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The Effectiveness of Partially Protected Marine Areas for Ecosystem Based Management

Davies, Bede Ffinian Rowe

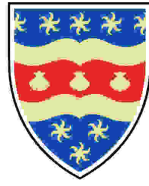
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UNIVERSITY OF
PLYMOUTH

**The Effectiveness of Partially Protected
Marine Areas for Ecosystem Based
Management**

by

Bede Ffinian Rowe Davies

A thesis submitted to the University of Plymouth
in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

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Authors declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Doctoral College Quality Sub-Committee. Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or at another establishment. Relevant scientific conferences were regularly attended at which work was often presented. One paper has been accepted for publication in a refereed journal and one is currently under review.

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Fieldwork, Video Analysis and Data Management:

Fieldwork The author participated in Lyme Bay Baited and Towed video fieldwork for the summers of 2018, 2019 and 2020.

Video Analysis The author was solely responsible for analysing all baited videos from 2009-2020. This created full consistency in analysis method and style throughout the Baited data. Quality control consisted of random selection of videos, re-analysis by other members of the team and comparison of data for both MaxN values and species identification.

Data Organisation The author organised all baited video data from raw data formats into a series of data bases within a research group repository. This involved converting data from per-minute relative abundances values into per video relative abundance values. These data were then combined into a large database of all years, sites and treatments.

Word count for the main body of this thesis: 51,431

A handwritten signature in black ink, consisting of several fluid, overlapping strokes. The signature is positioned above the printed name.

Signed: Bede Ffinian Rowe Davies

Dated: 31/03/2021

Abstract

Thesis Title: The Effectiveness of Partially Protected Marine Areas for Ecosystem Based Management

Author: Bede Ffinian Rowe Davies

The oceans provide highly important benefits to humans, ranging from sustenance and travel to livelihoods and spiritual wellbeing to climate stabilisation. Yet, globally the use of the marine environment has been unsustainable with extensive pressure being applied either directly or indirectly. This has led to the degradation of almost all marine ecosystems, with no system considered pristine from the depths of the Marianas trench to the inshore seas. Destabilisation of the ocean systems is jeopardising their ability to slow down the effects of climate change. This destabilisation is being driven in part by unsustainable and destructive human practises, such as: overfishing, pollution, coastal development, deep sea mining and habitat destruction. To counteract the negative effects of these practises, spatial management of the marine environment is highly important. The most common form of marine spatial management is the creation of Marine Protected Areas (MPAs).

MPAs are being championed as a method to decrease negative impacts to marine systems, while also allowing a certain level of benefit to humans, with inclusion to legislation guidance from organisations such as: Convention on Biological Diversity (CBD), the International Union for the Conservation of Nature (IUCN) and European Union (EU: Marine Strategy Framework Directive and Water Framework Directive). MPAs can be highly varied in multiple ways: geographic extent, from tens of square metres to thousands of square kilometres; level of protection, from total prohibition of all activities to personal quotas for specific activities; enforcement, from heavy military enforcement to no enforcement and designation rationale, from fisheries and conservation to personal or spiritual. This variety in MPAs, alongside the inherent variability of the marine environment in which they are applied, makes the application and assessment of successful MPAs a significant challenge. Therefore, effective and efficient MPA assessment is highly important, not only to allow for the adaptive management of current MPAs but also to inform the best approach for implementing new MPAs elsewhere.

Here a model system, Lyme Bay in the United Kingdom, is used to assess non-extractive MPA monitoring methods. The system includes multiple management strategies, with differing geographical, temporal and protection scales; many of the details are unique to the location but could, if beneficial, be applied more widely throughout the United Kingdom (UK) and potentially the globe. University of Plymouth staff, students and volunteers have applied a range of monitoring methods yearly to assess different MPA effects since the summer of 2008. Discussed is the assessment of the methods themselves, some of the potential analysis techniques and the use of these techniques to assess the different management strategies within the model system.

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Nomenclature

Acoustic Complexity Index (ACI): The relative complexity of sound energy of a recording (McWilliam and Hawkins 2013, Gage and Axel 2014, Lillis et al. 2014, Staaterman et al. 2014).

Acoustic Entropy: The total acoustic energy of a recording (McWilliam and Hawkins 2013, Gage and Axel 2014, Lillis et al. 2014, Staaterman et al. 2014).

Acoustic Richness: The diversity of acoustic energy of a recording (McWilliam and Hawkins 2013, Gage and Axel 2014, Lillis et al. 2014, Staaterman et al. 2014).

Aichi Sustainability targets: A series of internationally agreed targets towards sustainability.

Akaike Information Criteria (AIC): Estimator of prediction error and thereby relative quality of statistical models for a given set of data.

Attraction Range (AR): The maximum distance an organism could have been from the Baited Remote Underwater Video system while still managing to react to the bait and appear on the camera within the deployment time.

Baited Remote Underwater Video system (BRUVs): Underwater video survey method to assess mobile species' relative abundance, whereby a bait source is within the field of view of the camera.

Benthic: Relating to or occurring at the seabed.

Bernoulli Distribution: A Bernoulli distribution is a discrete probability distribution for a Bernoulli trial — a random experiment that has only two out-

comes (usually called a “Success” or a “Failure”). Where the probability of success is defined (p):

$$f(x; p) = px + (1 - p)(1 - x)$$

Beta Distribution: A family of continuous probability distributions defined on the interval $[0, 1]$. Where two shape parameters are defined (α & β):

$$f(x; \alpha, \beta) = \frac{x^{\alpha-1}(1-x)^{\beta-1}}{B(\alpha, \beta)}$$

where $B(\alpha, \beta) = \frac{\Gamma(\alpha)\Gamma(\beta)}{\Gamma(\alpha+\beta)}$ and $\Gamma(x) = (x-1)!$

Binomial Distribution: A probability distribution that summarizes the likelihood that a value will take one of two independent values under a given set of parameters or assumptions. Where the number of trials (n) and probability of success (p) are defined:

$$f(x, n, p) = \binom{n}{x} p^x (1 - p)^{n-x}$$

Biomass: The biological mass of a group or groups of individual species.

Biophony: The biologically produced elements of the soundscape.

Biotope: The region of a habitat associated with a particular ecological community.

Bottom Towed Fishing: Like Mobile Demersal Fishing, is a group of fishing methods that tow fishing equipment behind a vessel or vessels along the seafloor, such as scallop dredging or trawling.

Bray-Curtis Dissimilarity: Similarity/Dissimilarity metric often used on abundance data. Bray-Curtis dissimilarity between community i and j (BC_{ij}) where C_{ij} is the sum of only the lesser counts for each species found in both communities, S_i is the total number of species in community i and S_j is the total number of species in community j :

$$BC_{ij} = 1 - \frac{2C_{ij}}{S_i + S_j}$$

Bycatch: The incidental capture of non-target species.

Calibration lasers: Parallel lasers used to quantify the field of view area or measure the size of specific objects of interest.

Catch Per Unit Effort (CPUE): The total catch standardised by the amount of effort used to take that catch.

Conductivity Temperature Depth (CTD): Sensors used to measure temperature, conductivity and pressure. This then enables Depth to be calculated.

Convention of Biological Diversity (CBD): A convention with three main goals: the conservation of biological diversity; the sustainable use of its components; and the fair and equitable sharing of benefits arising from genetic resources.

Demersal: Something living or being close to the seabed.

Density: Number of Individuals per unit area or volume.

Department for Environment, Food and Rural Affairs (Defra): UK government department responsible for safeguarding the natural environment, supporting food and farming industry, and sustaining rural economy.

Digital SpectroGrams (DSG): Low-power acoustic recorders.

Distance Matrices: Symmetrical matrices populated by pairwise similarities or dissimilarity sites or groups of data, based on similarity or dissimilarity metrics. (See Bray-Curtis Dissimilarity and Euclidean Distance.)

Diurnal: A daily pattern.

Drop Camera: Simple underwater camera system dropped over the side of a vessel, which can have other recording equipment attached.

DSG2wav: Computer software to convert acoustic recordings to .wav files.

Ecosystem Approach to Fisheries Management (EAFM): An integrated management approach across coastal and marine areas and their natural resources that promotes conservation and sustainable use of the whole ecosystem.

Ecosystem Function: The capacity for natural processes and components to provide goods and services that satisfy human needs, either directly or indirectly.

Ecosystem Services: The benefits provided by ecosystems that contribute to human well-being.

Ecotourism: Tourism that is directly related to the quantity or quality of a natural resource.

Epibenthic: Organisms living on or near the seabed.

EU: European Union.

Euclidean Distance: Similarity/Dissimilarity metric often used on environmental data. Derived from Pythagoras' theorem: $A^2 = B^2 + C^2$ where Euclidean distance between $B_{xy...i}$ and $C_{xy...i}$ equals:

$$A = \sqrt{(B_x - C_x)^2 + (B_y - C_y)^2 + \dots (B_i - C_i)^2}$$

European Commission (EC): The executive branch of the European Union, responsible for proposing legislation, implementing decisions, upholding the EU treaties and managing the day-to-day business of the EU.

European Union Marine Strategy Framework Directive: A European directive aimed at achieving or maintaining good environmental status in European seas.

European Union Water Framework Directive: A European directive, which commits European Union member states to achieve good qualitative and quantitative status of all water bodies by 2015.

Feature Based Approach: Marine Spatial Management method where the protection serves to decrease or prohibit activities that endanger the integrity of a single feature of interest, specifically for the evidenced extent of the feature.

Field of View (FOV): Area shown by camera.

Fisheries: The collective noun for a group that extract species from the sea for sustenance or livelihood.

Functional Divergence: A univariate metric that enumerates how much abundance is attributed to rare traits within the multidimensional trait space occupied by a community of species (Villegger et al. 2008, Laliberté and Legendre 2010).

Functional Diversity: Generic term for the diversity of functional traits within a community.

Functional Evenness: A univariate metric that enumerates how evenly distributed abundance values are within the multidimensional trait space occupied by a community of species (Villegger et al. 2008, Laliberté and Legendre 2010).

Functional Redundancy: The amount of overlap in functional traits within the community (Micheli and Halpern 2005, Guillemot et al. 2011, Ricotta et al. 2016).

Functional Richness: A univariate metric that enumerates the multidimensional trait space occupied by a community of species (Villegger et al. 2008, Laliberté and Legendre 2010).

Gamma Distribution: A maximum entropy probability distribution where the values are greater than 0. Where a shape (α) and rate (β) parameter are defined:

$$f(x; \alpha, \beta) = \frac{\beta^\alpha x^{\alpha-1} e^{-\beta x}}{\Gamma(\alpha)}$$

where $\Gamma(x) = (x-1)!$

Gaussian Distribution: A type of continuous probability distribution for a real-valued random variable. Often referred to as the normal distribution. Where the probability function ($f(x)$) can be calculated from the mean (μ) and standard deviation (σ):

$$f(x) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{1}{2}\left(\frac{x-\mu}{\sigma}\right)^2}$$

Generalised Linear Mixed Effect Modelling (GLMM): An extension to the generalized linear model (GLM) in which the linear predictor contains random effects in addition to the usual fixed effects.

Generalised Linear Model (GLM): A flexible generalization of ordinary linear regression that allows for response variables that have error distribution models other than a normal or Gaussian distribution.

IUCN: International Union for the Conservation of Nature.

Keystone Species: Species that play a pivotal role in an ecosystem, meaning decreases or increases in their abundances can significantly alter the rest of the system.

Linear Regression: Method of modelling the relationship between a scalar response and one or more explanatory variables.

Marine and Coastal Access Act 2009 (MCAA): An act of the UK parliament, to make provision in relation to marine functions and activities within England and Wales.

Marine Conservation Zones (MCZs): Marine Protected Areas designated within English waters designated under the Marine and Coastal Access Act 2009.

Marine Renewable Energy Installations (MREI): Renewable energy that is installed and operated at sea and requires access to offshore grid and distribution systems.

MaxN: Maximum number of individuals seen on screen simultaneously, a measure of relative abundance derived from BRUVs.

Mobile Demersal Fishing: Like Bottom Towed Fishing, is a group of fishing methods that tow fishing equipment behind a vessel or vessels along the seafloor, such as scallop dredging or trawling.

Mono-BRUVs: A single camera Baited Remote Underwater Video system.

MPA: Marine Protected Area.

Multibeam sonar: Method similar to sidescan sonar, to assess the complexity of the seabed using acoustic backscatter.

Natura 2000 agreement: Network of protected areas developed under the European Commission's Habitats Directive (92/43/EEC) and Birds Directive (79/409/EEC). It forms the cornerstone of the European Union's biodiversity policy.

Nekton: Aquatic organisms that are able to swim and move independently of water currents.

No Take Zones: Marine Protected Areas where no extractive activities are allowed.

non-metric Multi-Dimensional Scaling: Method of ordination to display multivariate data in a two dimensional plane.

Open Controls (OC): Survey sites deemed to be comparable in their composition depth and other physical characteristics but are not protected.

Paper Park: A legally established protected area where experts believe current protection activities are insufficient to halt degradation.

Paper Reserve: See Paper Park.

Partially Protected Zones: Marine Protected Areas where certain extractive activities are permitted and others are prohibited.

Passive Acoustic Monitoring (PAM): Continuous or duty cycle acoustic recorders.

Pearson Correlation: Method for displaying the correlation between two univariate metrics.

Permutational Multivariate Analysis of Variance (PERMANOVA): Analysis method to assess multivariate data.

Pielou's Index (J): The evenness of abundance spread across all species calculated from Shannon's Index of Diversity (H' see below) divided by the natural log of the number of species (s):

$$J = \frac{H'}{\ln s}$$

Poisson Distribution: A probability distribution that can be used to show how many times an event is likely to occur within a specified period of time. Where the variance (γ) is defined:

$$f(x; \gamma) = \frac{\gamma^x e^{-\gamma}}{x!}$$

R: A statistical programming language.

Recruitment Subsidy: Larval export from a nearby Marine Protected Area.

Recruitment: The process by which an individual becomes an adult of a population.

Reef Life Survey (RLS): International collaboration to carry out volunteer diver surveys to produce scientific quality data.

Remote Sensing: The process of detecting and monitoring the physical characteristics of an area by measuring its reflected and emitted radiation at a distance (typically from satellite or aircraft).

Reserve: Here, a synonym for Marine Protected Area.

Root Mean Square: Acoustic entropy metric calculated using the root mean square of specific frequency bands.

SCUBA: Self-Contained Underwater Breathing Apparatus.

Shannon's Index (H'): Sometimes called Shannon-Weiner's diversity metric is a metric of diversity calculated from the sum of the proportion of abundance of each species (n_i) compared to the total number of individuals (N) from all species (s) in a community. Where the proportion (p_i) for each species (i) in the community is calculated as $p_i = \frac{n_i}{N}$:

$$H' = - \sum_{i=1}^s p_i \ln p_i$$

Sidescan sonar: Equipment that surveys the seafloor complexity using the backscatter of underwater acoustics.

Similarity Percentage (SIMPER): Method to assess the average percent contribution of individual variables to the dissimilarity between objects in a dissimilarity matrix.

Similarity/Dissimilarity Metrics: Suite of metrics that describe how similar to groups or sites of data are. Used extensively within multivariate data analysis.

Simpson's Index (D): Metric of diversity with more weighting for more dominant or common species from the inverse of the sum of the squared proportion of each species abundance (n) compared to the total number of individuals (N) from all species (s) in a community. Where the proportion (p_i) for each species (i) in the community is calculated as $p_i = \frac{n_i}{N}$:

$$D = \frac{1}{\sum_{i=1}^s p_i^2}$$

Site of Community Importance (SCI): Area proposed to the European Commission by the State Members and once approved can be designated as SACs.

Sound Pressure Level: Absolute acoustic energy from all frequency bands.

Soundscape: The combination of all sounds in the area.

Special Areas of Conservation (SAC): Marine Protected Areas created across the European Union.

Special Protection Areas (SPA): Protected Areas created across Europe specifically for the protection of birds.

Species Richness: The number of different species recorded.

Spillover: The process by which Marine Protected Areas lead to increases in abundance of species outside the area.

Stakeholders: The collective noun for all parties who contribute to and benefit from an area.

Statutory Instrument (SI): The principal form in which delegated legislation is made in the UK.

Stereo-BRUVs: Dual camera Baited Remote Underwater Video systems.

Target Species: Species actively sought after.

Taxonomic Distinctness: Univariate metric based upon the taxonomic distance between species or taxa.

Towed Underwater Video Survey (TUVS): Underwater videography towed behind a vessel to record species or habitats.

Trophic Cascade: When a species or group of organisms go past a threshold of abundance meaning there is a significant knock-on effect throughout the foodweb.

UK: United Kingdom of Great Britain and Northern Ireland.

Underwater Video Survey (UVS): Assessment by videography to quantify the distribution, species richness, abundance or organismal size distribution of the environment.

Underwater Visual Census (UVC): Assessment by either SCUBA or snorkelling to quantify the distribution, species richness, abundance or organismal size distribution of the environment.

University of Plymouth Marine Institute : Institute within the University of Plymouth specialising in marine and maritime subjects.

Vessel Monitoring Scheme (VMS): Method to record vessel movements over time and space.

Whole-Site Approach: Marine Spatial Management method where the site is protected rather than a single species or habitat.

Wildlife and Countryside Act 1981: An act of the UK parliament implemented to comply with the European Council Directive 2009/147/EC, which protects animals, plants and habitats.

Zero-Inflated Poisson (ZIP): Pertaining to a modelling approach that overcomes issues of overdispersion from data with excessive zero counts. Splits model into two. Firstly, assessing "success" or "failure" (see Bernoulli Distribution), then assessing, if "success", what change there is in the count (see Poisson Distribution).

"I was so busy making maps, I let them argue."

Marie Tharp

1

Introduction

1.1 Background

Humans have impacted the globe so significantly over recent decades that the current geological epoch has been classified as the Anthropocene (Crutzen 2006, Steffen et al. 2020). The most widely documented of these impacts, climate change (Zhang et al. 2015), caused by the increase of greenhouse gases absorbing solar radiation (Berger and Tricot 1992, Hertzberg et al. 2017), will certainly impact humans extensively in the coming decades (Schal-

egger et al. 2010, Princiotta 2011). The impacts will come in different forms and vary considerably over temporal and geographical scales (Giorgi and Mearns 1991). Impacts on the ocean from global climate change include ocean warming (Mertens et al. 2015, Connell et al. 2017), alterations to currents (Barcikowska et al. 2018), sea level rise (Moore et al. 2011, 2013), ocean acidification (Pimentel et al. 2016), sea ice loss (Screen et al. 2018), marine heat waves (Cheung and Frölicher 2020), hypoxia events (Du et al. 2018) and increases in frequency and intensity of extreme weather events (Xie et al. 2015).

The health of marine systems will be under increasing pressure, as many impacts of global climate change are felt and, in some cases, buffered or regulated by the oceans (Armour et al. 2016, Trossman et al. 2016), such as CO₂ and heat absorption (Jiao et al. 2018, John 2018). As such, marine systems will be more vulnerable to other impacts, whether anthropogenic (Halpern et al. 2015) or natural (Frölicher and Laufkötter 2018). Global fisheries consistently show evidence of overexploitation and have caused impacts on ecosystems globally, ranging from biodiversity loss to large shifts in species and ecosystem composition, which in turn leads to extensive trophic disruption (Worm et al. 2009, Ye et al. 2013).

Shifts in species composition can be caused by selective removal of large species (Cheung et al. 2005), as larger species or individuals are often highly important for ecosystem trophic dynamics, and selection by fishing will heavily decrease the abundance of keystone species (Valls et al. 2015). Keystone species are generally defined as species which will have a greater impact on an ecosystem when their abundance increases or decreases in comparison to other species (Valls et al. 2015). Selected removal of these highly important species by fisheries can, in extreme cases, lead to trophic disruption and even

trophic cascades, which rapidly change a whole ecosystem (Daskalov 2002, Bieg and McCann 2020). As larger individuals are generally older, removal of these individuals will increase the probability that only younger, or smaller, individuals will successfully breed (Berkeley et al. 2004). This pressure can select for both smaller individuals and individuals that reach sexual maturity quicker, or at smaller body size (Davis 1981, Uusi-Heikkilä 2020). Thus, selection of larger individuals can change a population's breeding and size dynamics, and can alter whole ecosystem trophic dynamics (Sinclair et al. 2002, Hutchings and Reynolds 2004). This is known as top-down trophic disruption.

Not only can fisheries cause top-down trophic disruption but they can also drive bottom-up changes (Allen and Clarke 2007). Fisheries often employ highly destructive methods for harvesting target species, such as mobile demersal fishing (Atkinson et al. 2011). Destructive forms of fishing can completely alter the habitat found in a region over very small timeframes (Moran and Stephenson 2000). This habitat destruction can be via changing the substrate type (Freese et al. 1999), smothering of sessile benthic organisms by re-suspension of particulate matter (Hinz et al. 2009) or by physical destruction of often fragile ecosystem-building organisms (Rosenberg et al. 2003), such as polychaete tubeworms, coral reefs, maerl beds, seagrass beds or mangrove networks (Watling and Norse 1998, Hall-Spencer and Moore 2000, Vorberg 2000, Fox and Caldwell 2006). Once the habitat is fully altered, this will have large knock-on effects to higher trophic organisms that rely on the habitats and the species they support (Moran and Stephenson 2000).

In reality, even with the relatively large technological advances in recent years, most fishing methods have relatively low selectivity (Broadhurst 2000, Davies et al. 2009), as these methods capture sexually immature individuals (Doherty

et al. 2014), non-target and thus less valuable species (Wakefield et al. 2017) and endangered species (Werner et al. 2006, Bull 2007, Gray and Kennelly 2018). This can lead to high levels of bycatch, the incidental capture of non-target species, which will most likely be discarded back into the sea, dead or alive (Bellido et al. 2011). The capture of high levels of sexually immature individuals can heavily decrease population stability by decimating recruitment into the population. Recruitment failure events can cause large declines and even collapses in local or regional populations (Serchuk et al. 1996, Myers et al. 1997, Liu and De Mitcheson 2008). The non-target taxa caught as bycatch can include: sharks (Baum et al. 2003, Worm et al. 2013), rays (Brander 1981, Dulvy et al. 2014), turtles (Spotila et al. 2000, Lewison et al. 2004), cetaceans (Zeeberg et al. 2006, Reeves et al. 2013) and even seabirds (Žydelis et al. 2009, Pott and Wiedenfeld 2017). All of these taxa contain highly endangered, even near extinction, species (Gray and Kennelly 2018).

Due to fisheries contributing to the food security and health of 3.1 billion people (FAO 2016), concerns over the level of overfishing and how to mitigate the ecological effects of fisheries has led to a United Nations resolution to facilitate the elimination of overfishing by 2020 and the development of sustainable fisheries in developing states by 2030 (UN News Centre 2015). Generally, the sustainable development of a fishery resource is a rarity; historically this was due to the emphasis on a single or a few species (Freshwater et al. 2020). However, Ecosystem Based Fisheries' Management (EBFM) is becoming more widespread (Worm et al. 2009, Solandt et al. 2020).

EBFM is the holistic management of a fishery that prioritises the ecosystem over the individual target resource, whether fisheries, tourism or coastal habitats (Pikitch et al. 2004b, Curtin and Prellezo 2010, Katsanevakis et al. 2011),

meaning the management of all sectors are combined rather than separate. Therefore, it strives to avoid degradation to the habitat, minimise non-target species bycatch, protect endangered species and avoid trophic disruption (Crowder et al. 2008, Durante et al. 2020).

One of the most common implementations of EBFM is the creation of Marine Protected Areas (MPAs). MPAs are becoming increasingly popular and have been advocated in international sustainability goals, such as: Aichi Sustainability targets, Convention on Biological Diversity (CBD), the International Union for the Conservation of Nature (IUCN), European Union (EU) Marine Strategy Framework Directive and EU Water Framework Directive. Collectively these aim towards a specific goal: 30% protection of the marine environment by 2030 (Brander et al. 2020, O'Leary et al. 2016, Rees et al. 2020, Waldron et al. 2020, Zhao et al. 2020). There are many reasons why an area of the marine environment would be protected. Broadly speaking, MPAs are a tool to safeguard the nature of the area (Agardy 1994, Badalamenti et al. 2000, Lubchenco and Grorud-Colvert 2015). There have been many ways of achieving this goal, each of which can be split into three general techniques: protecting a specific species; protecting a habitat or protecting the biodiversity found in the habitat (Rees et al. 2012b). The method used to safeguard the nature of an area will depend heavily on the motives behind the protection at its inception and any subsequent goals, set out by the stakeholders (Maxwell et al. 2015). The most common motive for protecting an area is for resource management, specifically fisheries' management (Sumaila et al. 2000).

