benthic monitoring at offshore renewable energy developments. *PLoS One*, *5*(12), e14461. https://doi.org/10.1371/journal.pone.0014461

Sheehan, E. V., Stevens, T. F., Gall, S. C., Cousens, S. L., & Attrill, M. J. (2013). Recovery of a temperate reef assemblage in a marine protected area following the exclusion of towed demersal fishing. *PLoS One*, *8*(12), e83883. https://doi.org/10.1371/journal.pone.0083883

Sheehan, E. V., Vaz, S., Pettifer, E., Foster, N. L., Nancollas, S. J., Cousens, S., Holmes, L., Facq, J.-V., Germain, G., & Attrill, M. J. (2016). An experimental comparison of three towed underwater video systems using species metrics, benthic impact and performance. *Methods in Ecology and Evolution*, *7*(7), 843–852. https://doi.org/10.1111/2041-210X.12540

Shojaei, M. G., Gutow, L., Dannheim, J., Pehlke, H., & Brey, T. (2015). *Functional diversity and traits assembly patterns of benthic macrofaunal communities in the Southern North Sea. In Towards an interdisciplinary approach in earth system science* (pp. 183–195). Springer International Publishing. https://doi.org/10.1007/978-3-319-13865-7

Skaug, H., Fournier, D., Bolker, B., Magnusson, A., & Nielsen, A. (2016). Generalized Linear Mixed Models using 'AD Model Builder'.

Smithson, M., & Verkuilen, J. (2006). A better lemon squeezer? Maximum likelihood regression with beta-distributed dependent variables. *Psychological Methods*, *11*(1), 54–71. https://doi.org/10.1037/1082-989X.11.1.54

Solandt, J.-L., Mullier, T., Elliott, S., & Sheehan, E. V. (2020). Managing marine protected areas in Europe. *Marine Protected Areas*, *157–181*, https://doi.org/10.1016/b978-0-08-102698-4.00009-5

Song, C., & Saavedra, S. (2018). Will a small randomly assembled community be feasible and stable? *Ecology*, *99*(3), 743–751. https://doi.org/10.1002/ecy.2125

Stevens, T. F., Sheehan, E. V., Gall, S. C., Fowell, S. C., & Attrill, M. J. (2014). Monitoring benthic biodiversity restoration in Lyme Bay marine protected area: Design, sampling and analysis. *Marine Policy*, *45*, 310–317. https://doi.org/10.1016/j.marpol.2013.09.006

Strong, J. A., Andonegi, E., Bizsel, K. C., Danovaro, R., Elliott, M., Franco, A., Garces, E., Little, S., Mazik, K., Moncheva, S., Papadopoulou, N., Patrício, J., Queirós, A. M., Smith, C., Stefanova, K., & Solaun, O., 2015). Marine biodiversity and ecosystem function relationships: The potential for practical monitoring applications. *Estuarine, Coastal and Shelf Science*, *161*, 46–64. https://doi.org/10.1016/j.ecss.2015.04.008

Stuart-Smith, R. D., Bates, A. E., Lefcheck, J. S., Duffy, J. E., Baker, S. C., Thomson, R. J., Stuart-Smith, J. F., Hill, N. A., Kininmonth, S. J., Airoldi, L., Becerro, M. A., Campbell, S. J., Dawson, T. P., Navarrete, S. A., Soler, G. A., Strain, E. M. A., Willis, T. J., & Edgar, G. J. (2013). Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature*, *501*(7468), 539–542. https://doi.org/10.1038/nature12529

Tillin, H. M., Hiddink, J. G., Jennings, S., & Kaiser, M. J. (2006). Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Marine Ecology Progress Series*, *318*, 31–45. https://doi.org/10.3354/meps318031

Törnroos, A., & Bonsdorff, E. (2012). Developing the multitrait concept for functional diversity: Lessons from a system rich in functions but poor in species. *Ecological Applications*, *22*(8), 2221–2236. https://doi.org/10.1890/11-2042.1

Törnroos, A., Bonsdorff, E., Bremner, J., Blomqvist, M., Josefson, A. B., Garcia, C., & Warzocha, J. (2015). Marine benthic ecological functioning over decreasing taxonomic richness. *Journal of Sea Research*, *98*, 49–56. https://doi.org/10.1016/j.seares.2014.04.010