The adoption of MPAs by fisheries' management organisations has commonly resulted in an increase in density, biomass and average size of the target species (Palumbi 2002, Gell and Roberts 2003, Michelli et al. 2004, Sale et al.

2005). However, many MPAs were not created based on scientific knowledge on how to effectively attain a sustainable fish population (Halpern 2003). Many were instead created by political or social demand (Agardy 1994), with no difference in protection compared to non protected areas (Claudet et al. 2020). However, development of MPAs established to support sustainable resource use has increased the success rate, with Halpern (2003) finding that the creation of a reserve doubled density, almost tripled biomass and increased diversity and organism size by 20-30% across a range of different taxa (fish and invertebrate). Likewise, Edgar and Stuart-Smith (2014) found that 87 MPAs, with at least four out of five key features, displayed twice as many large fish species, five times more large fish biomass and fourteen times more shark biomass compared to fished areas. These five key MPA features were: no take, well enforced, old (>10 years), large (>100km²) and isolated by water or sand.

It has been suggested that when a protected area is well managed and effective it can lead to increases in fish biomass and diversity in neighbouring non-protected areas (Davis 1981, Rowley 1994, Dee Boersma and Parrish 1999, Roberts et al. 2005). This is often referred to as 'spillover' (Rowley 1994, Gell and Roberts 2003). Similarly, increased larval/egg export or 'recruitment subsidy' from MPAs into surrounding areas has been discussed (Grüss et al. 2011). However, these phenomena are hard to test for, and have therefore been harder to prove empirically (Rowley 1994, Stobart et al. 2009, Di Lorenzo et al. 2020). Yet, studies are increasingly finding 'spillover' effects in recent years, evident from increases in nearby fisheries' yields (Stobart et al. 2009, Di Lorenzo et al. 2016, Lenihan et al. 2021).

The most consistent factor that appears to deliver a successful MPA is effective

governance, from implementation through to dynamic maintenance (Kelleher 1999, Cicin-Sain and Belfiore 2005, Edgar and Stuart-Smith 2014). Yet, this can be heavily influenced by compliance of local communities, meaning MPAs need to provide tangible benefits to surrounding areas and not just meet conservation or industrial scale fisheries' targets (McClanahan et al. 2006, Bennett and Dearden 2014, Barreto et al. 2020).

Increasingly, the marine environment is being protected for resource management, where financial gain from a fishery is not the only resource (Sumaila et al. 2000, Alder et al. 2002, Edgar and Stuart-Smith 2014). Ecotourism is now a large contributing factor to local economies, especially in areas that are protected from certain fishing practices (Merino et al. 2009, Oberholzer et al. 2010). Therefore, creation of an MPA should take these elements into account when being designed and designated. As such, the design process should involve as many different stakeholders as possible to involve all interested parties and maximise compliance within the protected area.

1.2 Levels of Protection

MPAs can cover many varying levels of protection, all of which are related to the aims of the protected area and the priorities of the stakeholders involved (Lester and Halpern 2008). They can be no-take zones, where no fishing is allowed, or partially protected zones where certain activities are prohibited (Claudet 2018). The level of protection found in partially protected zones can vary considerably from restrictions on commercial fishing equipment (Campbell et al. 2018), tourist activity (Dee Boersma and Parrish 1999) or recreational fishing (Cooke and Cowx 2006, Veiga et al. 2013) to regulations on vessel specifications (Milazzo et al. 2004), marine infrastructure (Inger et al. 2009) or rotation of open

and closed fishing grounds (Williams et al. 2006).

The majority of studies that consider the level of protection of an MPA conclude that the inclusion of no-take or full protection is more effective at achieving conservation targets than partial protection alone (Lester and Halpern 2008, Edgar and Stuart-Smith 2014, Costello et al. 2015, Sala et al. 2018). However, conflicts of interest between stakeholders often make the establishment of no-take zones problematic (Bohnsack et al. 2004). Thus, the use of MPA networks with varying levels of protection, from no-take to open access, depending on the MPA objectives, has been suggested (Gell and Roberts 2003, Lester and Halpern 2008). A successful example of this could be the Great Barrier Reef Marine Park, which consists of multiple different 'zones' with differing levels of protection throughout these zones, where density, mean length and biomass of an exploited fish were found to be greater than at adjacent fished areas by Emslie et al. (2015).

1.3 Enforcement

Enforcement can be highly linked to the level of protection, as a lower level of protection is generally easier to enforce (Bohnsack et al. 2004). Yet, enforcement has been consistently shown to increase the success of an MPA (Claudet et al. 2006, Guidetti et al. 2008, Edgar and Stuart-Smith 2014, Di Franco et al. 2016). Hence, MPAs without effective enforcement are often referred to as 'paper parks' or 'paper reserves' (Mora et al. 2006, Pieraccini et al. 2017, Álvarez-Fernández et al. 2020, Rife et al. 2013b). An example of a 'paper park', as outlined by Rife et al. (2013a), is the Gulf of California, Mexico, where a cumulative area of over 20,000km² has been protected, yet has failed to meet fishery and conservation targets. The lack of enforcement has led to high levels of illegal

fishing throughout this MPA network with the authors describing it as 'rampant'. The presence of these 'paper parks' can heavily change outcomes of studies, especially meta-analyses, looking at MPA impacts (Rife et al. 2013a). As most MPA analyses use an inside versus outside approach to assess impacts, the inclusion of non-enforced MPAs, as 'inside', is confounding and should be treated as a different treatment (Kareiva 2006, Guidetti et al. 2008, Gallacher et al. 2016). Thus, sampling efforts to study MPA effects need to take into consideration not only the level of protection but also the enforcement throughout the different levels of protection.

1.4 Monitoring Methodologies

To properly assess the effectiveness of an MPA and how to dynamically manage the area, temporally and spatially replicated monitoring following a robust sample design needs to be carried out (Claudet et al. 2006, 2010, Claudet and Guidetti 2010). However, this has not always been the case for many MPAs globally (Ahmadi et al. 2015). Yet, even as robust monitoring of MPAs increases, so does the number of different monitoring methodologies (Mascia et al. 2014, Hill et al. 2018), both in the field for data collection (Di Lorenzo et al. 2016) but also the way that this collected data is interpreted to assess specific ecological processes (Pelletier et al. 2005, Claudet et al. 2006). Adaptive management is vital for appropriately managing MPAs so that they can achieve their conservation and fisheries goals, which means that the ability to monitor these targets is equally important. Therefore, the methods for data collection and how that data is interpreted is highly important for how management can be carried out.

1.4.1 Data Collection

The most widely used data collection methods, set out by [Murphy and Jenkins \(2010\)](#), are Underwater Visual Census (UVC: [Sale and Douglas 1981](#), [Barrett and Buxton 2002](#), [Edgar et al. 2005](#), [Edgar and Stuart-Smith 2014](#)), Underwater Video Survey (UVS: [Malcolm et al. 2007](#), [Sheehan et al. 2010](#), [2013a,a](#), [Stevens et al. 2014](#)), remote sensing ([Elvidge et al. 2004](#), [Palacios et al. 2006](#), [Scopélitis et al. 2010](#)), underwater acoustics ([Kaplan et al. 2015](#), [Bertucci et al. 2016](#)), experimental fishing data ([McClanahan and Mangi 2000](#), [Kaunda-Arara and Rose 2004](#)) and fisheries data ([Schroeder and Love 2002](#), [Murphy and Jenkins 2010](#)).

Underwater Visual Census

Underwater Visual Census (UVC) is the assessment by either SCUBA or snorkelling to quantify the distribution, species richness, abundance or organismal size distribution of the environment. This is normally carried out by: strip (belt) transect, where the diver estimates density of target species along a known distance and width ([Samoilys and Carlos 2000](#), [Colvocoresses and Acosta 2007](#)); line transect, where the diver swims along a line and estimates distance and swimming direction of organisms from the line; or point counts, where the diver stays still or sinks to a point, continually rotating and estimating target species density and length ([Samoilys and Carlos 2000](#), [Colvocoresses and Acosta 2007](#)). Strip transects are the most widely used, such as Reef Life Survey (RLS: [Edgar and Stuart-Smith 2009](#), [2014](#), [2009](#), [Reef Life Survey 2015](#), [Duffy et al. 2016](#), [Mourier et al. 2016](#), [Staaterman et al. 2017](#)), as they do not rely on the diver's ability to estimate distance underwater, which can heavily bias the metrics ([Harvey et al. 2004](#)).

Less common forms of UVC include: rapid visual technique (RVT), where the diver is not constrained to a transect but swims throughout the specific habitat, recording species-time data (Jones and Thompson 1978); quadrat transects, where quadrats are placed along transects then photographed or assessed in situ for sessile organism densities; line-intercept, which measures the transition from one habitat to another and line-point, which quantifies organisms under specific points along the transect.

Of all the UVC methods, line-point transects are the fastest to carry out (Murphy and Jenkins 2010), point count is the best method for counting mobile species, strip transects are the best for counting sedentary fish species (Buxton and Smale 2006) and RVT identifies a more complete species list but at lower abundance and density than point counts (Baron et al. 2004). Disadvantages of these censuses are that they rely heavily on: diver abilities of identification, enumeration and distance; diver depth and time limits, and that the records cannot be reanalysed after the dive unless an underwater video camera is also used alongside the diver.

Underwater Video Survey

Underwater Video Surveys (UVS) are often utilised when the area to be sampled is too deep or dangerous for divers to access, or the target species' behaviour will be influenced by diver presence (Cole 1994, Willis et al. 2000, 2003). Similarly, they can be deployed for much longer timeframes (battery and storage dependent). UVS can be a combination of stationary or mobile, baited or un-baited, mono or stereo, and diver held or remotely deployed (Murphy and Jenkins 2010, De Vos et al. 2014).

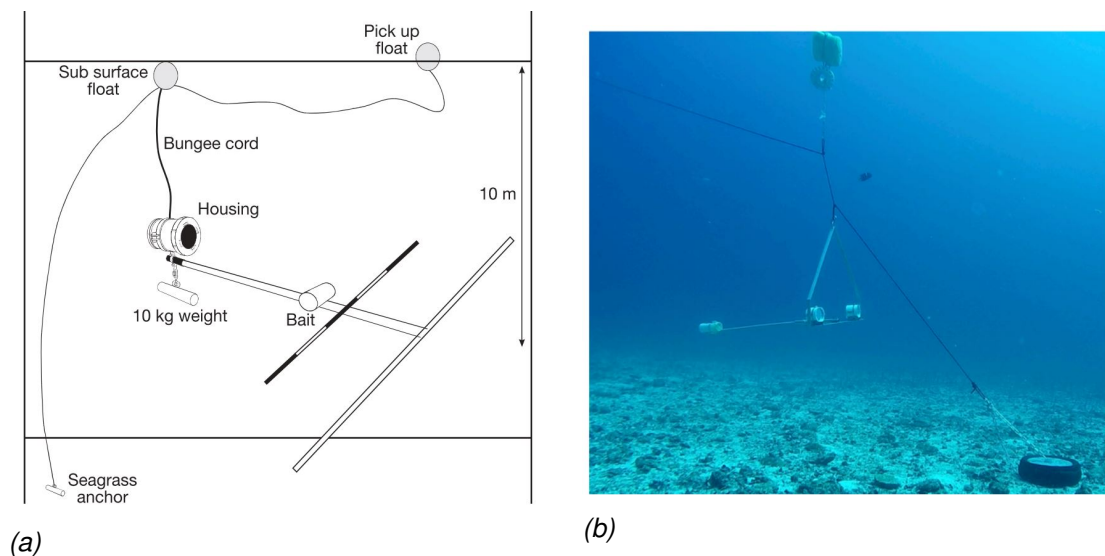


Fig. 1.1 Diagram of BRUVs (1.1(a): [Heagney et al. 2007](#)) and example of Stereo-BRUVs (1.1(b): [Acuña-Marrero et al. 2018](#)).

Baited Remote Underwater Video Systems Baited Remote Underwater Video systems (BRUVs) have been established as a non-extractive sampling method, with the ability to provide highly robust data and to sample a large proportion of the fish community ([Bernard and Götz 2012](#), [Cappo et al. 2003, 2004](#)), providing high statistical power when utilised within effective sampling designs ([Stobart et al. 2007](#)). The general set-up for a BRUVs is an underwater housing, containing a video camera, attached to a weighted frame with a pole extending from the camera to a receptacle containing bait (Fig. 1.1(a)). Hence, any organisms attracted to the bait will be in the field of view (FOV) of the camera. BRUVs produce relative abundance per unit time based on 'MaxN' values, the maximum number of individuals of a given species in a given time unit ([Cappo et al. 2003](#), [Stoner et al. 2008](#)). 'MaxN' is utilised to stop individuals being recorded multiple times, and, as such, is a conservative estimate of species' relative abundance ([Willis et al. 2003](#), [De Vos et al. 2014](#)).

Single camera BRUVs (mono-BRUVs) have had high popularity as a cost effective

tive, non-extractive and non-invasive sampling method, which samples species that may avoid diver surveys (Cole 1994, Willis et al. 2000, 2003). Furthermore, when deployed as stereo cameras (two converging cameras with a known distance calibration in the FOV; Fig. 1.1(b)), BRUVs can also provide highly accurate size data (Cappo et al. 2004, Malcolm et al. 2007, Watson et al. 2009, Acuña-Marrero et al. 2018). As such, stereo-BRUVs can be very useful for studying population size structure and dynamics of large mobile fish species (Cappo et al. 2004, Parker et al. 2016). Likewise, bespoke mono-BRUVs can be used to estimate fish size but may require added equipment or decrease the proportion of the useable FOV (Willis et al. 2003, Denny and Babcock 2004, Heagney et al. 2007, Stobart et al. 2007).

However, BRUVs are heavily biased towards larger piscivorous predators or scavengers that are attracted to the specific bait being used (Watson et al. 2009). The comparability of studies could be confounded by the difference in type, quantity and freshness of the bait. Commonly used bait types include mackerel *Scomber scombrus* (Priede et al. 1994, Stevens et al. 2014), pilchards *Sardinops neopilchardus* (Cappo et al. 2004, Malcolm et al. 2007, Hill et al. 2018), yellow fin tuna *Thunnus albacares* (Acuña-Marrero et al. 2018) and sardines *Sardinops sagax* (Stobart et al. 2007, Watson et al. 2009, De Vos et al. 2014), with quantities ranging from 100g to 1kg. Type, quantity and age of bait may also affect the plume dynamics, although localised currents will be much more influential (Watson et al. 2009). As such, local conditions confine BRUVs to produce relative values for density or biomass, so comparability between differing protocols can be problematic, even when used consistently (Watson et al. 2009).

There are a range of assumptions and limitations when using BRUVs to assess

mobile benthic communities. These themes can be split into three elements: practicalities of video collection and analysis; behavioural assumptions of organisms; physical conditions, and the interaction of these three elements. To get data from BRUVs the first hurdle is being able to record the video itself. This is highly dependent on prevalent weather conditions for safe fieldwork, such as wind and swell intensity. The second hurdle is being able to collect useable and useful videos, which is also highly linked to weather. For example, high wind or wave activity will lead to resuspension of particulate material in the water column even after a few days of fine weather rendering all videos unusable. Likewise, planktonic blooms will cause similar issues with visibility. Therefore, when using BRUVs in UK waters, months from June to August are the most ideal for fieldwork. This in itself has ramifications for any seasonal variation or behavioural patterns, such as changes in assemblage due to mating, spawning or migration patterns. However, to study trends of mobile fauna over larger temporal scales, this consistency will control for any season variation. Once a viable video is recorded, assuming no organism or physical structure is obscuring the view, the species attracted to the bait or incidental around the camera can then be enumerated. Yet, behaviour of individuals and species will influence the presence or absence and, if present, the abundance of species. Whether, organisms are attracted to the bait will influence their appearance on a BRUVs video but potentially so will the presence of other species or individuals near the bait, such as a predator or dominant member of the same species. These inter and intra specific behavioural interactions will potentially give elevated or diminished relative abundances of the species involved. The area of attraction of each individual BRUV will be dependant on the combination of local currents and passive diffusion to move the bait plume. The likelihood of an individual of a specific species being then recorded on the BRUV will be dependent on them

encountering the bait plume, their ability to detect the bait plume, the decision (conscious or subconscious) of the individual to move (swim or crawl etc.) towards the bait source and their speed allowing them to arrive in the FOV before the video finishes.

Towed Underwater Video Survey Towed underwater video survey (TUVS) has been utilised to assess the marine benthos since the middle of the 20th century (Machan and Fedra 1975). However, many of these early cameras were attached to trawls or dredges, often used to assess the efficiency of the method (trawl or dredge sampling) or to provide extra habitat data of the wider area surrounding grab samples. Subsequent developments in towed underwater video were used to validate habitats and biotopes mapped by acoustic techniques (e.g. Sidescan sonar) or aerial photography of littoral systems (Sotheran et al. 1997).

The main systems for deploying towed video to carry out transects of the benthic environment are: dragged sleds, which drag along the sea floor (Fig. 1.2) (Holme and Barrett 1977, Rosenkranz and Byersdorfer 2004, Spencer et al. 2005, Stoner et al. 2007); suspended sleds, which are kept floating just above the seafloor (Barker et al. 1999, Kenyon et al. 2006, Sheehan et al. 2010, 2016) and drop cameras, which are small self-contained cameras that can be deployed by hand (Lauth et al. 2007, Rooper 2008). A dragged or 'benthic contacting sled', is the most used but is restricted to homogenous seafloors and has been shown to heavily impact the seabed (Sheehan et al. 2016).

The dragged sled generally consists of a weighted frame on parallel runners, with a forward and slightly down-facing, camera and lights attached (Rosenkranz and Byersdorfer 2004), although they can be equipped with other sampling devices such as 'Tickler Chain' (Spencer et al. 2005, Stoner et al. 2007), FOV cal-

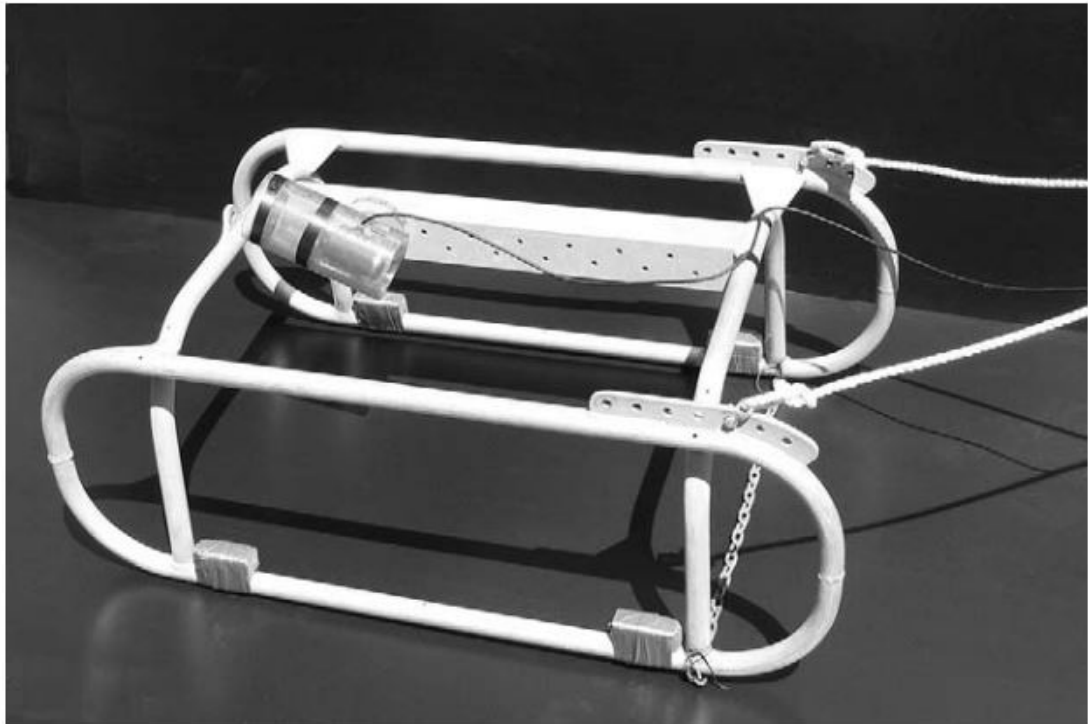


Fig. 1.2: Sled TUVS with tickler chain to disturb flatfish (Spencer et al. 2005).

ibration lasers (Rooper 2008) and physical oceanographic data loggers (Lauth et al. 2007).

Drop cameras are simpler, consisting of a camera in a metal protective frame. The camera is downwards facing and designed to drift with the currents (Rooper 2008). However, as with all of the TUVS, extra equipment can be attached (extra cameras, depth loggers or Conductivity Temperature Depth CTD sensors). Yet, this will increase the weight of the apparatus and thus detract from its main attraction: it can be deployed by hand.

Suspended towed arrays can range in their size and deployment style. Again, it follows the general TUVS pattern, of a camera in a frame, with any extra equipment the survey requires (Rooper 2008). However, suspended arrays also contain flotation devices to keep positively buoyant with an added weighted chain. The combination of the weighted chain and the positive buoyancy means

it will float at a desired distance from the seabed (Barker et al. 1999, Sheehan et al. 2010, Stevens et al. 2014). The use of a chain means that, although far less destructive, suspended TUVS still have a chain dragging along the seabed (Sheehan et al. 2016). Therefore, when a highly sensitive area is to be sampled, a diver 'towboard' can be used, where a diver moves with the cameras and maintains a safe distance from the seabed with all equipment (Kenyon et al. 2006).

All TUVS methods have advantages and disadvantages. Generally, data recorded will be limited by the specification of the cameras used (Sheehan et al. 2016); simple protocol adjustments can minimise this issue, yet the methods are still limited to individuals large enough to be visible and epifauna. Assuming a mid-range HD camera (720p Resolution), the issues can be addressed by the use of: lights in lowlight situations; low vessel/drag speeds; appropriate buoyancy/weighting to maintain frame stability, and parallel lasers to calibrate FOV size. Individual methodologies have their own considerations, such as the impact to the seabed, the financial cost to create and the lifting power necessary for deployment.

These methods have the distinct advantage over many census and physical catch surveys in that the video recording can be kept, reanalysed and shared long after the survey has taken place. Yet, the time and specialist knowledge needed to analyse the video can be considerable.

Remote Sensing Imagery

Satellite available Remote Sensing has been frequently used in the monitoring of terrestrial landscapes, and has been suggested as a possible method for MPA monitoring too. Remote Sensing can be used to sample many abiotic

factors of an environment, which are then used to infer biodiversity processes. The measured factors are: bathymetry (Knudby et al. 2011, Rowlands et al. 2012), ocean colour (Elvidge et al. 2004, Palacios et al. 2006, Rowlands et al. 2008, Scopéritis et al. 2010), sea surface temperature (Purkis and Riegl 2005, Palacios et al. 2006), surface wind vectors (Risien and Chelton 2008) and sea surface height (Palacios et al. 2006).

These factors and how they interact with each other can be used to infer many processes and biotic factors indirectly (Kachelriess et al. 2014). Ocean colour has often been used as a measure of chlorophyll in the surface oceans and thus is used to monitor phytoplankton populations and those organisms that rely on phytoplankton for sustenance, such as: whale sharks, basking sharks or manta rays (Sequeira et al. 2012). Remote Sensing allows sampling over large temporal and spatial scales, and allows hard-to-reach locations to be sampled with high replication. However, due to its visual nature, Remote Sensing is limited to relatively shallow waters, cloudless days and requires ground truthing (Murphy and Jenkins 2010).

Acoustics

The use of acoustics to monitor MPAs can be split into three distinct groups, each with different focuses: habitat/biotope mapping; acoustic telemetry of specifically tagged species and Passive Acoustic Monitoring (PAM).

Habitat Mapping Unlike satellite or aerial photography, acoustic mapping of the habitat can be applied in deep water and over large areas, most commonly by sidescan or multibeam sonar (Fig. 1.3) . They transmit pulses of sound to the sea bed (Murphy and Jenkins 2010), with the reflected ‘backscatter’ describing seafloor texture and density (Fakiris et al. 2019). This method, just like

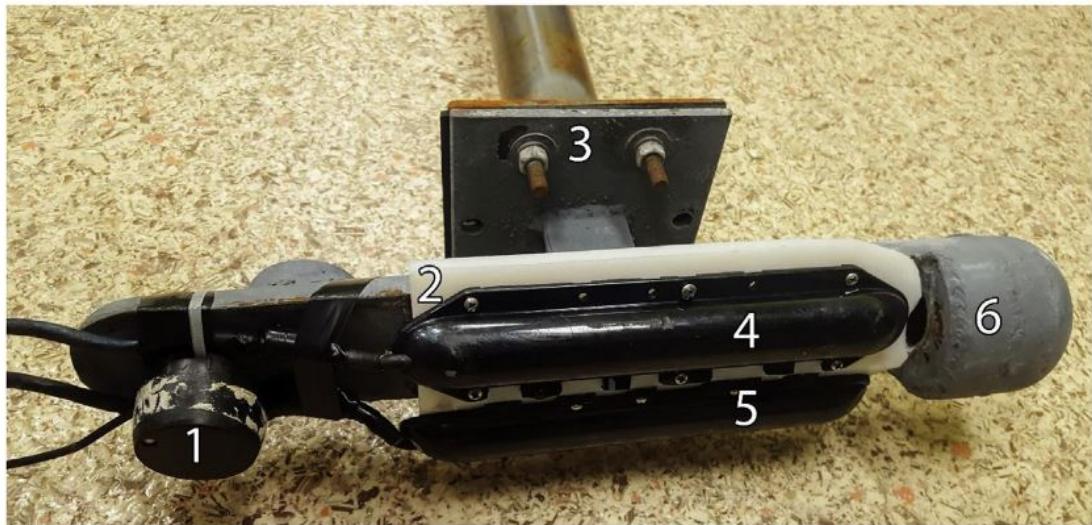


Fig. 1.3: Bow mounted Side Scan array from [Greene et al. \(2018\)](#). Numbered are the most important elements of the array 1- bathymetric sounder, 2- angled mount for transducers, 3- plate to attach to the bow, 4- starboard side scan transducer, 5- port side scan transducer and 6- smoothed 'head' to streamline flow over the transducers.

remote sensing imagery, relies on ground truthing of the different seafloor types to create a large scale habitat map. This process of ground truthing historically was carried out by grabs or point samples across the scanned area ([Pergent et al. 2017](#)). However, more recently, to negate damage caused by grabs or destructive point samples to sensitive habitats, video surveys or satellite Remote Sensing imagery have been used to 'ground truth' ([Lefebvre et al. 2009](#), [Smith et al. 2015](#), [Greene et al. 2018](#)). The process of mapping the seafloor acoustically, and subsequent 'ground truthing', can create a highly detailed and large biotope habitat map in a relatively small amount of time ([Anderson et al. 2007](#)).

Acoustic Telemetry Acoustic Telemetry consists of attaching tags to organisms of interest. Arrays of hydrophones are then set up in the area of interest. The tags will produce unique acoustic pings, which allow the hydrophones to track individuals (Fig. 1.4). This allows not only general trends in population



(a)



(b)

Fig. 1.4: V9 Transmitter or 'tag' (1.4(a)) and hydrophone (1.4(b)) to acoustically track sea bass (Vemco 2019).

movement to be tracked but also the movement of certain groups within the population (Lowe et al. 2003, Egli and Babcock 2004, Meyer et al. 2007). When the tag is attached, biometric information, such as size, sex and maturity, can be acquired, so that movements of specific age/size/maturity groups can be tracked. As the hydrophone arrays are deployed for long periods of time (multiple years depending on battery life), and tags can last similar timescales, this can allow high temporal resolution tracking over large temporal scales (Starr et al. 2005). These methods can inform management procedures, assess current protection measures and assess 'spillover' to surrounding areas (Zeller et al. 2003, Starr et al. 2005, Murphy and Jenkins 2010).

Passive Acoustic Monitoring Passive Acoustic Monitoring (PAM) is the recording of the marine soundscape, using post-processing to assess different elements of the ecosystem. The principle is relatively simple: a hydrophone is deployed, where it records the marine soundscape over pre-set specific frequency bands, schedules and timescales (Fig. 1.5). These recordings are

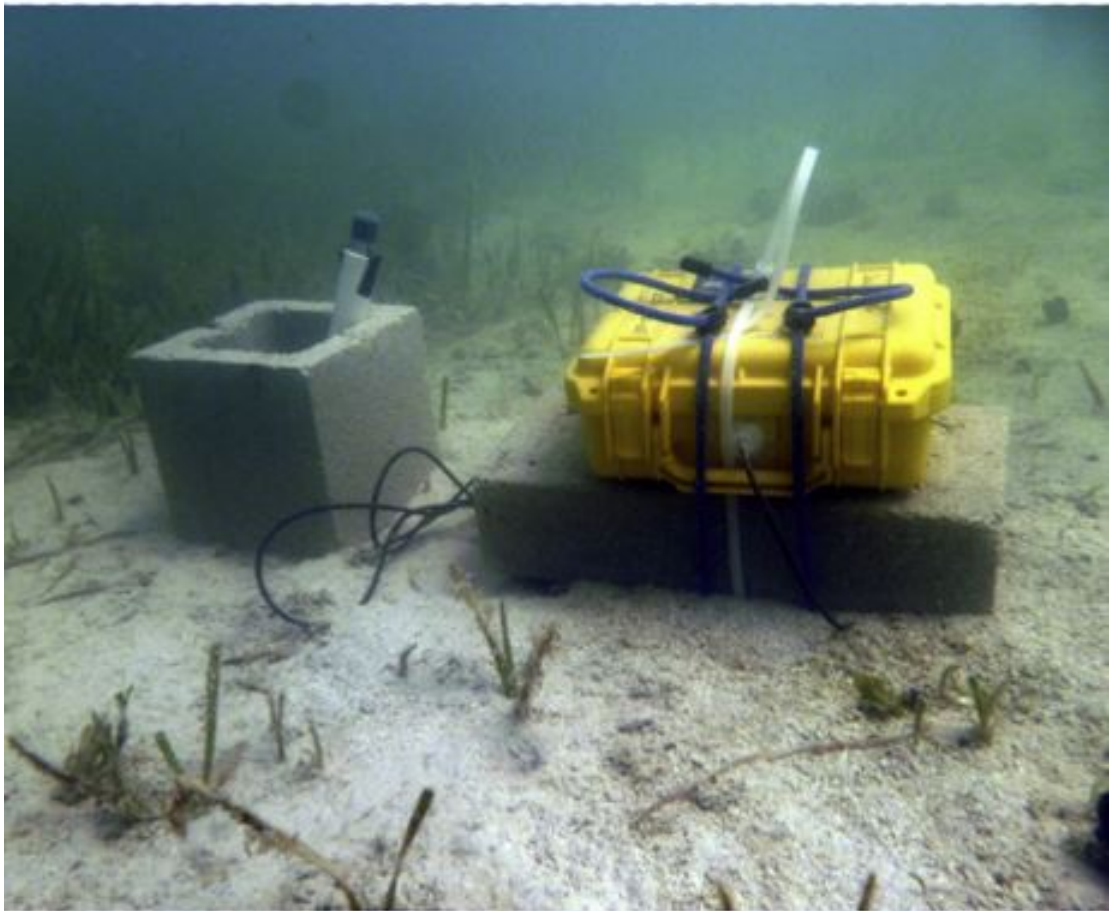


Fig. 1.5: Hydrophone deployed to sea floor for Passive Acoustic Monitoring (Butler et al. 2017).

then analysed by specific software or algorithms to create different metrics, which quantify elements of the soundscape of interest. PAM has been shown to describe biodiversity (Bertucci et al. 2016), courtship behaviour of certain fish (de Jong et al. 2018), habitat selection (Simpson et al. 2004, Vermeij et al. 2010, Barth et al. 2015), spawning (Hawkins and Amorim 2000, Casaretto et al. 2014) and predator-prey interactions (Nøttestad et al. 2002, Bernasconi et al. 2011, Giorli 2016, Giorli and Au 2017) .

Depending on the objectives of the study, post-processing of the recorded soundscape can specifically study one organism (Denes et al. 2014, Giorli

2016) or the whole soundscape (Kaplan et al. 2015, Bertucci et al. 2016). Single organism or group studies are restricted to those species that produce distinct and characteristic calls or songs, such as cetaceans (Samaran et al. 2013), snapping shrimp (Au and Banks 1998, Beng et al. 2003, Picciulin et al. 2013) or Gadoid fish: Atlantic Cod *Gadus morhua* and Haddock *Melanogrammus aeglefinus* (Radford et al. 2014). Whole soundscape analysis has been used to assess biodiversity (Bertucci et al. 2016, Harris et al. 2016), habitat biotopes (McWilliam and Hawkins 2013, Lillis et al. 2014) and anthropogenic noise pollution (Radford et al. 2014, Spiga 2016).

PAM is relatively easy to deploy and retrieve without any technical expertise needed. However, post-processing can be time intensive and requires specialist knowledge and software. This is partly due to the fact that underwater acoustic analysis, in relation to the biology of the ecosystem, is a relatively understudied discipline (Lillis et al. 2014). Yet, as research increases in the field, so does the number of indices that can infer biological characteristics of a whole ecosystem into one number (Harris et al. 2016), many of which can be processed utilising basic, open-source software and with less need for specialist training (PAMGuide: Merchant et al. 2015). However, there have been mixed results when showing correlations with these acoustic indices and the observed ecology (McWilliam and Hawkins 2013, Kaplan et al. 2015, Bertucci et al. 2016, Harris et al. 2016, Pieretti et al. 2017). This may be due to the differences in the taxa that the methods are potentially sampling (Staaterman et al. 2017) or the intensity of cycles found in the acoustic behaviours of specific organisms (Diurnal and lunar: Radford et al. 2014, Staaterman et al. 2014).

Physical Catch

Physically catching organisms, to assess populations or assessing what is already being caught and landed by fisheries, has been used extensively throughout fisheries' research. In recent years, the extraction of individuals from MPAs or fragile ecosystems has become less popular. Thus, analysing fisheries data can be more informative (Stobart et al. 2009). Yet, calculations to assess the amount of effort needed to catch a fish or catch per unit effort (CPUE) can be difficult. Furthermore, fisheries data will select for larger more profitable species and individuals, thus, not necessarily giving a full picture of the diversity or population structure.

Experimental fishing Experimental fishing surveys can either use traps, hook-and-line or trawling, and are carried out specifically for the experiment (Fig. 1.6). Standardised design and size of traps allows CPUE to be calculated, while population size and biomass can be calculated by catch and release tagging methods (Zeller et al. 2003). As hook-and-line is similarly less destructive to the individuals caught, depending on the species of interest and its resilience to capture, the same method of mark-recapture can also be employed to assess individual movements (Zeller et al. 2003), but has depth limitations. Hook-and-line CPUE can be calculated by standardising equipment, bait and time (Zeller et al. 2003, Götz et al. 2007). Similarly, trawl effort can be calculated when gear is standardised, and duration and depth of trawl are recorded (Depestele et al. 2016). Trawls are more selective of smaller demersal species, although less selective overall (Cappo et al. 2004), whereas hook-and-line and traps can be far more selective through their choice of bait and equipment design (Ralston 2008).



Fig. 1.6: Experimental trawl being deployed ([Katsanevakis et al. 2012](#)).

Fisheries On the whole, by virtue of MPAs excluding fisheries from certain areas, using fisheries' landings to assess MPAs is difficult. However, when the main objective of an MPA is to subsidise a nearby fishing area, assessing fisheries' data over time adjacent to an MPA may be a demonstration of 'spillover'. This is especially true if there is an increase in large bodied species and individuals in the fished area, as those species and individuals have been shown to be positively impacted by MPAs and selectively removed by fishing (Coleman et al. 2015).

Like experimental fishing, traps, hook-and-line and trawling may be the emphasis for fisheries-based catch data. This will rely heavily on the species being assessed. Often a fishery will be seasonally dominated by one or other of these techniques. To assess CPUE, fisheries will often use the amount of power used, or time taken, to catch a specific weight of fish. However, information on time under tow or power used can be hard to come by. Yet, in recent years, fisheries have started introducing Vessel Monitoring Systems (VMS), mostly on larger vessels. This allows distance travelled to be assessed but more specifically it allows behaviour of the boat to be analysed to estimate time under tow as opposed to time of steaming from one fishing ground to another (Dinmore et al. 2003, Murawski et al. 2005, Rijnsdorp et al. 2016).

1.4.2 Monitoring Indicators

Visual and Video Census

Depending on the aims and methodology of a monitoring scheme, different metrics will be more or less suitable, as such considerations must be made before choosing an appropriate indicator (Hayes et al. 2015, Hill et al. 2018). The most commonly used indicators for the monitoring of MPAS are abundance,

biomass, diversity indices (Species Richness, Shannon's Index and Pielou's Evenness, etc.) and mean size (Claudet et al. 2006). These indicators all display varying responses to impacted ecosystems, although most of the 'diversity' indices, Species Richness, Shannon's Index, Simpson's Index, Pielou's Index, rely heavily on the number of species recorded.

Some researchers use the abundance or biomass of specific 'indicator species' to highlight the effectiveness, or lack thereof, of the MPA to achieve its goals (Hill et al. 2018). However, this use of indicator organisms is often rooted in management of a specific resource, be it a target fishery species or a rare and fragile habitat type. As with EBFM being more effective than single species protection, so the assessment of a few individual species will not be able to indicate the fine-scale processes occurring within the MPA. These fine-scale changes are highly important for the effective management of the system.

Passive Acoustic Monitoring (PAM)

As with single number metrics, PAM is often assessed using individual metrics of the ecosystem soundscape, which define the diversity of a whole ecosystem to simplify the quantity of data often produced by surveys (Harris et al. 2016). These metrics have been tested alongside biodiversity measures from UVC and to try to relate elements of the acoustic output with the biota being surveyed by more historically used methods (Bertucci et al. 2015, 2016, 2017). The advantage is that indices produced from the soundscape can be quicker and easier to attain in terms of expertise and time (Pieretti et al. 2017). Indices such as, Acoustic Complexity Index, Acoustic Entropy and Acoustic Richness have gained popularity but are still understudied in most ecosystems, and can be heavily influenced by anthropogenic and biotic interference (McWilliam and Hawkins 2013, Gage and Axel 2014, Lillis et al. 2014, Staaterman et al. 2014).

Functional Trait Analysis

Within many of the objectives set out to manage MPAs using EBFM, recovery or maintenance of the ecosystem functioning and services is a high priority. Ecosystem function can be thought of as a complex system of interactions or individual functions, which combine to sustain the system as a whole, through multiple different processes (Jax 2005). As mentioned above, taxonomy based diversity is frequently used to monitor MPAs (Soykan and Lewison 2015, Starr et al. 2015, Ferreira et al. 2017). However, large changes in taxonomic biodiversity do not necessarily imply equally large changes to the ecosystem function (Solan et al. 2004, Törnroos and Bonsdorff 2012, Wong and Kay 2019), especially when an ecosystem contains high levels of functional redundancy or overlap of functions (Micheli and Halpern 2005, Guillemot et al. 2011). Hence, the use of functional or biological traits has been suggested to have potential for both monitoring and management (King and McFarlane 2003, Tillin et al. 2006, Bremner 2008, Wiedmann et al. 2014, Rijnsdorp et al. 2016), as the functional diversity of a system will dictate the ecosystem functioning (Díaz and Cabido 2001, Perović et al. 2018). To utilise this method, abundance (relative or absolute) data of species within the system under study are recorded. These data are then combined with known trait data of these species (Coleman et al. 2015, Benoit et al. 2013, Belley and Snelgrove 2016). This analysis has the potential to look at any trophic level in any system but is highly dependent on availability of trait information. Some popular metrics used to assess a community's functional diversity include functional richness, functional divergence, functional evenness, functional redundancy and functional dispersion (Mason et al. 2008, Villegger et al. 2008). These metrics have been used to indicate function in relation to ecosystem-wide processes, such as productivity and reg-

ulation of biogeochemical fluxes (Perović et al. 2018, Ricotta et al. 2016).

Multivariate Assemblage Analysis

Sampling methods focus on specific areas of the ecosystem. As such, the ability for an index or indicator to define the true diversity of an ecosystem will be highly dependent on the method or combinations of methods used. This dependence would not be an issue under non-EBFM objectives from many MPAs, whereby the area is designed to protect one species. However, when wanting to use EBFM, the whole ecosystem, or a representative portion, needs to be assessed to properly inform management regimes (Halpern et al. 2007). One method for assessing more of the ecosystem is to not convert the multivariate data into a single number, but rather, analyse it with multivariate statistics. This reduces inherent biases produced within most indicators and, using similarity matrices, allows the data to be plotted visually with multiple different ordination styles. The data can be formally analysed using different multivariate statistics. However, care needs to be taken with the sampling design, as specific assumptions must be met to be statistically robust. Likewise, care should be taken with the selection of the similarity measure used and the interpretation of two-dimensional ordination (Anderson 2001a). This method of analysing assemblage composition has been extensively used for the detection of assemblage level change (Anderson 2001a, Bicknell et al. 2019).

1.5 Marine Protected Area Legislation

1.5.1 United Kingdom

In the UK, Marine Protected Area legislation is a relatively novel concept, with the first statutory provision being created in 1981 and designated in 1986 with Lundy Marine Nature Reserve (Jones 2008). Subsequently, European leg-

islation has created Special Areas of Conservation (SAC) and Special Protection Areas (SPA), driven by the Natura 2000 agreement (Gall and Rodwell 2016) under the EU Habitats Directive of 1992 (European Commission 1992). Since 2009, England, Scotland, Wales and Northern Ireland have been developing processes to designate a network of MPAs throughout the UK. In England and Wales this has been under the Marine and Coastal Access Act 2009 (MCAA). English designations since 2009 have primarily been Marine Conservation Zones (MCZs), which rely on both top-down and bottom-up involvement from multiple groups, such as the UK Government, Department for Environment, Food and Rural Affairs (Defra), statutory nature conservation bodies and regional stakeholders (Gall and Rodwell 2016). Therefore, within English waters there are three main types of MPA: SACs, SPAs and MCZs. Protection from SACs, SPAs and MCZs all focus on specific 'features', and managing activities, which affect these 'features', within the designated area as they are based within either the EU Habitats Directive or the MCAA (Solandt et al. 2020). The extent of the protection can be highly variable with the protection of the 'feature' including surrounding areas of 'non-feature'. This is seen by the Start Point SAC, where a mosaic of reef ('feature') and adjacent areas of sand, cobbles and smaller boulders are all protected from mobile demersal fishing gear (dredges, trawls, etc: Solandt et al. 2020). However, other examples provide little protection to the 'feature', such as Wash and North Norfolk SAC, where 1.5% of the reef extent is protected (Solandt et al. 2020). When an MPA applies consistent legislation over the whole of the designated area, unlike SACs, SPAs and MCZs where only the extent of the 'feature' is protected, it is known as the whole-site approach. This form of marine spatial management is extremely rare especially within the UK, yet shows evidence of being a 'win-win' scenario for a range of stakeholders, conservationists, commercial fishers, tourists and recre-

ational fishers (Solandt et al. 2020, Rees et al. 2010b, Sheehan et al. 2013a, Beukers-Stewart et al. 2005, Howarth et al. 2015). One of the few cases of this whole-site approach to MPA management started in 2008 in Lyme Bay (Sheehan et al. 2013a,b, Anon 2008).

1.6 Lyme Bay: A Case Study

1.6.1 Background

Lyme Bay constitutes a large portion of the South UK coastline, and is noted as a marine biodiversity hotspot (Singer and Jones 2018). In 2001 the Devon Wildlife Trust helped to set up a voluntary closure of 7 km² of the seabed, incorporating two reef areas (Jones et al. 2012). The voluntary closure was not deemed to be sufficient to protect the large areas of ecologically important rocky reef (Hiscock and Breckels 2007), which included pink sea fans *Eunicella verrucosa*, a species listed under the species protection provision of the Wildlife and Countryside Act 1981 (Wildlife and Countryside Act 1981). As such, fishers formed an association that agreed to voluntarily close 41 km² of the bay across four areas (Jones et al. 2012). Subsequently, Defra designated 206 km² of the bay under a Statutory Instrument (SI) in 2008, prohibiting all mobile demersal fishing gear (Rees et al. 2012b, Anon 2008). In 2010, an extended area of 312km², encompassing the SI, was designated under the European Commission (EC) as a candidate SAC, which followed a 'feature' based approach to protection (Fig. 1.7: Rees et al. 2012b). The value of Lyme Bay MPA, both for fisheries and recreational users, has been assessed extensively (Rees et al. 2010b, 2012b, 2010b, Mangi et al. 2011, Rees et al. 2012b), as well as the effect of its governance (Singer and Jones 2018, Jones et al. 2012) and the success of the MPA generally (Gallacher et al. 2016).

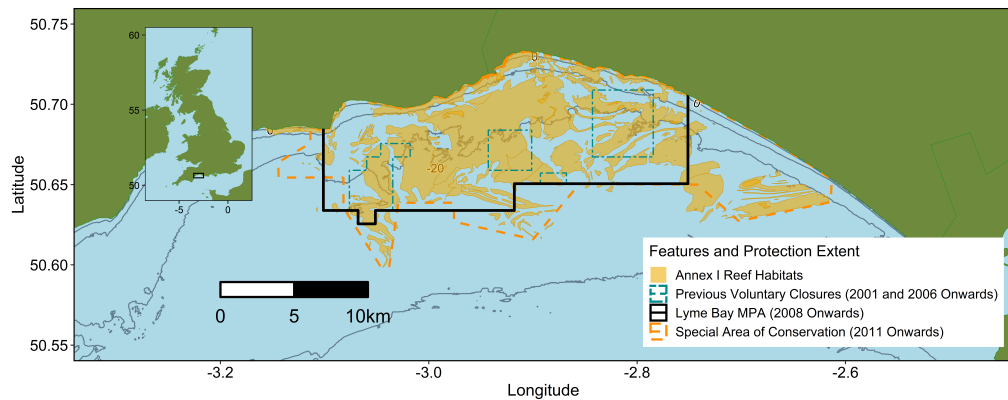


Fig. 1.7: Lyme Bay, its reef habitat extent and designation levels.

The long-term goal of the Lyme Bay MPA is to allow the recovery of the temperate rocky reef habitat and the associated biodiversity, by excluding the use of mobile demersal fishing gear, namely scallop dredging and trawling (Fleming and Jones 2012, Gallacher et al. 2016). Thus, the aim of the ongoing monitoring project is to assess the SI and SAC in comparison with nearby fished areas to monitor recovery. Simultaneously, it acts as an almost unique case study for MPA monitoring and protection, due to the longevity, consistency and robust design of the sampling carried out. To effectively monitor the whole rocky reef habitat, as much of the ecosystem as possible must be sampled; hence, the use of multiple techniques in this monitoring programme. This combination of methods has been shown as an effective control of the biases inherent within each sampling style, while increasing the range and detail of the data produced (Zeller and Russ 1998, Willis et al. 2000, Watson et al. 2005, Murphy and Jenkins 2010). Thus, the continued combination of sampling methods and the post-processing methodologies is of very high importance.

1.6.2 Monitoring Programme

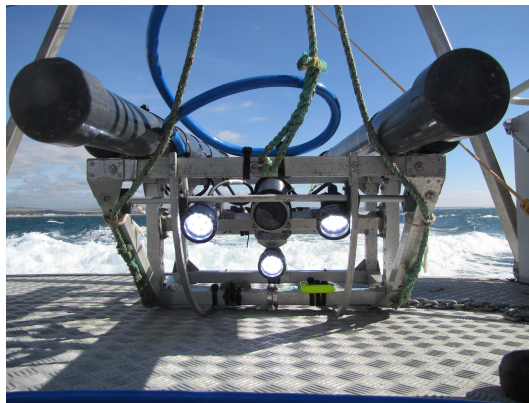
A consortium led by the University of Plymouth Marine Institute was funded in 2008 to assess the effect of the Lyme Bay MPA on the associated nekton and

epibenthic communities (Stevens et al. 2014). The aim was to monitor the protected area in a non-invasive and non-extractive way (Sheehan et al. 2013a, Stevens et al. 2014). Underwater videography, in the form of a towed flying array to sample the epibenthos (Sheehan et al. 2010, 2013a,a) and Baited Remote Underwater Video system (BRUVs) to sample the nekton (Stevens et al. 2014), have been deployed annually since the protected area's designation. Since 2014, Passive Acoustic Monitoring has also been deployed annually.

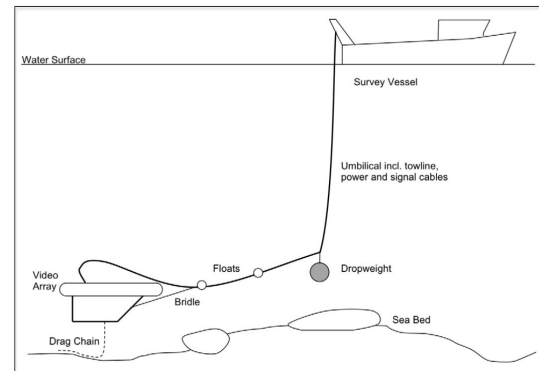
Towed Flying Array

To assess the impacts of Marine Renewable Energy Installations (MREI), Sheehan et al. (2010) developed a bespoke TUVS to sample the benthic environment in a non-extractive, cost-effective and accurate way. The array, a 1.5x scale version of the array detailed by Stevens (2003), consists of: an aluminium frame; a Surveyor-HD-J12 colour zoom titanium camera (6000 m depth rated, 1080i/720p); a mini Conductivity-Temperature-Depth profiler (CTD: Valeport Ltd); three LED lights (Bowtech Products limited, LED-1600-13, 1600 Lumen underwater LED); parallel lasers; two positively buoyant ballast tubes and a drag chain to automatically control distance to seabed (Fig. 1.8(a)). The camera and LEDs are connected via an umbilical cord to the boat, where the video is viewed in real time, allowing the control of camera focus and illumination, as well as the speed of the boat (Fig. 1.8(b)). The whole system is powered from the surface by an onboard generator (2 kW Honda Generator).