Trindade-Santos, I., Moyes, F., & Magurran, A. E. (2020). Global change in the functional diversity of marine fisheries exploitation over the past 65 years. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1933), 20200889. https://doi.org/10.1098/rspb.2020.0889

Ulman, A., & Pauly, D. (2016). Making history count: The shifting baselines of Turkish fisheries. *Fisheries Research*, *183*, 74–79. https://doi.org/10.1016/j.fishres.2016.05.013

Vackár, D., Brink, B., Loh, J., Baillie, J. E., & Reyers, B. (2012). Review of multispecies indices for monitoring human impacts on biodiversity. *Ecological Indicators*, *17*, 58–67.

van Denderen, P. D., Bolam, S. G., Hiddink, J. G., Jennings, S., Kenny, A. J., Rijnsdorp, A. D., & van Kooten, T. (2015). Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. *Marine Ecology Progress Series*, *541*, 31–43. https://doi.org/10.3354/meps11550

Villeger, S., Mason, N. W., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, *89*(8), 2290–2301. https://doi.org/10.1890/07-1206.1

Violle, C., Thuiller, W., Mouquet, N., Munoz, F., Kraft, N. J. B., Cadotte, M. W., Livingstone, S. W., & Mouillot, D. (2017). Functional rarity: the ecology of outliers. *Trends in Ecology & Evolution*, *32*(5), 356–367. https://doi.org/10.1016/j.tree.2017.02.002

Wahl, M., Link, H., Alexandridis, N., Thomason, J. C., Cifuentes, M., Costello, M. J., da Gama, B. A. P., Hillock, K., Hobday, A. J., Kaufmann, M. J., Keller, S., Kraufvelin, P., Krüger, I., Lauterbach, L., Antunes, B. L., Molis, M., Nakaoka, M., Nyström, J., bin Radzi, Z., … Lenz, M. (2011). Re-structuring of marine communities exposed to environmental change: A global study on the interactive effects of species and functional richness. *PLoS One*, *6*(5), 3–5. https://doi.org/10.1371/journal.pone.0019514

Wang, Z., Leung, K. M., Sung, Y. H., Dudgeon, D., & Qiu, J. W. (2021). Recovery of tropical marine benthos after a trawl ban demonstrates linkage between abiotic and biotic changes. *Communications Biology*, *4*(1), 1–8. https://doi.org/10.1038/s42003-021-01732-y

Wiedmann, M. A., Aschan, M., Certain, G., Dolgov, A., Greenacre, M., Johannesen, E., Planque, B., & Primicerio, R. (2014). Functional diversity of the Barents Sea fish community. *Marine Ecology Progress Series*, *495*, 205–218. https://doi.org/10.3354/meps10558

Willis, T. J., Millar, R. B., & Babcock, R. C. (2000). Detection of spatial variability in relative density of fishes: Comparison of visual census, angling, and baited underwater video. *Marine Ecology Progress Series*, *198*, 249–260. https://doi.org/10.3354/meps198249

Wong, M. C., & Kay, L. M. (2019). Partial congruence in habitat patterns for taxonomic and functional diversity of fish assemblages in seagrass ecosystems. *Marine Biology*, *166*(4), 46. https://doi.org/10.1007/s00227-019-3488-2

BIOSKETCH

Bede F. R. Davies is a researcher at the University of Plymouth who recently handed in his PhD thesis entitled: 'The Effectiveness of Partially Protected Marine Areas for Ecosystem Based Management'. Bede's work focusses on assessing the impacts to environments of different practices and processes, both anthropogenic and natural, including improving methodologies for detecting change, both through field research and analytical techniques. This work has ranged from Passive Acoustic Monitoring of the Marine Benthos to plastic pollution on the top of Mount Everest.

Author contrubutions: EVS and MJA conceived the ideas and monitoring design; EVS, LH and BFRD collected data; LH, AB and BFRD organized and analysed data; BFRD, EVS, AB and LH led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Davies, B. F. R., Holmes, L., Bicknell, A., Attrill, M. J., & Sheehan, E. V. (2021). A decade implementing ecosystem approach to fisheries management improves diversity of taxa and traits within a marine protected area in the UK. *Diversity and Distributions*, 00, 1–16. https://doi.org/10.1111/ddi.13451