The array can be used to sample deep high-energy systems, as well as shallow calmer waters with minimal modifications (Sheehan et al. 2010). It has also been tested in comparison with other similar towed video transects and shown to be far more successful at sampling the heterogeneous seabed while being relatively less destructive (Sheehan et al. 2016).



(a)



(b)

Fig. 1.8: TUVS system used for Benthic Survey (1.8(a)) and diagram of its deployment (1.8(b): Sheehan et al. 2010, 2016).

Experimental Design This towed flying array has been used annually to monitor the Lyme Bay MPA since 2008. Each tow records a $\sim 200\text{m}$ transect carried out at an optimum speed of 0.2 ms^{-1} . The sampling design (Fig. 1.9) has been consistent across all levels of protection, with sites within the Previous Voluntary Closure (PVC), Statutory Instrument (SI), and Open Control (OC). In 2011, a Site of Community Importance (SCI) that turned into a Special Area of Conservation (SAC) was established surrounding the original SI. Thus, a subset of OC sites were changed to SAC sites and extra Open Control sites were added. From 2011 there were 15 PVC sites, 18 SI sites, 15 SAC sites and 18 OC sites (Fig. 1.10). As they were provided the same protection throughout the survey, PVC and SI were grouped as MPA throughout.

Data Extraction Two different data extraction methods are used: 30 frame grabs taken from each $\sim 200\text{m}$ transect (Cybertronix frame extractor), where a digital quadrat is superimposed on the image and all visible sessile fauna are enumerated (individual or discrete taxa, as counts, and cover forming taxa, as percentage cover); to count infrequent or conspicuous fauna, the video was played at normal speed and all taxa that passed through the ‘gate’ made by

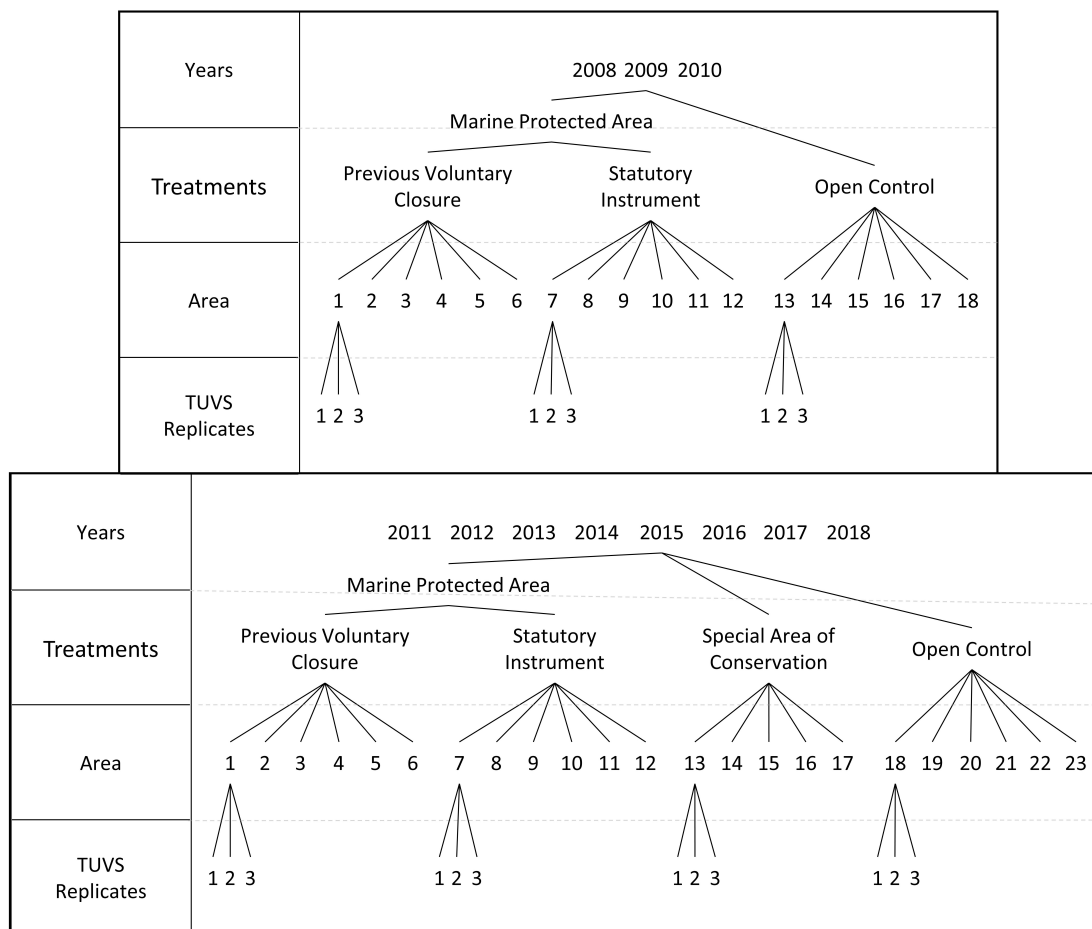


Fig. 1.9: Sampling effort of different years, treatments and areas for the Towed Flying Array for 2008-2010 (above) and 2011-2018 (below). Three replicates were taken at every area sampled.

the lasers were counted. For both methods, taxa were recorded by density, using the distance of the transect and the distance between the lasers or by calculation of the area of the electronic quadrat used. 30 quadrats per transect were calculated to be optimal for time expenditure and accuracy (Stevens et al. 2014).

Baited Remote Underwater Video Systems

BRUVs are a widely used non-extractive methodology for sampling mobile fauna communities, especially in protected areas (Acuña-Marrero et al. 2018). As

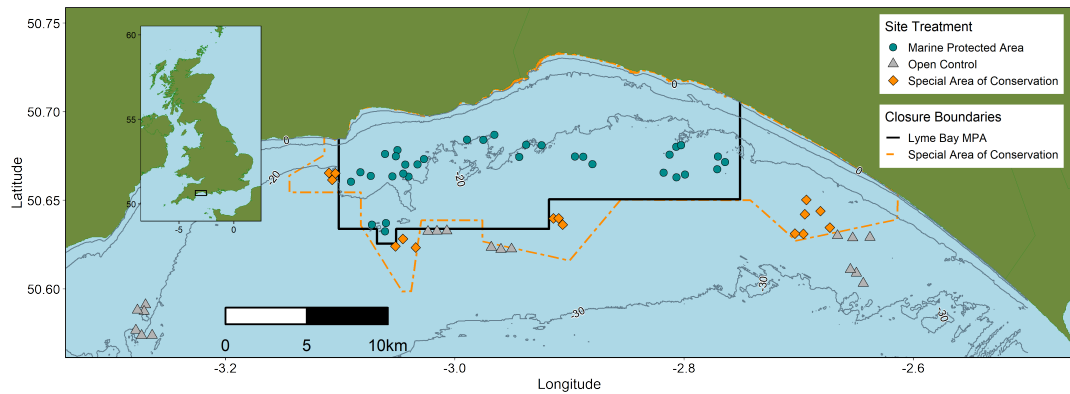


Fig. 1.10: Sampling sites for the Towed Flying Array inside Lyme Bay MPA (Blue circles), inside the Special Area of Conservation (Orange squares) and Open Controls (Grey triangles).

such, BRUVs have consistently been used in Lyme Bay since 2009, with sites in the PVC, SI and OC. From 2011 onwards, the OC sites became incorporated within the new SAC, hence more OC sites were added. Six sites are within each protection level (Fig. 1.11). Three BRUVs were deployed together at each site, with cameras spaced appropriately to stop an organism being recorded in more than one BRUVs (~100m). As they were provided the same protection throughout the survey, PVC and SI were grouped as MPA throughout.

The BRUVs used from 2011 comprised an HD video camera (Panasonic HDC-SD60) inside an underwater housing (Seapro Subsea Video Camera Module), with an underwater torch (Seapro wideangle 50 watt diffused LED) connected to an enclosed 10 hour battery pack. Bait consisted of ~100g of fresh Atlantic mackerel *Scomber scombrus* contained in a wire-mesh box mounted on a pole, which extended 1m from the camera lens (Fig. 1.12). Cameras were deployed to the seafloor at each site for 45 minutes then recovered (Fig. 1.13). In the first two years (2009 & 2010), the HD camera from the towed flying array (Surveyor-HD-J12), which was connected via umbilical cord to the boat, was mounted on a static frame with the 1m bait box arm. Decreased times were also used in the

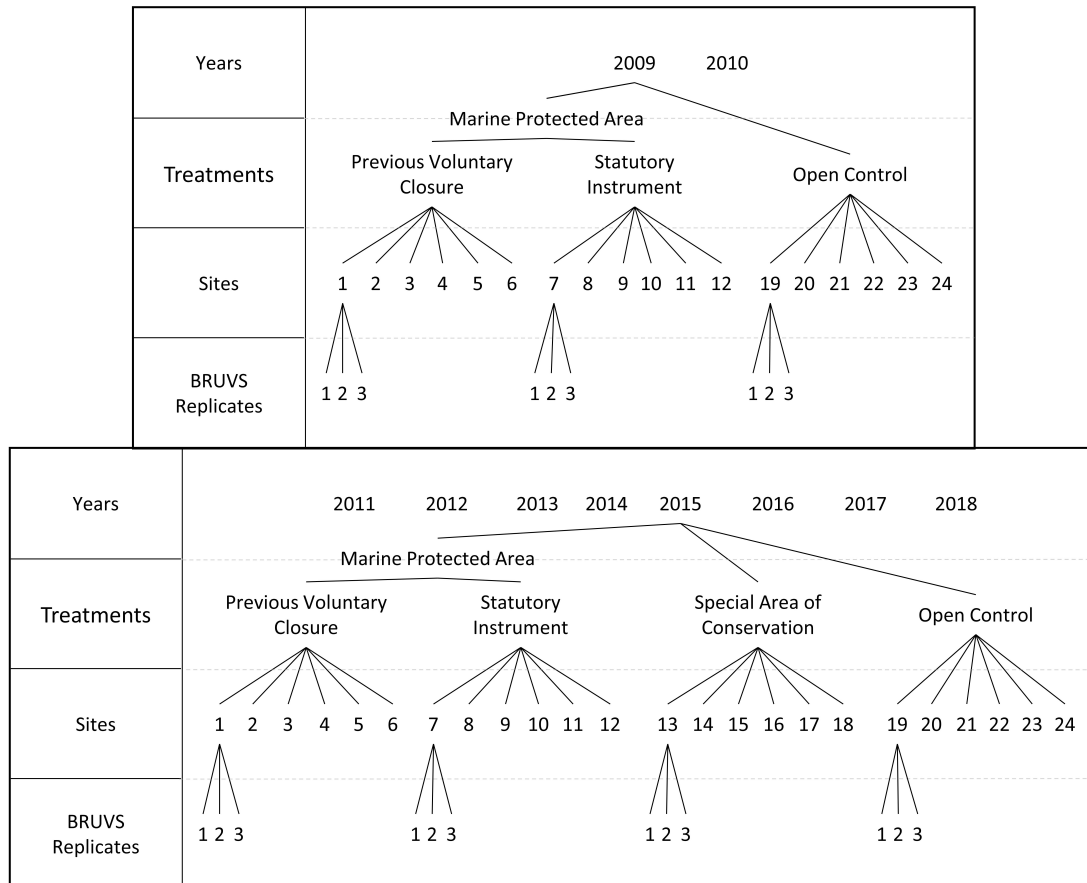


Fig. 1.11: Sampling effort of different years, treatments and sites for the Baited Remote Underwater Video Systems for 2009- 2010 (above) and 2011- 2018 (below). Three replicates were taken at every site sampled.



Fig. 1.12: Six individual BRUVs with associated rope and buoys.

first two years, so the cameras were only deployed for 20 minutes.

After a preliminary settling period of 5 minutes (2 minutes in 2009 & 2010), all mobile benthic organisms were recorded as counts per minute for 30 minutes (15 minutes in 2009 & 2010). All organisms were identified to the highest taxonomic resolution possible. Nekton relative abundance was calculated from the maximum number of individuals (MaxN) of a species across all of the individual minute segments (15 in 2009 & 2010 and 30 afterwards). This MaxN per species for each individual video deployment was used as relative abundance.

Digital Spectrogram Acoustic Recorders

From 2014 until 2018, acoustic recorders were deployed alongside the BRUVs. Digital SpectroGrams (DSG) are low-power acoustic recorders (Hydrophone

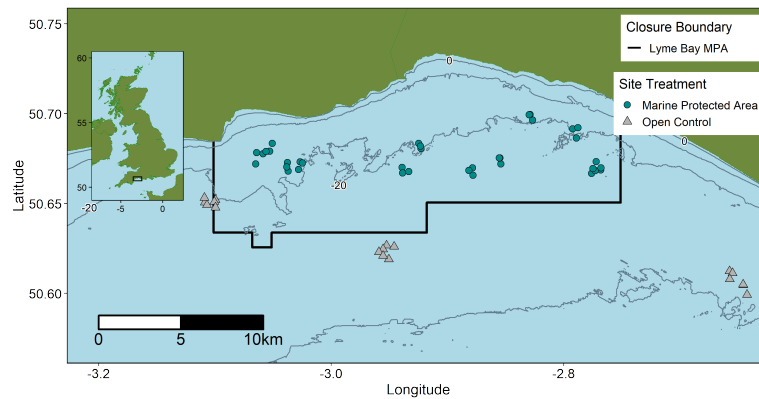


Fig. 1.13: Sampling locations for the Baited Remote Underwater Video Systems inside Lyme Bay MPA (Blue triangles) and Open Controls (Grey circles).

Calibration Sensitivity=-190dBV/uPa, Sample rate= 50 kHz, System Gain =20; Loggerhead Instruments, Sarasota, FL, USA). These loggers were programmed to record 16 seconds every 2 minutes for the duration of the sampling period. This duty cycle was used to minimise battery usage. The loggers were attached to one BRUVs for every site, to sample identical locations (Fig. 1.13). DSG acoustic recorders sample a larger area, 1.7km^2 (Simard et al. 2015), than the BRUVs, 0.2km^2 maximum effective range of attraction (AR) (Cappo et al. 2004), so a single acoustic recording was used across the three BRUVs replicates (Fig. 1.14).

Data were extracted by first selecting files recorded at the corresponding times of cameras being on the seafloor. For each deployment, all these files were grouped and then converted to wav files, using the computer software 'DSG2wav'.

1.7 Chapter Overview

The aim of this thesis was to assess the effectiveness to fisheries and conservation of a partially protected area where an ecosystem approach to management has been applied. Benthic monitoring methodologies were assessed and recommendations were given with relation to the lessons learned in Lyme Bay

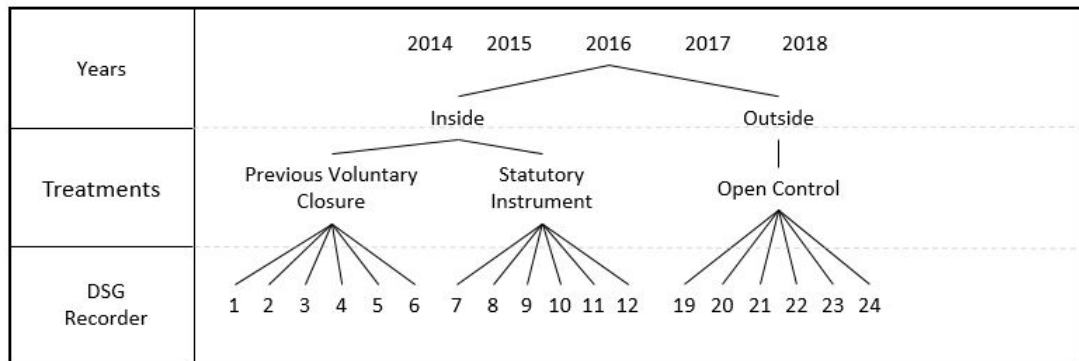


Fig. 1.14: Diagram showing the sampling effort of different years and treatments for the DSG Acoustic Recorders for 2014-2018. One recording was taken at every site.

and how best to improve monitoring and management of MPAs.

In **Chapter 2**, a relatively novel methodology, PAM, was compared to the established method BRUVs. PAM has the potential to provide substantial quantities of data, enumerating the diversity, abundance and behaviour of mobile species, with small time and effort expenditure in the field and computer processing stages of analysis. Yet, as a relatively novel area of marine ecology, it is understudied and therefore relatively poorly understood, especially when applied over multiple year time scales. By comparing the Acoustic Complexity Index, measured with PAM, to the ecology, surveyed by the BRUVs, from 2014 to 2018, PAM's utility and efficacy as a rapid MPA monitoring tool was assessed. It was expected that inside the MPA in comparison to nearby controls: i) Acoustic Complexity Index (ACI) would increase over time; ii) biodiversity would increase over time; iii) biodiversity and ACI would correlate and iv) mobile benthic assemblage composition would correlate with ACI.

In **Chapter 3**, the complete complement of BRUVs data from 2009 to 2019 were assessed, with specific focus on elements of the mobile assemblage most likely to have been impacted by the MPA. Thus, exploited and non-exploited

taxa were analysed over 11 years, inside vs outside the MPA. The exploited and non-exploited taxa were split into fish and invertebrates, as these groups were expected to respond differently to the protections due to their ecology, as well as the differences in fisheries exploitation rates. It was expected that: i) over time assemblage composition of mobile species would change in the MPA progressively in comparison with nearby open controls and ii) number of taxa and total abundance of all taxa, exploited and non-exploited fish and invertebrates would increase over time in the MPA relative to the open controls.

In **Chapter 4**, the functional change of the whole benthic assemblage covering sessile, sedentary and mobile fauna, surveyed by the towed flying array and the BRUVs, was assessed over 11 years, using metrics based on the abundance and diversity of specific biological traits. These traits can be used to enumerate specific functional metrics looking at the amount of different traits (functional richness), the spread of relative abundances of traits (functional evenness and functional divergence) and the relative overlap of the traits (functional redundancy). Traits were selected for their importance in ecosystem process, such as environmental position (benthic, pelagic etc.) or feeding habit (predator, grazer, filter feeder). Furthermore, the relative proportion of specific traits known to be affected by mobile demersal fishing were assessed over time. It was expected that: i) over time the number of taxa, functional richness and functional redundancy would increase over time in the MPA relative to the open controls; ii) functional divergence and functional evenness would decrease over time in the MPA in relation to the open controls and iii) the relative proportion of sessile filter feeding long-lived trait modalities would increase over time in the MPA, while mobile scavenging trait modalities would decrease, relative to the open controls

In **Chapter 5**, the effect of the 'feature' based SAC to the benthic ecosystem was assessed, using the towed flying array and BRUVs. The arrangement of protections within Lyme Bay also allowed the unique co-located comparison of the older whole-site MPA with the newer 'feature' based SAC and their effect on the benthic ecosystem with age of protection. It was expected that: i) the number of taxa, total abundance, functional richness and functional redundancy would increase from before to after designation in the SAC in comparison to the open controls; ii) assemblage composition of the SAC would significantly change from before to after designation in comparison to the open controls; iii) number of taxa, total abundance, functional richness and functional redundancy would increase with age of protection in the SAC and older MPA relative to the open controls; iv) the rate of increase in number of taxa, total abundance, functional richness and functional redundancy with age of protection would be greater in the older MPA than the SAC and v) the assemblage composition would significantly change with age of protection in the SAC, becoming more similar to the older MPA and less similar to the open controls.

Finally in **Chapter 6**, these results are synthesised and discussed in relation to each other and relevant literature, emphasising how this research fits within current MPA evaluation, management practices and policy. Furthermore, recommendations for future research, as direct and indirect outcomes of this work, are discussed.

"We go to war with the data we have, not the data we wish we had."

Richard McElreath

2

Acoustic Complexity Index to assess Benthic Biodiversity of a Partially Protected Area in the Southwest of the UK

Status: Published

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Authors' Contributions

EVS and MJA conceived the ideas and monitoring design; MJW provided technical advice regarding acoustic analytical methods; EVS, LH, AR and BFRD collected data; BFRD and LH organized and analysed data; BFRD, EVS and LH led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

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Abstract

1. The environmental noise, or soundscape, of the marine environment is a relatively understudied area of ecology that has the potential to provide large amounts of information on biodiversity, reproductive behaviour, habitat selection, spawning and predator-prey interactions. Biodiversity is often visually assessed and used as a proxy for ecosystem health. Visual assessment using divers or remote video methods can be expensive, and limited to times of good weather and water visibility. Previous studies have concluded that acoustic measures, such as the Acoustic Complexity Index (ACI) correlate with visual biodiversity estimates and offer an alternative to assess ecosystem health.
2. Here, the ACI measured over 5 years in a MPA in the UK, Lyme Bay, was analysed alongside another monitoring method, Baited Remote Underwater Video Systems (BRUVs). Two treatments were sampled annually in the boreal summer from 2014 until 2018 with sites inside the MPA, as well as Open Control sites outside of the MPA.
3. Year by year correlations, which have been used elsewhere to test ACI, showed significant correlations with Species Richness and ACI. However, the sign of these correlations changed almost yearly, showing that more in-depth analyses were needed. Multivariate analysis of the benthic assemblage composition (from BRUVs) was carried out by Permutational Multivariate Analysis of Variance using Distance Matrices (PERMANOVA).
4. These analyses showed that, although not consistently correlating with univariate measures, the ACI was significantly interacting with the chang-

ing benthic assemblage composition, as it changed over time and protection (Inside vs Outside the MPA). This acoustic index shows potential to allude to shifting benthic communities, yet with no consistency when used alongside univariate measures of diversity. Although it is not without its own disadvantages, the ACI is demonstrating more complex changes to the benthos than simply the overall diversity and thus should be developed further before implementation.

2.1 Introduction

Biodiversity provides a useful measure to assess ecosystem health (Worm et al. 2006), and is increasingly being used for conservation and monitoring purposes, as an observed decrease often being a proxy for a degraded or negatively impacted ecosystem (Wabnitz et al. 2018). To quantify and compare these changes in diversity, many univariate indices have been produced, which simplify an assemblage of taxa into a single value. The most commonly used being number of species present often referred to as Species Richness (Hall and Mainprize 2004, Pieretti and Farina 2013, Sheehan et al. 2013a, Kaplan et al. 2015), Shannon-Wiener's diversity index (Spellerberg and Fedor 2003, De-La-Ossa-Carretero et al. 2012), Simpson's diversity index (Zahl 1977, Miralles et al. 2016) and taxonomic distinctness (Clarke and Warwick 1998, 2001, Leonard et al. 2006).

Historic methods for assessing marine biodiversity have often used destructive practices (Francour 1994, Lipej et al. 2003), such as poisoning (Diamant et al. 1986) or trawling (Van Dolah et al. 1987, Wassenberg et al. 1997, Cappo et al. 2004). However, for the study of recovering and fragile benthic systems, such as those in Marine Protected Areas (MPAs), non-invasive, non-extractive meth-

ods such as Underwater Visual Census (UVC) or Underwater Video Survey (UVS) are considered more appropriate (Edgar and Stuart-Smith 2009, Sheehan et al. 2010, Hill et al. 2018). Solely visual methods will always have the drawback that there is no physical sample taken and thus those species that are harder to visually identify will always be under-sampled; yet this lack of physical sample means the populations being researched are almost or completely unaffected by the survey taken. A potential addition to supplement visual survey would be the assessment of the marine soundscape (Staaterman et al. 2017). This method for sampling the marine environment is similarly non-extractive and non-invasive, while sampling areas of the ecosystem potentially under-represented by visual methods alone.

The marine soundscape comprises both natural and anthropogenic noise. Assessment of the biological element (biophony) of the marine soundscape has been used to describe overall biodiversity (Bertucci et al. 2016), reproductive behaviour (de Jong et al. 2018), habitat selection (Simpson et al. 2004, Vermeij et al. 2010, Barth et al. 2015), spawning (Hawkins and Amorim 2000, Casaretto et al. 2014) and predator-prey interactions (Bernasconi et al. 2011, Giorli 2016, Giorli and Au 2017). Biophony is produced by a wide range of taxa ranging from large cetaceans producing low frequency (20Hz) calls or songs (Samaran et al. 2013), that can be detected up to thousands of kilometres away (Clark 1995, Rivers 1997), to crustaceans creating loud (190 dB re 1 μ Pa), broadband (2kHz up to 300kHz) ‘snaps’ and ‘pops’ (Au and Banks 1998, Beng et al. 2003, Picciulin et al. 2013).

Acoustic indices have been developed and utilised in marine (Nedelec et al. 2015, Pieretti et al. 2017) and terrestrial (Pieretti et al. 2011, 2015, Pijanowski et al. 2011, Pieretti and Farina 2013, Merchant et al. 2015) environments to

assess whole ecosystem biodiversity. The use of these indices is perceived to allow hidden or shy species, overlooked by other survey methods, to be accounted for (Staaterman et al. 2017). The ACI as set out in Pieretti et al. (2011) quantifies the relative change in noise intensity across all frequencies of a soundscape, while being minimally affected by constant anthropogenic noise. The ACI was developed on the assumption that with increased diversity of species, there would be an increase in the complexity of biological noises produced. So far, most analyses of ACI have shown a positive correlation with a variety of biodiversity indices (Bertucci et al. 2016, Harris et al. 2016).

The two survey methods, visual and acoustic, are thought to complement each other by overlapping, as well as covering differing spatial scales and taxonomic groups (Staaterman et al. 2017). However, the majority of studies to date regarding this interaction have been based either in areas of very high biodiversity, such as coral reef systems (Bertucci et al. 2016, Kaplan et al. 2015), or only focused on fish diversity (Harris et al. 2016). As such, the transferability to other habitats and ecosystems is limited. Both survey methods have been carried out simultaneously as part of a long term monitoring project of the Marine Protected Area (MPA) in Lyme Bay since 2014.

In the winter of 2013/2014, the south coast of the UK experienced high storm activity that was observed to have heavily impacted benthic assemblages inside and outside of the MPA (Sheehan et al., unpublished data). This effect to both the protected and non-protected ecosystems provided an opportunity to start a new monitoring strategy. This incorporated acoustic recording and assessment of the marine soundscape inside and outside of the MPA and allowed the assessment of the emerging acoustic analyses. Thus, the study aimed to assess the efficacy of using acoustic recording as a monitoring methodology.

It was expected that the ACI and two visual biodiversity indices, Species Richness and Shannon's Diversity Index, derived from BRUVs data ('visual biodiversity indices' from now on), would increase over time in the MPA relative to the areas that continue to be fished. Therefore, the following hypotheses were assessed for inside vs outside the MPA:

1. The ACI will increase over time,
2. The visual biodiversity indices will increase over time,
3. The visual biodiversity indices and the ACI will correlate with each other,
4. Changes in the mobile benthic assemblage composition will result in similar changes to the ACI.

2.2 Materials and Methods

2.2.1 Study Location

Lyme Bay (Fig. 2.1), is located on the south coast of England, and contains areas of rocky reef habitat known to include nationally important fragile reef building species (Hiscock and Breckels 2007). A Statutory Instrument (SI), a type of MPA, was established in 2008 in Lyme Bay. The SI excluded all towed demersal fishing equipment (scallop dredging and trawling) in an area of the bay measuring 206km².

Site selection for BRUVs deployments was based on similar biotope classifications to negate any confounding effects of habitat heterogeneity (Claudet et al. 2008), with all sites being on either hard or 'mixed' substrate (Sheehan et al. 2013b). There were two treatments: Inside the MPA (n=12) and Outside the MPA (n=6). Geographically similar pairs of sites were grouped into 'Areas'.

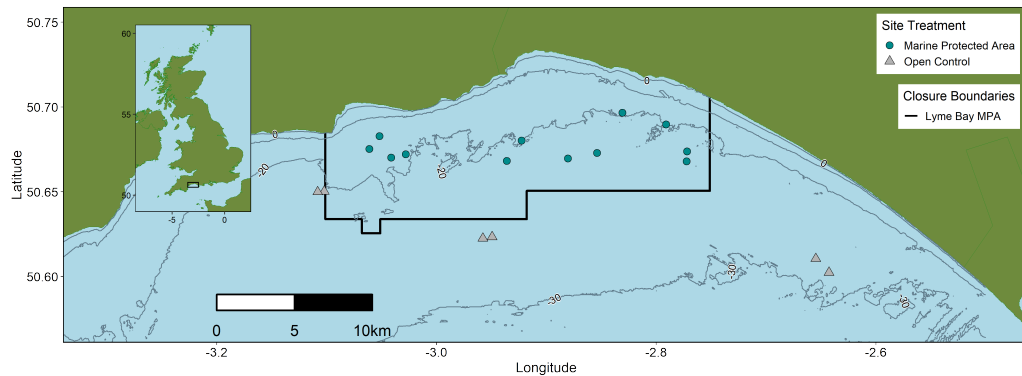


Fig. 2.1: Map of the UK inlaid in a map of Lyme Bay, showing site locations and their treatments (Blue: Marine Protected Area, Grey: Open Control). Solid line shows the Statutory Instrument Boundary.

2.2.2 Data Collection

Acoustic Recorder Deployment

At each site, an acoustic recorder was attached and deployed with one of the three replicate BRUVs (Fig. 2.2). The acoustic recorders used were low power Digital SpectroGrams (DSG) (Hydrophone Calibration Sensitivity= $-190\text{dBV}/\mu\text{Pa}$, Sample rate= 50 kHz, System Gain =20; Loggerhead Instruments, Sarasota, FL, USA), which were used to record DSG files. The recorders were attached to one BRUVs for every site, to sample identical locations (Fig. 2.2), but, as DSG acoustic recorders sample a larger area, 1.7km^2 (Simard et al. 2015) than the BRUVs 0.2km^2 maximum effective range of attraction (AR) (Cappo et al. 2004), single acoustic recordings were used across the three BRUVs replicates (Appendix A).

For each deployment, corresponding audio files were selected, grouped and converted to WAV files, using the computer software 'DSG2wav'. Auditory and visual examinations were then used to remove any dominant anthropogenic interference using 'seewave' package in R (Sueur et al. 2008). The Acoustic Complexity Index was then calculated for each deployment (ACI: Pieretti et al.

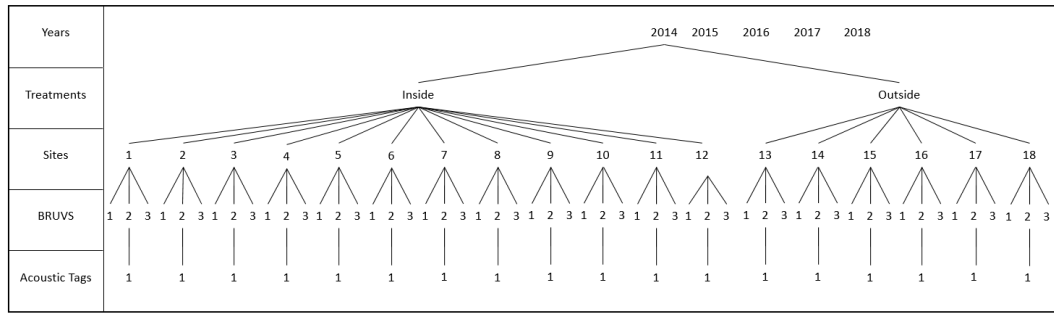


Fig. 2.2: Sampling design for BRUVs and Acoustic Tags.

2011), using the R packages ‘tuneR’ and ‘seewave’ (Sueur et al. 2008, Ligges et al. 2016). Originally developed to analyse terrestrial avian communities, the ACI quantifies the change in adjacent spectrogram intensities for all temporal steps and frequency bins (Pieretti et al. 2011).

Acoustic Complexity Index

The Acoustic Complexity Index (ACI) was chosen for the current study since the hydrophones used were encased in resin and could not be calibrated. As such, the acoustic files created could not be analysed with any of the other popular acoustic measures such as Acoustic Entropy, Acoustic Richness, Root Mean Square or Sound Pressure Level.

Sounds files were split into frequency bins and temporal steps. The change in adjacent intensities are then summed across these frequency bins and temporal steps. Thus, high ACI values are produced by large variations in sound intensity across many frequencies and times, whereas constant levels of similar intensity, such as most anthropogenic sources (e.g. boat engine), will produce low values of ACI (Bertucci et al. 2016).

Baited Remote Underwater Video Systems

Baited remote underwater video (BRUV) systems are a non-destructive method for sampling mobile communities (Babcock et al. 1999, Heagney et al. 2007). Three replicate BRUVs were deployed at each site for 45 minutes then recovered. Specifications of equipment are described in Bicknell et al. (2019).

Video analysis

After a preliminary settling period of 5 minutes, 30 minutes of video were analysed in 1 minute segments. For each segment, all mobile benthic organisms were identified and recorded. All organisms were identified to the highest taxonomic resolution possible. Abundance (MaxN) was calculated for each species from the maximum number of individuals of each species observed across all of the 30 minute segments.

2.2.3 Statistical Analysis

Permutational Analysis of Variance (PERMANOVA) was used to test differences in between years and treatments for the ACI, Shannon's Diversity Index, Species Richness and the abundance composition. Year and Treatment were fixed factors with five and two levels respectively (Year: 2014, 2015, 2016, 2017 and 2018; Treatment: MPA and Open Control) using Primer v7 and PERMANOVA+ (Anderson et al. 2008, Clarke and Gorley 2015). The assemblage composition analysis also included a random factor Area, which was nested inside Treatment (MPA= 6 areas, OC= 3 areas). For Shannon's Index, Species Richness and assemblage composition, the ACI was included as a covariate. The statistical significance of the variance components were tested using 9999 permutations under a reduced model (Anderson 2001b, Anderson and ter Braak 2002). The analyses of the ACI and the two visual biodiversity in-

dices were done on the basis of a Euclidean distance matrix calculated from the Index values. The assemblage composition analysis was done on the basis of Bray-Curtis dissimilarity matrix calculated from dispersion weighted, fourth root transformed abundance data. Significant interactions ($p < 0.05$) of fixed terms were tested using PERMANOVA pairwise tests.

To assess correlations between visual biodiversity measures and the ACI, scatter plots were created with linear Pearson correlations showing R^2 values and significance ($p < 0.05$). Assemblage composition was visualised using non-metric Multi-Dimensional Scaling (nMDS).

2.3 Results

2.3.1 Acoustic Complexity Index

The interaction between year and treatment had a significant effect on the ACI (Table 2.1: Pseudo- $F = 2.6766$, $p = 0.0351$). The MPA was more acoustically complex in 2014 and 2018 (Table 2.1; 2014: $p = 0.009$; 2018: $p = 0.0288$), whereas the OC was more complex in 2016 (Fig. 2.3A, Table 2.1; 2016: $p = 0.0218$). Overall, ACI shows a lower percentage mean inside the MPA (1.40% lower than outside: Fig. 2.3A).

2.3.2 Visual Biodiversity Indices

Both indices of diversity (Shannon's Diversity Index and Species Richness) were greater inside vs outside the MPA, with a mean percentage difference from outside to inside of: 20.03% for Shannon's and 8.40% for Species Richness (Fig. 2.3B & 2.3C).

Table 2.1: Results table of PERMANOVA analysis of Euclidean distances assessing Acoustic Complexity Index with Year and Treatment as interactions and Pairwise comparisons of yearly differences between Treatments for the ACI. (Bold p values denotes significance, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$). Year and Treatment are abbreviated throughout to Yr and Tr.

Source	PERMANOVA				Pairwise Comparisons		
	df	MS	Pseudo-F	p	Year	MPA vs OC	
						t	p
Yr	4	849.5	8.6736	0.0001***	2014	2.7956	0.009**
Tr	1	255.76	2.6113	0.1121	2015	0.33271	0.9741
Yr x Tr	4	262.15	2.6766	0.0351*	2016	2.3627	0.0218*
					2017	1.6034	0.1182
					2018	2.2848	0.0288*

When all diversity indices, both acoustic and visual biodiversity, are assessed by year and split into treatments, there is no significant trend with year displayed by the ACI, either inside or outside the MPA (Fig. 2.4, Inside: $R^2 = 0.02$, $p = 0.11$; Outside $R^2 = 0.034$, $p = 0.19$). Whereas Species Richness significantly increased with time, both inside and outside the MPA (Fig. 2.4: Inside: $R^2 = 0.046$, $p = 0.017$, Outside: $R^2 = 0.1$, $p = 0.02$). Outside the MPA, Shannon's index shows no significant trend with time and has a small significant increase with time inside the MPA (Fig. 2.4: Inside: $R^2 = 0.046$, $p = 0.017$; Outside: $R^2 = 3.3 \times 10^{-7}$, $p = 1$).

2.3.3 Visual Biodiversity against Acoustic Complexity

Shannon's Index was greater in the MPA than the Open Controls but did not change with Year (Table 2.2; Treatment: Pseudo-F=10.726, $p=0.0013$; Year:

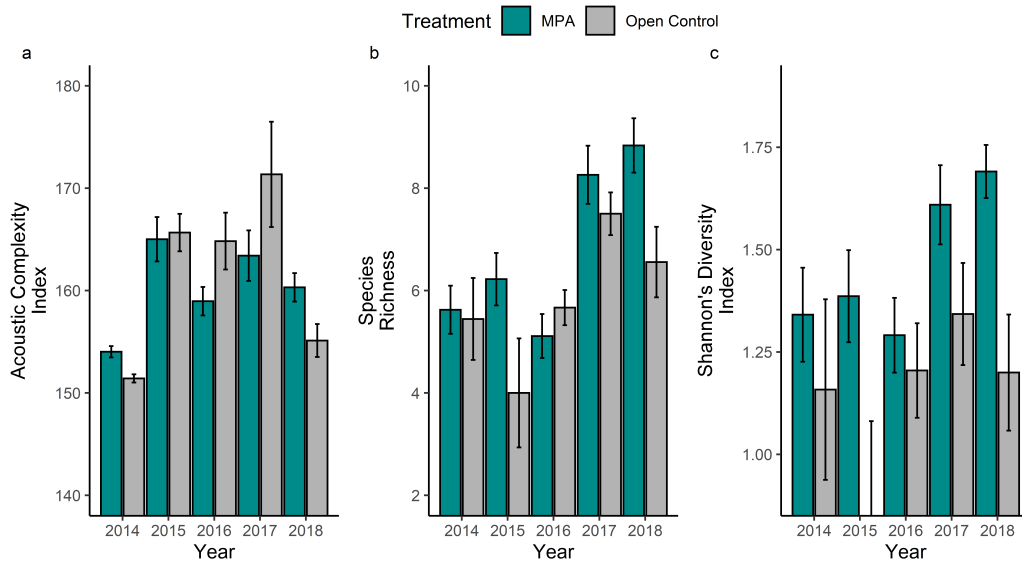


Fig. 2.3: Mean Acoustic Complexity (a), Species Richness (b) and Shannon's Diversity (c) inside and Outside the MPA across all years. Error bars show standard error.

Pseudo- $F=2.3123$, $p=0.0564$). Whereas, Species Diversity showed interaction between the Year and the ACI (Pseudo- $F=6.4837$, $p=0.0002$) as well as ACI and treatment (Pseudo- $F=6.1875$, $p=0.0157$).

Neither Species Richness nor Shannon's Index correlated with the ACI when compared across all the years and treatments (Fig. 2.5; Shannon's Index: $R^2=0.0045$, $p=0.37$ and Species Richness: $R^2=0.0014$, $p=0.63$). However, within each year, Species Richness did correlate with ACI with the exception of 2016. However, the orientation of this correlation was inconsistent; it was positive for 2014 and 2018, and negative for 2015 and 2017 (Fig. 2.6; Positive- 2014: $R^2=0.13$, $p=0.041$; 2018: $R^2=0.16$, $p=0.041$; Negative- 2015: $R^2=0.17$, $p=0.017$; 2017: $R^2=0.32$, $p=0.00032$). In contrast, Shannon's Index correlated with ACI in only 2017; this correlation was negative (Fig. 2.6; 2017: $R^2=0.16$, $p=0.017$).

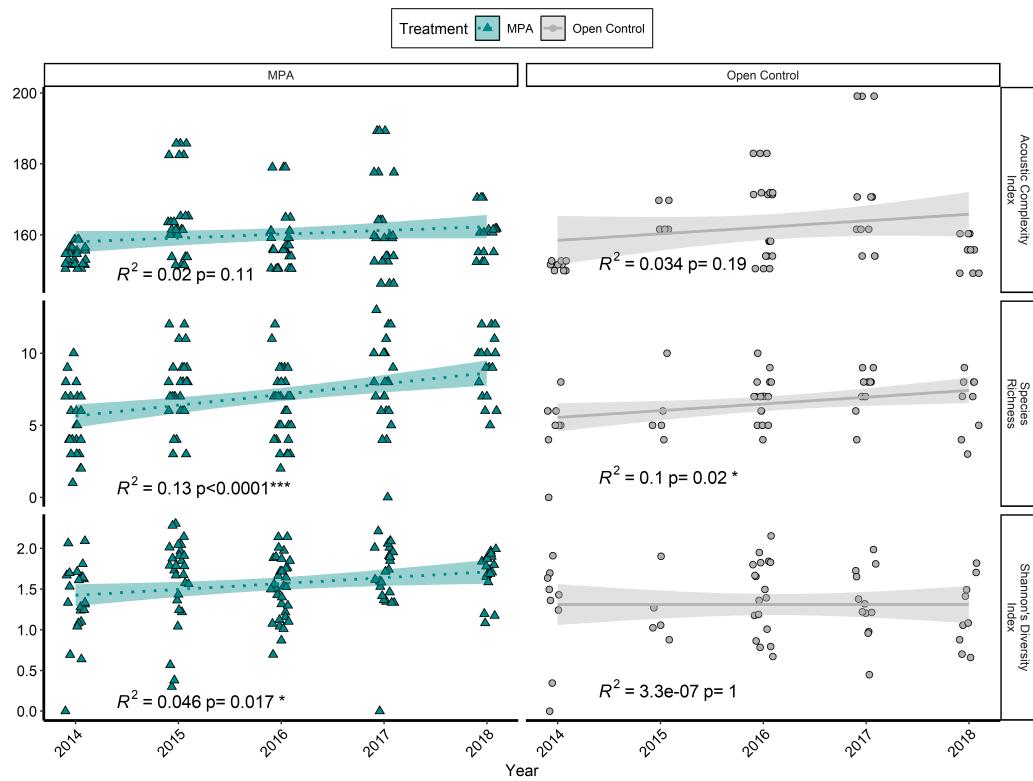


Fig. 2.4: Pearson correlation of Year against Acoustic Complexity Index (top), Species Richness (middle) and Shannon's Diversity Index (bottom) split by treatment (Outside: blue and left, Inside: grey and right). R^2 values are shown and significance denoted by *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$, $p < 0.0001$ ***: $p < 0.0001$. Shading around regression line shows 95% confidence interval.

Table 2.2: Results table of PERMANOVA analysis on Euclidean distance assessing Shannon's Diversity Index and Species Richness with Year and Treatment as interactions and ACI as a covariate. (Bold p values denotes significance, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$). Year and Treatment are abbreviated throughout to Yr and Tr.

Source	df	Shannon's Diversity Index			Species Richness		
		MS	Pseudo-F	p	MS	Pseudo-F	p
ACI	1	0.17249	0.89629	0.3526	1.5537	0.34091	0.5553
Yr	4	0.445	2.3123	0.0564	53.05	11.64	0.0001***
Tr	1	2.0641	10.726	0.0013 **	6.3986	1.4039	0.2415
ACI x Yr	4	0.30352	1.5771	0.1812	29.55	6.4837	0.0002**
ACI x Tr	1	0.21135	1.0982	0.2936	28.2	6.1875	0.0157*
Yr x Tr	4	0.25056	1.3019	0.2712	10.249	2.2487	0.0635
ACI x Yr x Tr	4	0.27228	1.4148	0.2248	5.133	1.1262	0.3408

2.3.4 Mobile Benthic Assemblage Composition

The assemblage compositions of the two treatments diverge with increasing time with the two treatments changing at different rates (Fig. 2.7; Table 2.3: ACI x Year x Treatment: Pseudo-F: 1.7682, $p=0.0482$). Similar to previous analyses, 2014 and 2018 seem to be the most distinct assemblages inside the MPA, which is much less defined outside the MPA (Fig. 2.7). However, the ACI in 2014 and 2018 for both treatments are the most similar (Fig. 2.7). *Inachus spp.* and *Pagurus spp.* were most important to the Open Control composition (Fig. 2.7). Whereas, the species most important for the MPA assemblage were *Labrus mixtus*, *Labrus bergylta* and *Ctenolabrus rupestris* (Fig. 2.7). This shows differences between treatments were driven by small scavenging crustaceans in the MPA, whereas the MPA was driven by reef dwelling wrasse species.

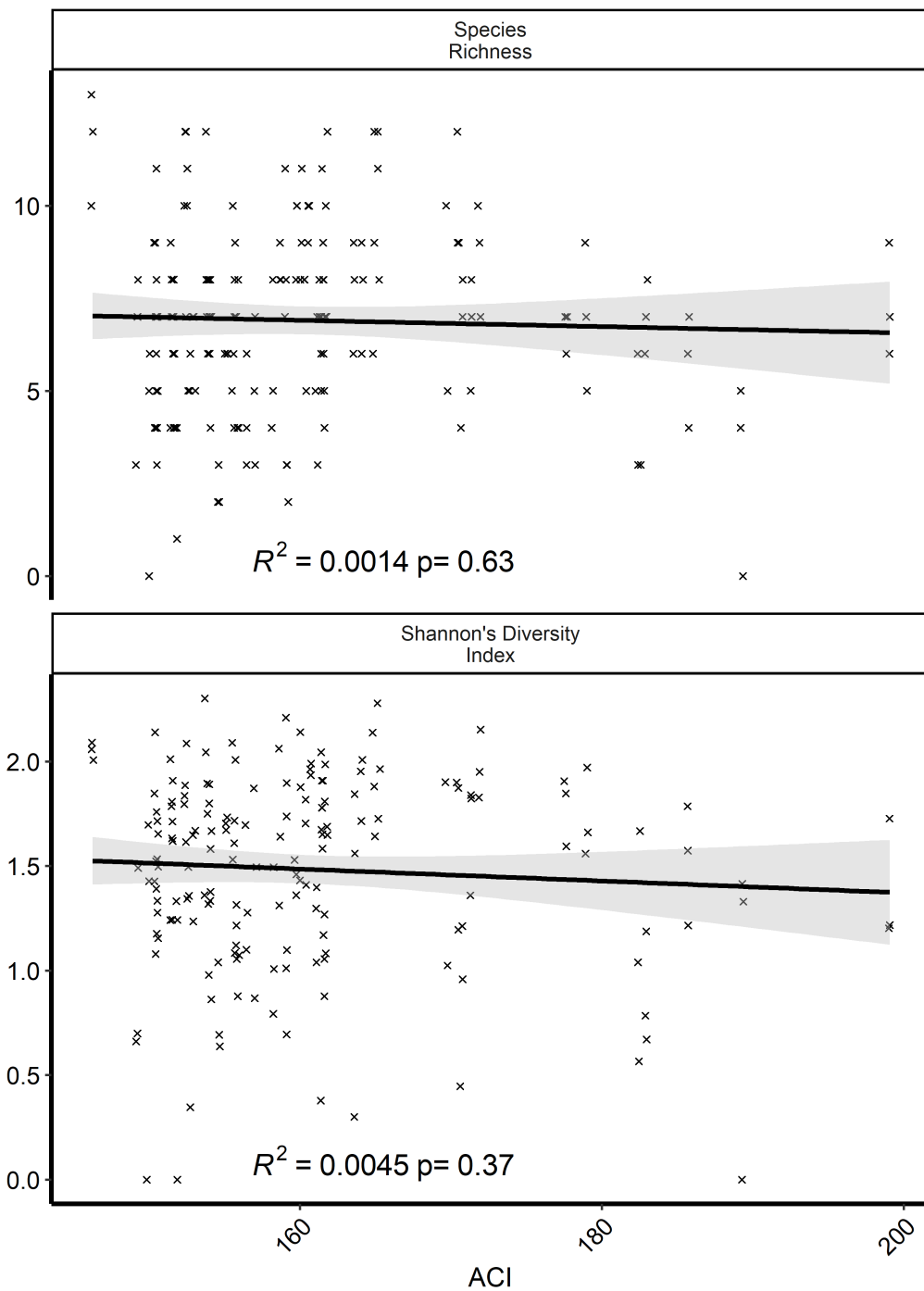


Fig. 2.5: Pearson correlation of Acoustic Complexity against Species Richness (above) and Shannon's Diversity Index (below). R^2 values are shown and significance shown by *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$, ****: $p < 0.0001$. Shading around regression line shows 95% confidence interval.

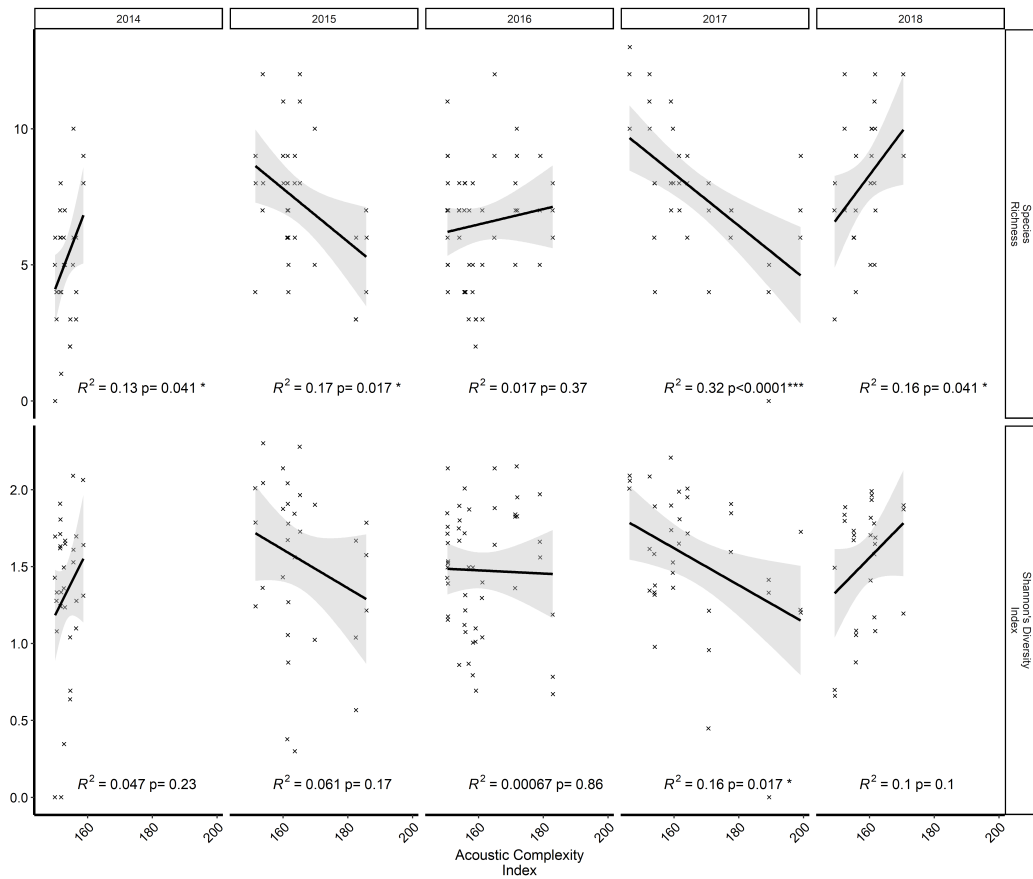


Fig. 2.6: Yearly Pearson correlation plots of Species Richness (above) and Shannon's Diversity Index (below) against Acoustic Complexity Index. R^2 values are shown and significance shown by *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$, $p < 0.0001$ ***: $p < 0.0001$. Shading around regression line shows 95% confidence interval.

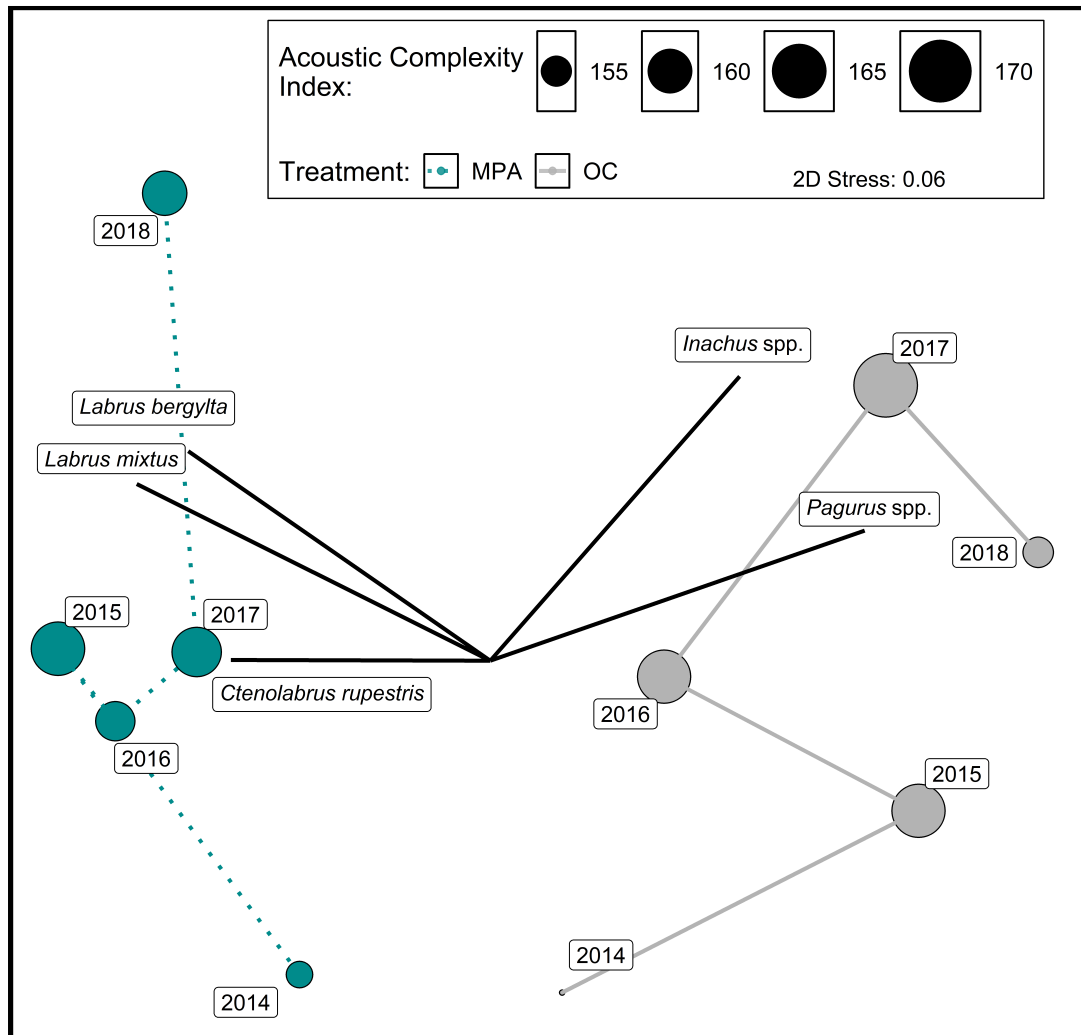


Fig. 2.7: Non-Metric Multidimensional Scaling plot of distance to centroids split by Year and Treatment from adjusted Bray-Curtis similarity of fourth root transformed abundance data. Points are label by Year and coloured by treatment (Blue: Inside MPA, Grey: Outside MPA) and scaled according to mean ACI values. Vectors overlaid display 0.85 pearson correlation for the species driving the difference in the assemblage composition.

Table 2.3: Results table of PERMANOVA analysis on adjusted Bray-Curtis similarity assessing mobile benthic assemblage composition with Year and Treatment as fixed interactions, area as a random interaction nested within treatment and ACI as a covariate. (Bold p values denotes significance, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$). Year and Treatment are abbreviated throughout to Yr and Tr.

Source	df	Assemblage Composition		
		MS	Pseudo-F	p
ACI	1	4003.3	2.0845	0.0457*
Year	4	9011.3	3.4253	0.0001***
Tr	1	29580	3.652	0.0003***
Area(Tr)	7	8302.8	8.974	0.0001***
ACI x Yr	4	2167.7	1.5326	0.0607
ACI x Tr	1	2296.2	2.4819	0.0177*
Year x Tr	4	1883.9	1.1026	0.3666
ACI x Area(Tr)	7	1338.7	1.4469	0.0328*
Year x Area(Tr)	23	1419.6	1.5344	0.0001***
ACI x Yr x Tr	2	1635.9	1.7682	0.0482*

2.4 Discussion

After high storm activity impacted both protected and non-protected areas of Lyme Bay, acoustic and BRUVs monitoring was carried out. It was hypothesised that the Acoustic Complexity Index would increase over time as the biodiversity of the area increased. Further, the ACI was expected to be greater inside the protected area in comparison to the surrounding fished areas. Finally it was hypothesised that the ACI would change in a similar pattern to that of the mobile benthic assemblage composition recorded by BRUV systems.

The primary hypothesis was rejected as the ACI was not significantly increasing with time (Fig. 2.4). However, the ACI did show a significant interaction between year and treatment (Table 2.1). Inside the MPA, the ACI in 2014 and 2018 was greater while 2016 was lower (Table 2.1; Fig. 2.3). As hypothesised, Pearson's correlation showed that both Species Richness and Shannon's Index significantly increased with time, inside the MPA, whereas only Species Richness showed a significant increase outside the MPA (Fig. 2.4). Likewise, the two visual biodiversity indices were significantly changing with year (Table 2.2). Shannon's index was not significantly interacting with ACI, whereas the Species Richness was (Table 2.2). The ACI correlated with Species Richness in four of the five years studied (Fig. 2.6) though only with Shannon's index in one: 2017. However, the slope of ACI against Species Richness changed yearly. As hypothesised, ACI significantly interacted with the changing benthic composition across years and treatments (Table 2.3), but the correlations with the univariate metrics were not consistent.

Visual Biodiversity and Acoustic Indices

The Acoustic Complexity Index did not show the patterns displayed by the visual biodiversity indices (Fig. 2.3). Instead, it stayed relatively constant over time with higher values outside the MPA versus inside. Both Shannon's Diversity and Species Richness showed similar trends, with greater 'diversity' inside the MPA than outside (Fig. 2.3). At the treatment level, the ACI is not displaying the same trends, with marginally greater levels outside the MPA versus inside, which was not expected as there was greater visual biodiversity inside the MPA (Bertucci et al. 2016).

The Acoustic Complexity Index showed a greater number of significant interactions with Species Richness than Shannon's Diversity (Fig. 2.4 & 2.6; Table

2.2). This relationship between ACI and Species Richness implies that the ACI is less affected by abundance and more by the number of species present. This is to be expected as the ACI was developed under the theory that many differing biological noises in an environment imply many different species (Pieretti et al. 2011, Lindseth and Lobel 2018). However, the yearly correlations between ACI and Species Richness, although often significant, changed orientation (between positive and negative) throughout the study. This complete reversal, at times, of the relationship between the acoustics and the number of species could mislead results if studies testing this relationship do not cover an appropriate temporal scale. This inconsistency may be the result of specific species or behaviours dominating the soundscape, meaning the presence of specific species in the acoustically sampled area, but not recorded by the BRUVs, could be driving this inconsistent pattern. Although recordings were evaluated for consistent anthropogenic or abiotic noise prior to ACI calculation and the metric itself was designed to be insensitive to these types of noises, anthropogenic and abiotic sources of noise may have also caused this annual inconsistency. However, by virtue of sampling being carried out in summer and in weather conditions preferable for underwater videography, any abiotic factors (such as wind, swell or rain) would be consistent across different years.

Shifting Benthic Composition

There is a clear divergence of assemblage compositions, with the inside and the outside treatment moving further apart year on year (Fig. 2.7). However, without data on the 'before fishing' assemblage, it would be very difficult to suggest whether this separation is recovery of the ecosystem. Yet, Pearson's correlations would suggest that the species most associated with the MPA are classed as reef dwelling species (Darwall et al. 1992). Specifically, *Ctenolabrus*

rupestris remain in the same local area for several years, thus, these species will be localised to their own ‘territory’. The Open Controls were showing dominance by *Inachus* spp. and *Pagurus* spp. (Fig. 2.7); both have broad habitat preferences although *Inachus* spp. is more likely to be found on mixed coarse substrata (Rowley 2008).

As shown above, inside the MPA there was higher Species Richness and Shannon’s Diversity (Fig. 2.3). Pearson’s correlation reported both indices increasing with treatment and time, especially Richness, this shows that the MPA in Lyme bay is acting as a refuge to allow biodiversity to increase (Fig. 2.4). The assemblage composition does not interact with changing ACI alone, but is significant when aligned with year and treatment (Table 2.3). This would suggest that, although it did not correlate overall with visual biodiversity, the index is sensitive to some level of the non-background variation in the assemblage composition.

The ability for the acoustics to infer information about local assemblage structure, is the reason this is such a growing area of research (Pijanowski et al. 2011, Sueur and Farina 2015). Yet, as with most areas of ecology, the transition from the terrestrial to the marine poses a new range of obstacles to overcome (Radford et al. 2011, Stanley et al. 2012, McWilliam and Hawkins 2013, Parks et al. 2014, Giorli 2016, Ricci et al. 2017). Bearing that in mind, many different indices have been produced to quantify marine biological processes, such as Acoustic Richness, Acoustic Entropy Index and Acoustic Complexity Index (McWilliam and Hawkins 2013, Gage and Axel 2014, Lillis et al. 2014, Staaterman et al. 2014). Their use as proxies for marine biodiversity is already being assessed (Harris et al. 2016), with the Acoustic Complexity Index being the most favoured (Lindseth and Lobel 2018).

The Acoustic Complexity Index has been shown to have a number of drawbacks (McWilliam and Hawkins 2013, Kaplan et al. 2015), which may have been the reason for the lack of concurrence between the ACI and visual biodiversity in this case. For example, the ACI is prone to being increased heavily by snapping shrimp, which produce a high intensity broadband ‘snap’, meaning an increased ACI when diversity has only marginally increased (McWilliam and Hawkins 2013). In contrast, chorusing behaviour of fishes can heavily decrease ACI (Kaplan et al. 2015). Hence, ACI in certain situations can be dominated by either few or many species, producing opposing changes in the ACI and the observed biodiversity. The assemblage composition outside of the MPA, in this case, was heavily dominated in abundance by hermit crabs of the genus *Pagurus*. It is possible that these large aggregations of *Pagurus* spp. (up to 70 in one video), which ‘rap’ on others’ shells for shell competition (Edmonds and Briffa 2016), are dominating the ACI in a similar way to snapping shrimps. Snapping shrimp heavily dominating the marine soundscape (Au and Banks 1998, Radford et al. 2008, Lindseth and Lobel 2018) won’t just affect the ACI but also most other indices of acoustic energy currently being investigated as proxies for biodiversity. Thus, this issue needs to be overcome for multiple different methods to be unbiased.

All recordings here were made during the day and, as such, not at the highest acoustic activity times, which for most fish are dawn and dusk (Radford et al. 2014, Bertucci et al. 2015, 2016, 2017). Further investigation into this index should include high activity times, while also taking into consideration the activity cycles based upon lunar phase (Staaterman et al. 2014, Harris et al. 2016). As shown here, correlations between the ACI and other diversity measures can occur, but can vary considerably in their orientations over years. Thus, higher

temporal scales, across lunar and daily cycles, should be used to assess these indices.

The use of ACI in this MPA, off the south coast of the UK, has not shown the direct relationship with the observed ecology as demonstrated elsewhere indices (Picciulin et al. 2013, Harris et al. 2016) yet did show significant interactions across treatments and years. For this, or another, acoustic index to be used as a fast and cheap monitoring tool, the drawbacks mentioned here need to be addressed within the algorithm that creates the ACI itself. Subsequently, thorough experimental assessments of such alterations to the algorithm will be needed, with robust spatial and temporal coverage. This is essential, as based on a single year of this study (e.g. 2014 or 2018), ACI would have shown a positive correlation with Species Richness that has been found elsewhere. Again, this shows that temporal and geographical scales are important considerations for the development of any such index or methodology.

In conclusion, the Acoustic Complexity Index is not as yet ready to be used as a marine diversity monitoring tool, even in conjunction with other methods, such as BRUVs, which showed the recovery and increased diversity within the Lyme Bay MPA. However, this acoustic index shows potential to allude to shifting benthic assemblage compositions, yet with no consistency when used alongside univariate measures of diversity. This implies that although it is not without its own disadvantages, the ACI is demonstrating more complex changes than overall univariate diversity. For it to be used as a monitoring tool, the information it provides regarding these shifting compositions needs to be fully researched and understood.

"It is a curious situation that the sea, from which life first arose, should now be threatened by the activities of one form of that life. But the sea, though changed in a sinister way, will continue to exist; the threat is rather to life itself."

Rachel Carson

3

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.

Authors' Contributions

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

Author	Institution	% Contribution
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Adam Rees	University of Plymouth	5
Amy Y. Cartwright	University of Plymouth	5
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Emma V. Sheehan	University of Plymouth	10

Abstract

Designated using a Statutory Instrument in 2008, Lyme Bay Marine Protected Area (MPA) is the UK's first and largest example of an ambitious, whole-site approach to management, to recover and protect reef biodiversity. The whole-site approach applies consistent management, in this case excluding bottom towed fishing, across the full 206 km² extent of the MPA, thus protecting a mosaic of reef associated habitats from regular damage, while still allowing less destructive fishing methods, such as static gear, rod and line, and diving. To assess the effectiveness of this management strategy for mobile taxa and the sustainability for those taxa that continue to be targeted, Exploited and Non-Exploited species' populations were compared inside the MPA, relative to open control sites spanning 11 of the 12 years of designation. Baited Remote Underwater Video systems (BRUVs) were deployed annually to assess mobile benthic and demersal fauna. Overall, the number of taxa significantly increased in the MPA relative to the open controls, while total abundance increased in both treatments. Exploited fish showed increases in number of taxa (430%) and total abundance (370%) inside the MPA over 11 years. Likewise, but to a lesser degree in the Open Controls, number of taxa of commercially exploited fish increased over time, potentially showing 'spillover' effects from the MPA. Non-Exploited fish did not show such changes. Regardless of constituting the majority of the fishery value, highly valuable Exploited invertebrates showed no significant changes over time.

Synthesis and applications: The Lyme Bay MPA shows that protection of a whole-site, comprising mosaics of different benthic habitats, through protection of sessile organisms that contribute to Essential Fish Habitats (EFH). This Ecosystem Approach to Fisheries Management can benefit and maintain sus-

tainable fisheries and species of conservation importance.

Keywords:

Biodiversity, BRUVs, Conservation, Monitoring, Whole-Site Approach.

3.1 Introduction

Globally, the implementation of Marine Protected Areas (MPAs) to conserve and protect marine biodiversity and aid fishery management has increased rapidly over the last 25 years (Halpern et al. 2010, Da Silva et al. 2015). By protecting vulnerable species and habitats, MPA management strategies have successfully increased the abundance and size of fisheries' target species and increased resilience to natural and anthropogenic disturbance (Edgar et al. 2014, Sheehan et al. 2013a). Thus, depending on how they are managed and enforced, MPAs have the potential to simultaneously benefit fisheries and conservation (Babcock et al. 2010). However, only 7.9% of the oceans are designated as MPAs (UNEP-WCMC and IUCN (2020); ~ 17,000 MPAs covering 28.6 million km²), over 2% short of the 10% target for 2020, set by the convention of Biological Diversity's Aichi Target 11 (Lubchenco and Grorud-Colvert 2015). Furthermore, 'paper parks' (MPAs established without appropriate management and or resources to monitor, maintain or enforce protection) are prevalent despite increased global pressure to protect ecosystems using the MPA approach (Rife et al. 2013a).

Permitted activities vary between different MPA designations and are typically zoned within MPAs, whereby only listed features such as specific habitats are afforded protection (Solandt et al. 2020), particularly within European waters. Partial protection can also include seasonal closures, specific species protection and fishing practice restrictions (Williams et al. 2006, Hattam et al.

2014, Dinmore et al. 2003, Topor et al. 2019). This form of management limits its recovery potential as the presence, extent and condition of features are required to be evidenced. A more ambitious approach is the whole-site approach, a method for applying the Ecosystem Approach to Fisheries Management (EAFM: Serpetti et al. 2017) through consistent protection, across the whole seabed, acknowledging that habitats and species can recover beyond their current status when protected (Sheehan et al. 2013a). Therefore, this approach protects a range of species and habitats across a larger area than the current evidenced extent of the 'feature' of interest (Solandt et al. 2020), including species or habitats that are highly important to the 'feature' of interest. The most extreme example are No Take Zones (NTZs) that exclude all extractive or destructive practices (Sale et al. 2005, Harasti et al. 2018). However, partial protection that only excludes the most destructive fishing activities has also been shown to be highly effective at protecting conservation features, yet evidence of benefits to fisheries are rare (Beukers-Stewart et al. 2005, Sheehan et al. 2013b,a). MPAs are often seen as a compromise between conservationists and groups with direct fishing interests (Denny and Babcock 2004, Sciberras et al. 2015). This compromise can lead to less protection for partial MPAs and decreased spatial extent for NTZs (Hamel et al. 2013), and has led to a debate as to the effectiveness of these areas (Edgar 2011, Turnbull et al. 2021). The level of protection and enforcement of an MPA, alongside the size, age and isolation, determines how species and habitats recover following designation, with greater protection generally causing a more positive response (Edgar and Stuart-Smith 2014). Most studies to date considering the effectiveness of 'feature-based' partial MPAs have found them ineffectual at achieving the conservation or fisheries' goals that instigated their designation (Shears et al. 2006, Piet and Rijnsdorp 1998, Turnbull et al. 2021) and, in some cases,

even increased the human threats to the system inside the protected zone (Zupan et al. 2018). Thus, it has been suggested that the whole-site approach can more adequately achieve the goals of both fisheries and conservation management (Solandt et al. 2020, Rees et al. 2020). Yet, due to the rarity of MPAs that have adopted the whole-site approach, few studies have assessed this style of marine management.

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

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

ter visual census (Kough et al. 2017), underwater video survey (Sheehan et al. 2010, 2013a), and fisheries' acoustic surveys (Erisman and Rowell 2017).

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

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

Non-Exploited mobile species (Solandt et al. 2020).

To assess this prediction the following hypotheses were tested:

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

3.2 Methods

3.2.1 Survey Location and Design

Lyme Bay MPA (Fig. 3.1), located on the southwest coast of England, covers 206km² of nationally important rocky reef habitat (Hiscock and Breckels 2007). For site selection, suitably comparable rocky reef regions comprising bedrock, boulders and cobbles were identified by utilising fishing effort and habitat data (Stevens et al. 2014, & Appendix B Fig. B.1). Within these broadly defined regions, sites were spread across each treatment (MPA and Open Controls:

OC) to ensure that sites were spatially interspersed as much as possible (Fig. 3.1). BRUVs were deployed each summer from 2009 to 2019. Sites of three replicate BRUVs, spaced $\sim 100\text{m}$ apart, were deployed, to depths ranging from 14m to 29m, for 45 minutes before being recovered. Twelve sites were inside the MPA (36 BRUVs) and six were in the OC (18 BRUVs). Annually, the same latitude and longitude of sites were used as targets, yet each replicate is considered independent as location will be influenced by the prevalent tidal and atmospheric conditions during deployment.

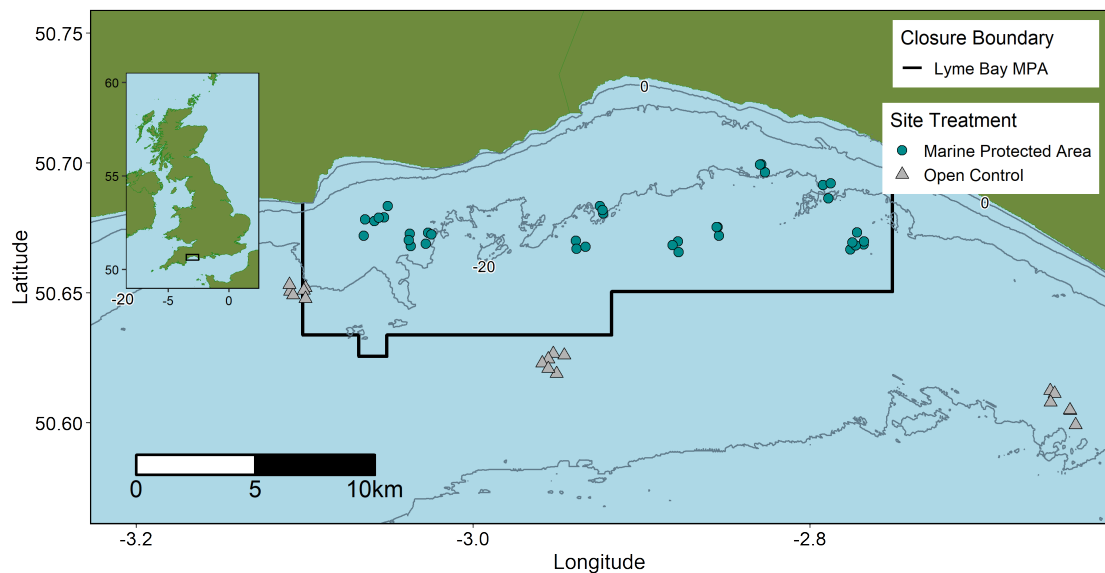


Fig. 3.1: Baited Remote Underwater Video system locations within Lyme Bay MPA (blue circles) and Open controls (grey triangles).

3.2.2 Equipment

Baited Remote Underwater Video systems (BRUVs) consisted of a metal frame, lead weights ($\sim 30\text{kg}$), underwater wide-angle camera housing with horizontal facing camera (Panasonic HDC-SD60 and HDC-SD80), LED lights and a fixed bait pole (Bicknell et al. 2019). Metal bait boxes were fixed on the pole one metre from the camera filled with $\sim 100\text{g}$ of Atlantic mackerel *Scomber scombrus* cut into segments. Fresh bait was replenished for each deployment. Videos

from BRUVs were assessed *in situ* to ensure that the camera had landed and recorded a viable sample. Failed attempts were repeated to ensure that all samples were suitable.

3.2.3 Video Analysis

Videos were subject to quality control checks according to the following requirements. Videos must: be in focus; have adequate visibility to discern the bait box clearly (potentially caused by suspended sediment from nearby fishing activity or high levels of plankton); have no fauna or flora obscuring the view and have the seafloor within view (Fig. 3.3: Examples of unacceptable (a & b) and acceptable (c-f) videos). All criteria must be maintained for a minimum of 30 minutes across the recording. Videos which did not meet these requirements were repeated in the field to record a viable sample. Videos which did meet the requirements were watched at normal speed for 30 minutes, after a preliminary 5 minute settling period. Videos were analysed using dual monitors. One screen displays the video (Windows Media Player), the other the raw dataset for input (Microsoft Excel, Fig. 3.2). After the settling period, videos were watched at normal speed in one minute increments. For every minute all mobile fauna were identified to the highest taxonomic resolution possible, and counted. Mobile species were categorised as taxa that were deemed able to continuously move, either in response to the bait or in response to other taxa, which are themselves reacting to the bait. Thus, benthic taxa such as *Pecten maximus*, *Aequipecten opercularis* and *Ophiothrix fragilis* were not included. For every one-minute segment of the video, the MaxN (maximum number of individuals on screen) for each taxon was recorded. Relative abundance of each taxa was recorded as the greatest MaxN value in any one minute, within the 30 minutes analysed. MaxN is considered a conservative estimate of relative

abundance of mobile species attracted to the bait, which decreases the chance of an individual being repeatedly recorded (Cappo et al. 2004).

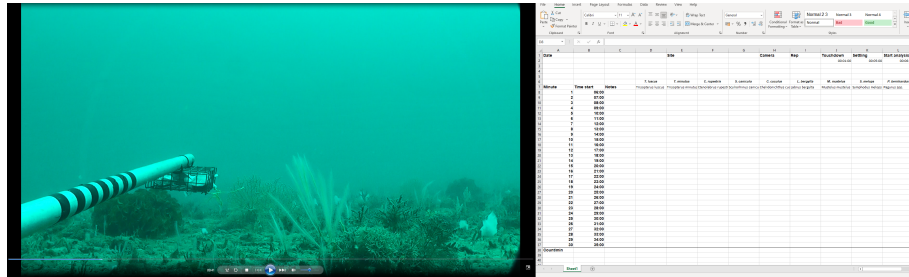


Fig. 3.2: Example screen grab of Dual Monitor video analysis.

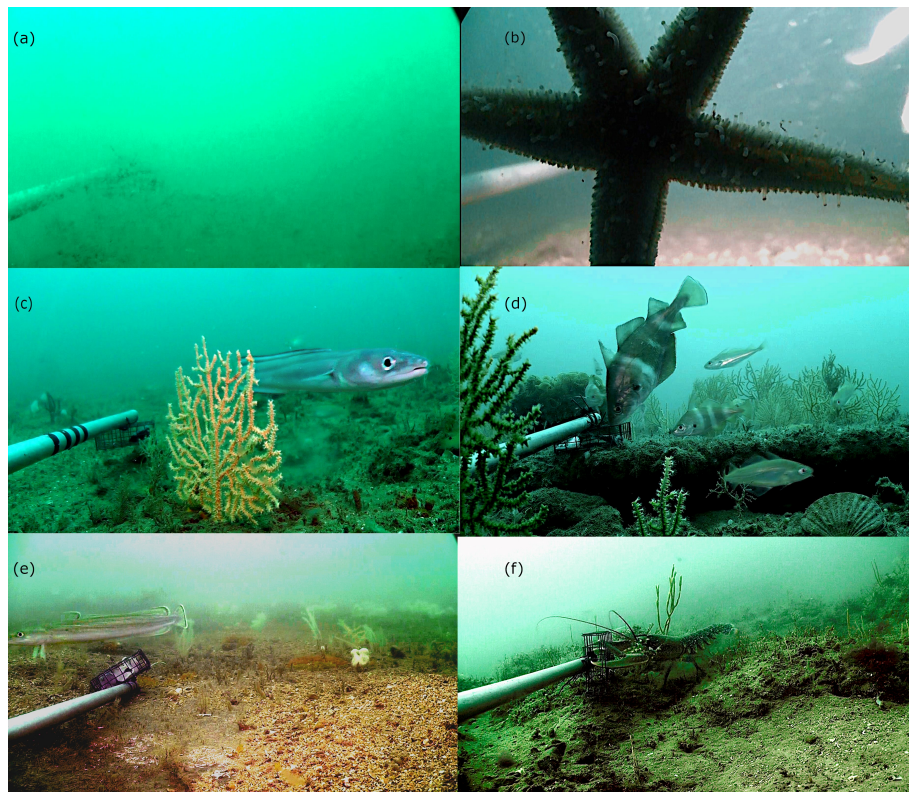


Fig. 3.3: Example screen grabs from BRUVs: poor visibility (a: unacceptable), a seastar *Asterias rubens* obscuring the field of view (b: unacceptable), a Conger Eel *Conger conger* behind of a Pink Seafan *Eunicella verrucosa* (c: acceptable), multiple fish, *Trisopterus luscus* and *Trisopterus minutus*, amongst Pink Seafans *Eunicella verrucosa* and a King Scallop *Pecten maximus* (d: acceptable), a Common Ling *Molva molva* (e: acceptable) and a European Lobster *Homarus gammarus* (f: acceptable).

3.2.4 Statistical Analysis

The univariate metrics, number of taxa and total abundance, were calculated in 'dplyr' and 'vegan' in R using BRUVs MaxN values (Oksanen et al. 2019, Wickham et al. 2019b). Unless stated otherwise, total abundances were fourth root transformed to meet assumptions of normality. Exploited taxa were defined as taxa which are either landed by fishers or caught and used as bait to catch other species in Lyme Bay (*Personal Communication with Lyme Bay fishers*, Table 3.1). As the BRUVs enumerated a wide range of species (Table 3.1), from sharks (*Mustelus mustelus*) and wrasse (*Labrus bergylta*, *Ctenolabrus rupestris* etc) to echinoderms (*Asteria rubens*) and hermit crabs (*Pagurus spp.*), Exploited and Non-Exploited species were classified as either fish (Actinopterygii and Elasmobranchii) or invertebrates (Asteroidea, Cephalopoda, Echinoidea, Gastropoda, Holothuroidea, Malacostraca and Ophiuroidea). Thus, taxa were grouped as Exploited or Non-Exploited fish, or Exploited or Non-Exploited invertebrates.

Permutational Multivariate Analysis of Variance (PERMANOVA Anderson et al. 2008, Clarke and Gorley 2015) was used to test differences between years and treatments for both multivariate (Assemblage composition) and univariate (number of taxa and total abundance) response variables for all taxa, then just univariate response variables for Exploited and Non-Exploited fish and Non-Exploited invertebrates. Year and Treatment were fixed factors (Year, 11 levels: 2009-2019; Treatment, 2 levels: MPA and Open Control). Multivariate analyses were carried out on the basis of a Bray–Curtis dissimilarity matrix, calculated from dispersion weighted fourth root transformed abundance data. Univariate analyses were carried out based on Euclidean distances. The statistical significance of the variance components was tested using 9999 permutations under

a reduced model (Anderson 2001a). Visualisation of multivariate data was carried out by a non-metric multidimensional scaling (MDS) ordination. Percentage contribution of taxa to dissimilarity between sites was assessed using the SIMPER (Similarity Percentages) method within each year and treatment (Clarke and Gorley 2015).

Due to a high proportion (~60%) of zero values when the data were split into Exploited invertebrates, Zero-Inflated Poisson (ZIP) regression models were used from the 'pscl' package in R to assess the data (Achim et al. 2008, Zuur and Ieno 2016). Model selection utilised Akaike Information Criteria (AIC) for both the Poisson "count" and binomial (Bernoulli) "zero" portions of the model (Appendix B Table B.1).

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

Table 3.1 Exploited and Non-Exploited Fish and Invertebrates. Information based on use and landings of fishers in Lyme Bay. Symbols denote species which were exclusively recorded in the MPA (^m) and OC (^o).

Fish		Invertebrates	
Exploited	Non-Exploited	Exploited	Non-Exploited
<i>Chelidonichthys cuculus</i>	<i>Blenniidae</i> spp ^(m)	<i>Buccinum undatum</i>	<i>Asterias rubens</i>
<i>Chelidonichthys lucerna</i>	<i>Callionymus lyra</i>	<i>Cancer pagurus</i>	<i>Calliostoma</i>
			<i>zizyphinum</i> ^(m)

Table 3.1 Exploited and Non-Exploited Fish and Invertebrates. (continued)

Fish		Invertebrates	
Exploited	Non-Exploited	Exploited	Non-Exploited
<i>Conger conger</i>	<i>Centrolabrus exoletus</i> ^(m)	<i>Homarus gammarus</i>	<i>Goneplax rhomboides</i>
<i>Eutrigla gurnardus</i>	<i>Ctenolabrus rupestris</i>	<i>Maja squinado</i>	<i>Hyas coarctatus</i> ^(o)
<i>Labrus bergylta</i> ^(m)	<i>Gaidropsarus</i> spp ^(m)	<i>Sepia officinalis</i> ^(m)	<i>Inachus</i> spp
<i>Limanda limanda</i>	<i>Gobiidae</i> spp		<i>Liocarcinus depurator</i>
<i>Mullus surmuletus</i>	<i>Labrus mixtus</i> ^(m)		<i>Loligo</i> spp ^(m)
<i>Pollachius pollachius</i>	<i>Lepadogaster</i> spp		<i>Luidia ciliaris</i>
<i>Raja clavata</i>	<i>Merlangius merlangus</i>		<i>Necora puber</i>
<i>Scyliorhinus canicula</i>	<i>Molva molva</i> ^(m)		<i>Macropodia</i> spp
<i>Scyliorhinus stellaris</i> ^(m)	<i>Symphodus melops</i> ^(m)		<i>Neopentadactyla mixta</i> ^(m)
<i>Solea solea</i> ^(o)	<i>Triakidae</i> spp		<i>Ophiuroidea</i> spp
<i>Spondyliosoma</i>	<i>Trisopterus minutus</i>		<i>Pagurus</i> spp
<i>cantharus</i>			
<i>Trachurus trachurus</i>			<i>Psammechinus miliaris</i>
<i>Trisopterus luscus</i>			<i>Porcellana platycheles</i>
<i>Zeus faber</i> ^(m)			<i>Tritonia nilsodhneri</i> ^(m)
			<i>Tritia reticulata</i>
			<i>Xantho hydrophilus</i>

3.3 Results

A total of 13175 individuals from 39 families were recorded during the study with 25 species (15 families) from the class Actinopterygii, 4 species (3 families) from the class Elasmobranchii, 12 species (10 families) from the class Malacostraca and 4 species (4 families) from the class Gastropoda. Hermit crabs *Pagurus* spp. were the most abundant taxa (2820 individuals), followed

by Pouting *Trisopterus minutus* (1595 individuals) and Nettle Dogwhelk *Tritia reticulata* (1120 individuals). Across both treatments the most ubiquitous taxa was *Scyliorhinus canicula* with 869 individuals across 71% of sites, followed by *Pagurus* spp. and Gobiidae spp. (2820 & 1012 individuals: both across 58% of sites). Inside the MPA the most common taxa were *Trisopterus minutus* (1135 individuals), *Tritia reticulata* (1043 individuals) then Gobiidae spp. (1012 individuals). For the OC the most common taxa were *Pagurus* spp. (2267 individuals), *Trachurus trachurus* (634 individuals), then *Merlangius merlangus* (589 individuals).

3.3.1 All Species

Assemblage Composition

Assemblages at MPA sites were always different from those in Open Controls (Fig. 3.4 & Table 3.2), but over time the assemblage composition of the two treatments also shifted in differing ways, shown by a significant year:treatment interaction (Table 3.2). The MPA showed large shifts in assemblage in the first years, then after five years proceeded to become consistent over time, unlike the OC, which showed random annual assemblage shifts with little to no consistency over time (Fig. 3.4). Assemblage similarities, within sites across years and treatments, were driven primarily by the Small-Spotted catshark *Scyliorhinus canicula* and Gobiidae spp (Fig. 3.5). Most of the remainder of the similarity within the MPA sites was driven by reef associated wrasse species (dark blues, Fig. 3.5), whereas in the OC this was driven by scavenging crustaceans, echinoderms and gastropods (yellows, oranges & dark browns, Fig. 3.5). Excluding *Scyliorhinus canicula*, the vast majority of the similarity within the OC sites was driven by the scavenging crustacean, *Pagurus* spp. (Fig. 3.5).

Table 3.2 PERMANOVA results for All Species (Assemblage, Number of Taxa and Total Abundance); Exploited and Non-Exploited Fish (Number of Taxa and Total Abundance) and Non-Exploited Invertebrates (Number of Taxa and Total Abundance), as well as Zero-Inflated Poisson Generalised Linear Mixed Effect model results for Exploited Invertebrates (Number of Taxa and Total Abundance). Year, Treatment, Site and Residual are abbreviated throughout to Yr, Tr, Si(Tr) and Res.

Source	df	Assemblage			Number of Taxa			Total Abundance		
		SS	Pseudo F	p value	SS	Pseudo F	p value	SS	Pseudo F	p value
All Species										
Yr	10	117000	6.56	<0.0001***	487	9.57	<0.0001***	21.4	11.5	<0.0001***
Tr	1	88900	12.80	<0.0001***	18.3	0.808	0.38	6.35	7.64	0.013*
Si(Tr)	17	157000	11.10	<0.0001***	509	10.8	<0.0001***	18.7	10.2	<0.0001***
YrxTr	10	32200	1.81	<0.0001***	74.6	1.47	0.16	2.6	1.4	0.18
YrxSi(Tr)	156	278000	2.15	<0.0001***	794	1.84	<0.0001***	29	1.73	<0.0001***
Res	387	320000			1070			41.5		

Table 3.2 PERMANOVA and ZIP results (*continued*)

Source	df	Assemblage			Number of Taxa			Total Abundance		
		SS	Pseudo F	p value	SS	Pseudo F	p value	SS	Pseudo F	p value
Fish										
Exploited										
Yr	10				93.8	8.35	<0.0001***	53	15.8	<0.0001***
Tr	1				24.1	14.5	0.0015**	0.825	2.42	0.14
Si(Tr)	17				35.2	3.73	<0.0001***	6.91	2.51	0.0011**
YrxTr	10				16.8	1.49	0.14	4.67	1.4	0.19
YrxSi(Tr)	156				175	2.02	<0.0001***	52.3	2.07	<0.0001***
Res	387				215			62.8		
Non-Exploited										
Yr	10				51.8	3.2	<0.0001***	27	6.83	<0.0001***
Tr	1				106	28.9	<0.0001***	3.52	6.89	0.021*
Si(Tr)	17				79.6	4.95	<0.0001***	10.5	2.73	<0.0001***
YrxTr	10				23.8	1.48	0.15	13.3	3.35	0.0012**
YrxSi(Tr)	156				252	1.71	<0.0001***	61.8	1.75	<0.0001***
Res	387				366			87.4		
Invertebrates										
Non-Exploited										
Yr	10				6.1	1.68	0.088	7	2.28	0.016*
Tr	1				0.197	0.1	0.75	0.215	0.149	0.7
Si(Tr)	17				44	8.96	<0.0001***	32.3	8.7	<0.0001***
YrxTr	10				8.37	2.3	0.015*	7.26	2.37	0.015*
YrxSi(Tr)	156				56.7	1.26	0.04*	47.9	1.41	0.0039**
Res	387				112			84.5		
Exploited										
					Estimate (SE)	z value	p value	Estimate (SE)	z value	p value
Zero Model (Bernoulli)										

Table 3.2 PERMANOVA and ZIP results (*continued*)

Source	df	Assemblage			Number of Taxa			Total Abundance		
		SS	Pseudo F	p value	SS	Pseudo F	p value	SS	Pseudo F	p value
Intercept					-0.725(0.0596)	-12.2	<0.0001***	0.656(0.0898)	7.31	<0.0001***
Tr								-0.744(0.136)	-5.47	<0.0001***
Count Model (Poisson)										
Intercept					-11.6(59.3)	-0.195	0.84	0.163(0.302)	0.541	0.59
Yr								-0.0284(0.0404)	-0.704	0.48
Tr								-0.754(0.326)	-2.31	0.021*

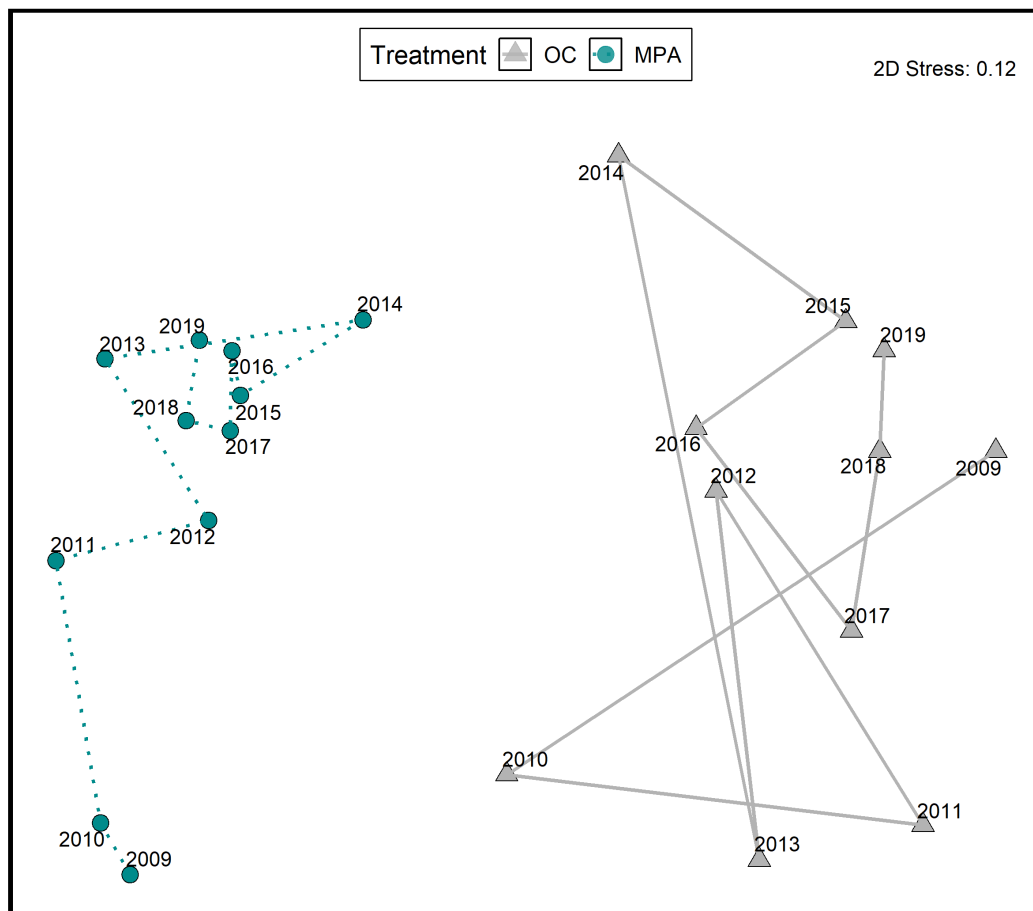


Fig. 3.4: MDS ordination showing the differences of assemblage composition over eleven years between the two treatments (MPA shown by blue circles and OC shown by grey triangles). Lines show yearly progression from 2009 to 2019.

Number of Taxa and Total Abundance

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

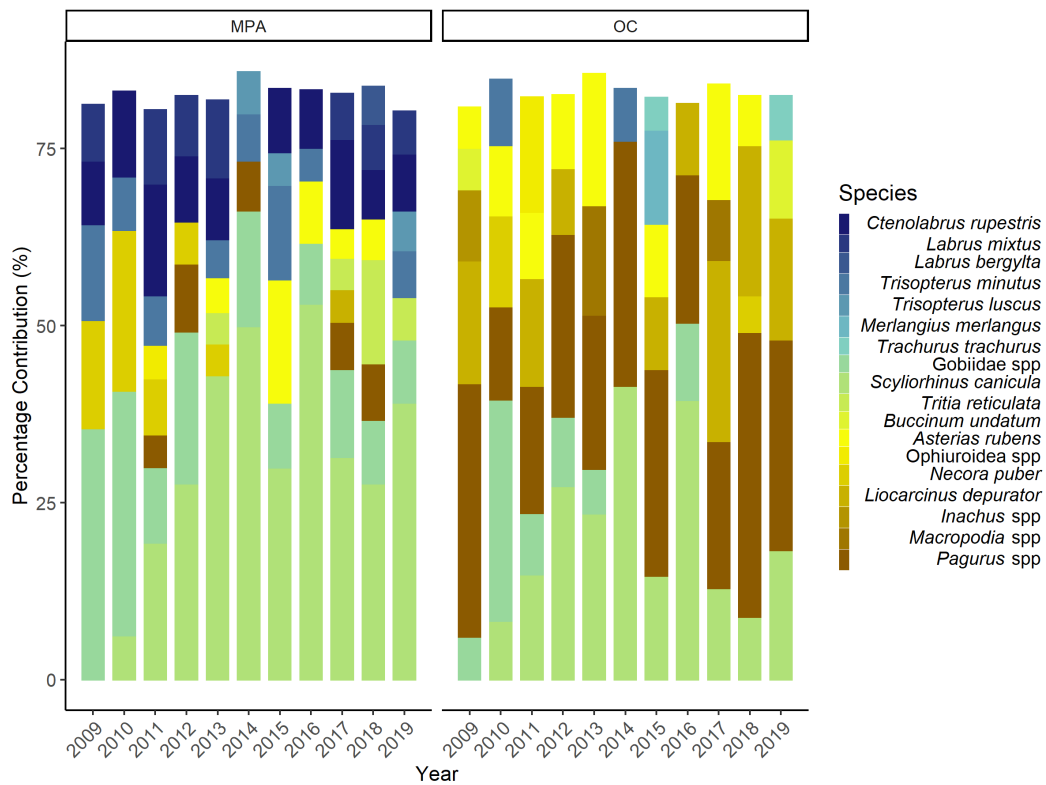


Fig. 3.5: SIMPER results for the top 80% contributions of species driving the similarities of assemblage compositions of sites within year and treatment.

± 0.301 & 2.44 ± 0.0958 in 2019 (15.8% & 23.4% increase in the number of taxa and total abundance respectively).

This change over time was significant in both the number of taxa and total abundance, yet neither metric showed a significant year:treatment interaction (Table 3.2). However, the total abundance was significantly different between treatments (Table 3.2). The number of taxa showed a significant linear increase over time inside the MPA, while the total abundance showed a significant linear increase in both treatments over time (Fig. 3.6a and 3.6b).

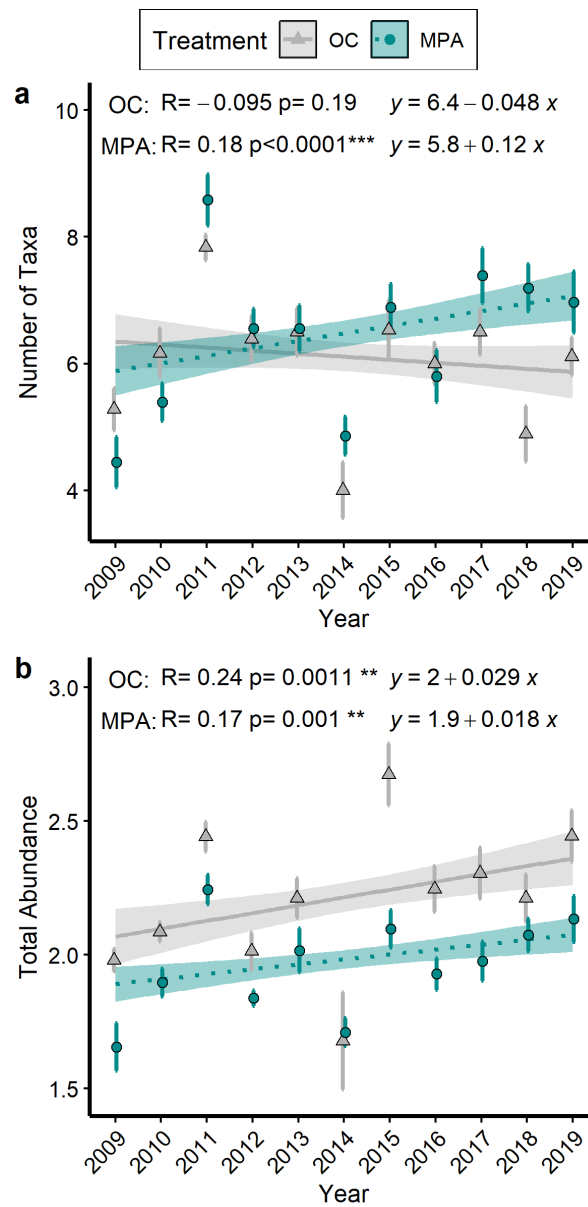


Fig. 3.6: Number of taxa (a) and total abundance (fourth root transformed: b) by year across treatments (MPA: blue circles, OC: grey triangles). Lines and equations show linear regression equation coefficients. Points with errors bars show mean values and standard errors.

3.3.2 Fish

Number of Taxa and Total Abundance

In the MPA, the mean number of taxa and mean total abundance of Exploited fish changed from 0.417 ± 0.122 & 0.311 ± 0.0856 in 2009 to 2.23 ± 0.184 & 1.45 ± 0.0486 in 2019 (430% & 370% increase in the number of taxa and total abundance respectively). For the Non-Exploited fish, in the MPA, the mean number of taxa and mean total abundance changed from 2.33 ± 0.211 & 1.46 ± 0.0916 in 2009 to 2.23 ± 0.225 & 1.41 ± 0.103 in 2019 (4.5% and 3.3% decrease in the number of taxa and total abundance respectively). In the OC, the mean number of taxa and mean total abundance of Exploited fish changed from 0.278 ± 0.109 & 0.316 ± 0.125 in 2009 to 1.61 ± 0.216 & 1.63 ± 0.165 in 2019 (480% and 420% increase in the number of taxa and total abundance respectively). In the OC, the mean number of taxa and mean total abundance of Non-Exploited fish changed from 1.28 ± 0.24 & 1.14 ± 0.156 in 2009 to 1.28 ± 0.195 & 1.56 ± 0.175 in 2019 (0% & 37% increase in the number of taxa and total abundance respectively). This change over time in the number of taxa of Exploited fish in both treatments was significant (Table 3.2). The MPA showed a much greater increase over time (gradient of 0.14: Fig. 3.7a) than that of the OC (gradient of 0.062: Fig. 3.7a). The number of taxa of Non-Exploited fish was significantly different across years and treatments but, like the Exploited fish, showed no year:treatment interaction. However, the change over time inside the MPA, unlike that of the Exploited fish, was expressed as a significant linear decrease (Fig. 3.7b). The total abundance of Exploited fish showed a significant difference between years but not between treatments (Table 3.2). Both treatments showed significant linear increases over time (Fig. 3.7c). There was a significant year:treatment interaction for the total abundance

of Non-Exploited fish (Table 3.2), which was expressed as a significant linear decrease over time inside the MPA (Fig. 3.7d).

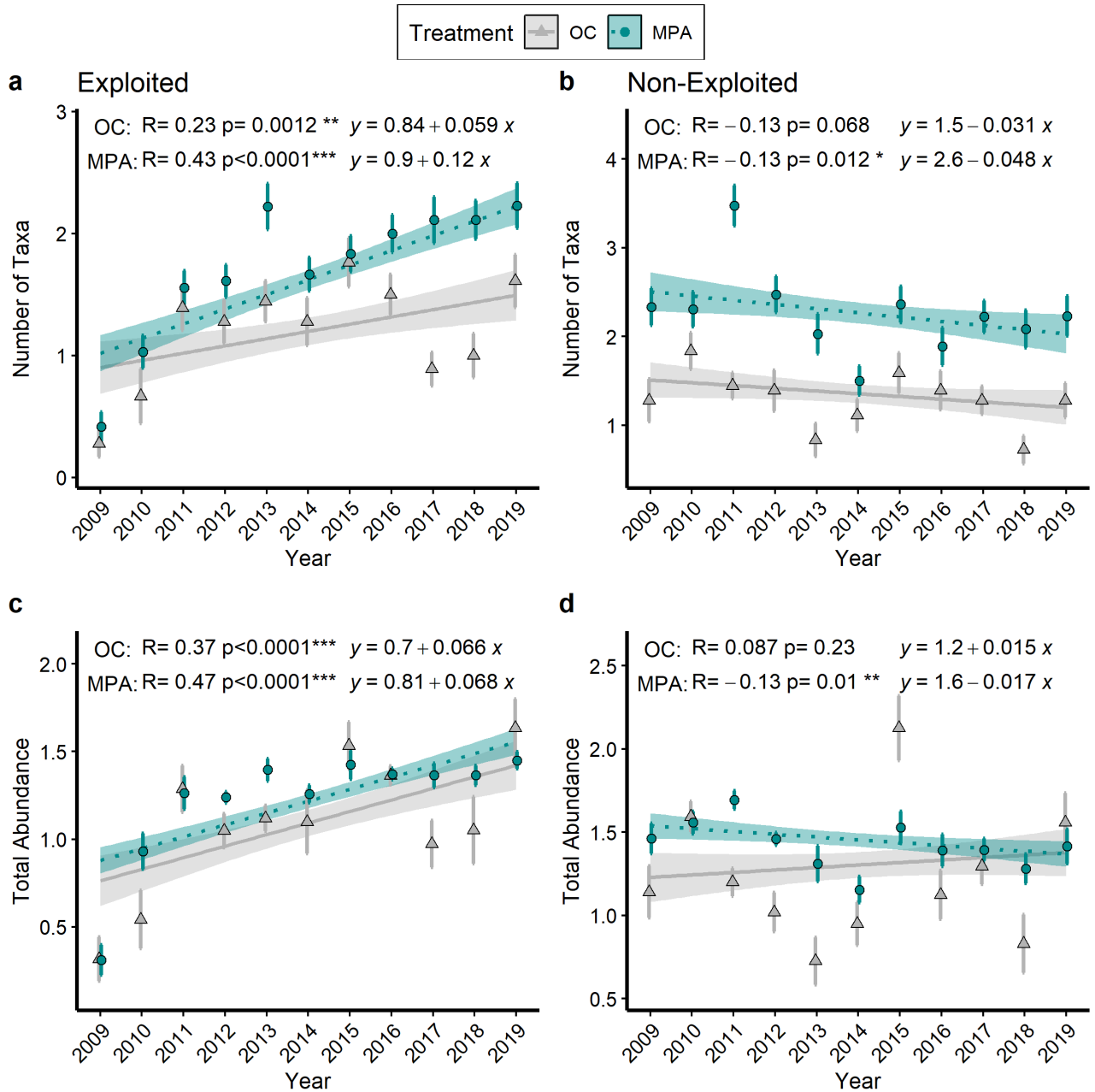


Fig. 3.7: Number of taxa (a) and total abundance (c) of Exploited fish by year and treatments, and number of taxa (b) and total abundance (fourth root transformed: d) of Non-Exploited fish by year and treatments (MPA: blue circles, OC: grey triangles). Lines and equations show linear regression equation coefficients. Points with errors bars show mean values and standard errors.

3.3.3 Invertebrates

Number of Taxa and Total Abundance

In the MPA, the mean number of taxa and mean total abundance of Exploited invertebrates changed from 0.333 ± 0.0797 & 0.333 ± 0.0797 in 2009 to 0.543 ± 0.118 & 0.686 ± 0.182 in 2019 (63% & 110% increase in the number of taxa and total abundance respectively). For the Non-Exploited invertebrates, in the MPA, the mean number of taxa and mean total abundance changed from 1.36 ± 0.196 & 0.985 ± 0.104 in 2009 to 1.97 ± 0.297 & 1.35 ± 0.16 in 2019 (45% and 37% increase in the number of taxa and total abundance respectively). In the OC, the mean number of taxa and mean total abundance of Exploited invertebrates changed from 0.5 ± 0.121 & 0.722 ± 0.24 in 2009 to 0.667 ± 0.14 & 1.33 ± 0.362 in 2019 (33% and 85% increase in the number of taxa and total abundance respectively). For the Non-Exploited invertebrates in the OC, the mean number of taxa and mean total abundance changed from 3.22 ± 0.25 & 1.76 ± 0.0588 in 2009 to 2.56 ± 0.294 & 1.77 ± 0.123 in 2019 (21% decrease & 0.47% increase in the number of taxa and total abundance respectively). Neither year nor treatment could be fitted to model the number of exploited invertebrate taxa, with the 'best' ZIP model utilising only the intercept for both the count and zero parts of the model (Table 3.2). However, there was a significant year:treatment interaction for the number of taxa for Non-Exploited invertebrates (Table 3.2), with a significant linear decrease with time in the OC (Fig. 3.8b). The total abundance of Exploited invertebrates was significantly lower in the MPA compared to the OC (Table 3.2 & Fig. 3.8c). The total abundance of Non-Exploited invertebrates did show a significant year:treatment interaction (Table 3.2) but there was no significant linear trend over time (Fig. 3.8d).

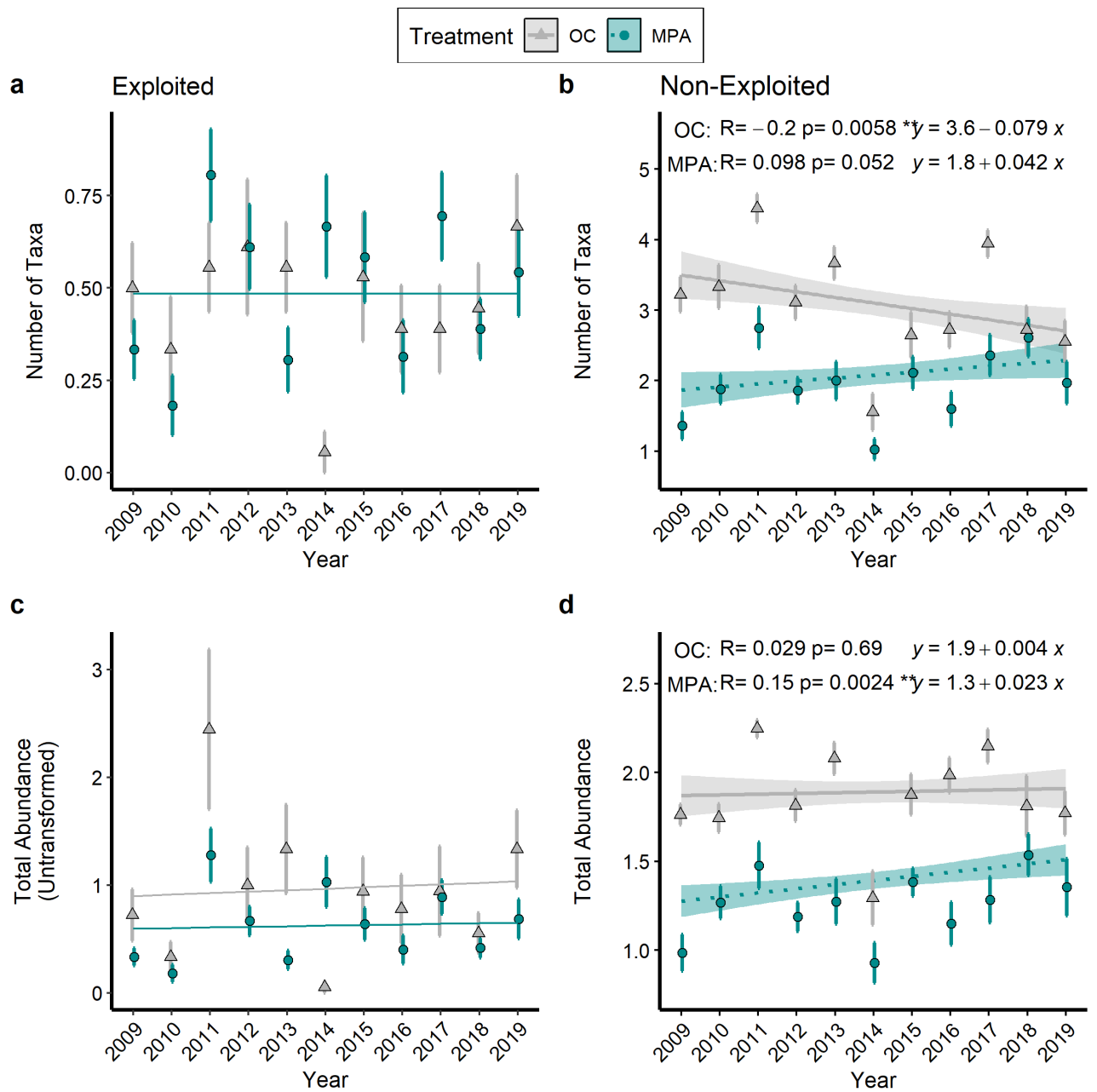


Fig. 3.8: Predicted vs observed number of taxa (a) and total abundance (c) of Exploited invertebrates over time for ZIP models and observed number of taxa (b) and total abundance (fourth root transformed: d) of Non-Exploited invertebrates across year and treatment (MPA: blue circles, OC: grey triangles). Lines show linear and Zero-Inflated Poisson regressions. Points with errors bars show mean values and standard errors.

3.4 Discussion

Over the course of the 11 year study, the exclusion of bottom towed fishing inside the MPA significantly altered the assemblage composition and increased the diversity (number of taxa) of mobile taxa, relative to areas that remained open to these fishing practices (Open Controls: Table 3.2 & Fig. 3.6a). The total abundance of these mobile taxa significantly increased over time in both treatments (Table 3.2 & Fig. 3.6b). When specifically assessing Exploited fish, which continue to be exploited and fished within the protected area, there was a significant increase over time in the number of taxa and total abundance across both treatments (MPA and Open Controls). Non-Exploited fish significantly decreased over time in the MPA, although there was a small R value for this trend (Table 3.2 & Fig. 3.7). Exploited invertebrates had lower total abundance inside the MPA compared to the OC, but neither treatment showed any change over time in the number of taxa or total abundance (Table 3.2 & Fig. 3.8a & c). Non-Exploited invertebrates showed a lower number of taxa and total abundance in the MPA but with a decreasing number of taxa in the Open Controls (Table 3.2 & Fig. 3.8b & d).

The Lyme Bay Statutory Instrument, was designated to allow recovery and protect the biodiversity of fragile sessile reef fauna across 206km² from further damage by bottom towed fishing gear. The protection has shown to positively benefit sessile reef fauna (Sheehan et al. 2013b,a) and the effects of this protection have now led to positive increases to the mobile fauna over time, with increases in the number of taxa in the MPA. This is likely to be due to a combination of direct displacement of species, from areas subject to bottom towed fishing to areas not subject to bottom towed fishing (Dinmore et al. 2003), and through indirect protection and proliferation of the sessile reef habitat, which, in

turn, increases survivorship of mobile taxa (Sheehan et al. 2013a, Wilson et al. 2010, Howarth et al. 2015).

Fish assemblages are dependent on depth, habitat complexity and availability, competition/predation and larval/recruitment variability (Harasti et al. 2018, Meekan et al. 2018), and, as such, can be highly variable (Stige et al. 2019). However, in this case, over time the number of taxa and total abundance of Exploited fish increased across both treatments. The whole-site approach employed in Lyme Bay has led to the increase of the functional reef area within the bay (Sheehan et al. 2013b,a). The increase in Exploited fish will likely have been driven by this increase in functional reef area, which is known to be an EFH (Rabaut et al. 2010). The increase seen in the OC was found to be at a slower rate than the MPA and may have been due to 'spillover' effects, likely driven by a combination of increased larval export and direct adult movement from the MPA to the surrounding area (Berkeley et al. 2004, García-Rubies et al. 2013). Thus, the simultaneous increase in EFH and reduction in collateral damage to habitat complexity associated with seabed dredging and trawling may have contributed to this general increase in taxa and abundance of around 400%. This co-occurred with a decrease in the number of taxa and total abundance of non-exploited fish over time, potentially indicating competitive exclusion by the commercially exploited fish, which are more likely to be larger higher trophic predators (Baudron et al. 2019).

As an indirect effect of exclusion of towed bottom fishing within Lyme Bay, decreases in conflict between towed fishers and potters led to increases in potting levels within the MPA (Mangi et al. 2011). Although less destructive than bottom towed fishing, potting at high densities can have impacts to sensitive habitats (Gall et al. 2020) and target species have harvest-associated selection applied

to them, which could lead to alterations in population size and behavioural selection (Meekan et al. 2018, Madin et al. 2010). The three main fisheries in Lyme Bay, which continue to be carried out within the MPA, utilise pots and target whelks *Buccinum undatum*, brown crab *Cancer pagurus* and European lobster *Homarus gammarus*, which constitute three of the five taxa classed as Exploited invertebrates in this study. Yet, regardless of potentially higher fishing levels, Exploited invertebrates showed no significant temporal trends over the 11 years of study, although there was significantly greater total abundance in the OC.

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

Previous studies of the ecological response to MPAs with partial protection have had varying results (Sciberras et al. 2013), with some, like the current study, finding increases in Exploited taxa (Pipitone et al. 2000, Beukers-Stewart et al. 2005), and others finding no difference between MPAs with partial protection and control sites (Denny and Babcock 2004, Piet and Rijnsdorp 1998). This variability in effects of MPAs with partial protection could be attributed to many factors, such as pre designation fishing pressure, enforcement/adherence level,

age of protection, size of protected area, the level of protection, as well as the sensitivity/appropriateness of the monitoring effort to detect protection effects (Edgar et al. 2014, Claudet et al. 2008, Babcock et al. 2010). Utilising a whole-site approach, such as in Lyme Bay, is being advocated to better protect the whole ecosystem and, by extension, lead to fisheries' increases (Solandt et al. 2020), particularly for larger ($>100\text{km}^2$) MPAs (Edgar et al. 2014).

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

In conclusion, after 11 years of BRUVs monitoring and 12 years of protection, Lyme Bay MPA is showing a positive response in the number and total abundance of Exploited fish taxa. Increases in the number of taxa and total abundance of Exploited fish ($\sim 400\%$ increase over 11 years) inside the MPA, which happened at the same time as an increase in static fishing, show that the protection and enforcement of the area provide benefits to both conservation and fisheries alike. Yet, inconclusive results regarding the main targeted

taxa by value, namely Whelks, Brown Crab and Lobster, require further assessment, alongside fisheries landings data, to fully quantify any benefits the protection has granted the local fishery. Regardless, this study provides further evidence of the capabilities of well enforced and monitored partial protection, which follow an Ecosystem Approach to Fisheries Management, and how the compromise between conservation and fisheries management can benefit benthic ecosystems when the whole-site approach is employed, as opposed to individual feature protection. Furthermore, it illustrates the importance and necessity of monitoring MPAs over appropriate temporal and spatial scales to aid management.

“Ecosystems are not only more complex than we think, ecosystems are more complex than we can think.”

Frank B Golley

4

A Decade Implementing Ecosystem
Approach to Fisheries Management
Improves Diversity and Ecosystem
Function Within a Marine Protected
Area in the UK.

Status: To Be Submitted

Authors' Contributions

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 and LH led the writing of the manuscript.

Author	Institution	% Contribution
Bede F. R. Davies	University of Plymouth	75
Luke Holmes	University of Plymouth	5
Anthony Bicknell	University of Exeter	5
Martin J. Attrill	University of Plymouth	5
Emma V. Sheehan	University of Plymouth	10

Abstract

The Ecosystem Approach to Fisheries Management (EAFM) has highlighted the importance of studying ecosystem functions and services. Yet, ecosystem services and the associated benefits that they provide are rarely the motive for creating Marine Protected Areas (MPAs). Therefore, many MPA monitoring projects do not explicitly study these functions and services. Lyme Bay MPA, located in the SW of England, was established in 2008 to protect the reef biodiversity across a 206 km² 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. Using a combination of towed underwater video and Baited Remote Underwater Video Systems (BRUVs) changes in diversity (taxonomic and functional) and functional traits affected by mobile demersal fishing were assessed in Lyme Bay MPA over 10 years. There was a consistent increase in the number of taxa and the functional traits they provide within the MPA as well as an increase in the overlap of these traits, which increases 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. The MPA showed a trend towards more diverse and resilient rocky reef habitats. This study constitutes a novel MPA assessment ranging across multiple sampling methods to encompass a wide range of taxa using a combination of taxonomic and functional analysis methods. It also reinforces the importance of effective MPA monitoring, which has demonstrated the changes in functional diversity driven by changes in taxonomic diversity.

4.1 Introduction

Coastal areas of the marine environment have historically been over-exploited and subjected to high levels of pressure, such as commercial fishing, nutrient loading and noise from shipping (Pine et al. 2016, Letessier et al. 2019, Brown et al. 2001). Arguably the most destructive impacts to the marine environment have come from unsustainable commercial practices, such as 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 (MPAs: Jones 2008, Cleguer et al. 2015, Gallacher et al. 2016). 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 activity in a whole area (Boonzaier and Pauly 2016). By excluding the most destructive human activities to protect sensitive biogenic habitats, which 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-Based Fisheries Management (EBFM) 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.

To monitor and assess whether ecosystems are recovering under the protection that a MPA has provided, taxonomy-based biodiversity metrics such as, Species Richness or Shannon's Diversity, are often used (Ferreira et al. 2017). Higher levels of taxonomy-based biodiversity are often linked to higher ecosystem functioning and increased productivity (Vačkář et al. 2012). However, large changes in taxonomy-based biodiversity do not necessarily imply equally large changes to ecosystem function (Törnroos and Bonsdorff 2012, Wong and Kay 2019), especially when an ecosystem contains high levels of functional redundancy: when many different species share the same functional traits (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, assessing the change in the functional diversity, the combination of functional richness, functional evenness and functional divergence (Laliberté and Legendre 2010), of a system will 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), with specific traits, modalities (e.g. filter feeding modality within the feeding trait) or groups of traits being heavily linked to specific processes and fluxes. For example: feeding habit has been linked to benthic-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 enumerates the number of different functional traits used by the community, while Functional Evenness and Functional Divergence indicate how the abundance is distributed across the different functional traits. Evenness increases as organism abundance is spread more evenly across all the traits present within the community, whereas Divergence increases as specific

rarer traits become more abundant in relation to others (Laliberté and Legendre 2010, Mason et al. 2008, 2007). Further, the study of functional redundancy, or the overlap of these traits, can indicate the resilience of a MPA to perturbations, such as destructive fishing, biological invasions and storm events (Tillin et al. 2006, McLean et al. 2019). Hence, the study of functional traits by biological trait analysis has been suggested for both monitoring and management (Tillin et al. 2006, Wiedmann et al. 2014, Rijnsdorp et al. 2016).

The most common form of MPAs in Northern Europe follow the ‘feature’ based approach, where the whole ecosystem is not 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 et al. 2013a), 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. 2004a), meaning MPAs which 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. Initially consisting of four, small, voluntary closures of reef areas (22km²), these were later superseded and enveloped within a larger area (206 km²) designated using a Statutory Instrument (SI) in 2008. 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 (His-

cock and Breckels 2007), which can be severely damaged by the mobile fishing gear that was prevalent throughout the bay. 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 fauna were monitored using a towed underwater video system ('towed flying array' henceforth) while mobile species were monitored with Baited Remote Underwater Video systems (BRUVs)(Sheehan et al. 2013b, 2010, 2016, Stevens et al. 2014, & chapter 3). The combination of these data collection methods, which enumerate species ranging from sessile branching sponges to highly mobile elasmobranchs, allow the assessment of a large proportion of the benthic ecosystem. These were originally carried out to perform taxonomic based assessments, evaluating the change in the species or taxa present (Sheehan et al. 2013a, 2010, & chapter 3). In the present study, biological trait analysis was carried out, analysing change in functional traits. Furthermore, as mobile demersal fishing gear is known to significantly impact the relative proportion of specific trait modalities present within an ecosystem (van Denderen et al. 2015, Howarth et al. 2018), 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.

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 (De-La-Ossa-Carretero et al. 2012,

Belley and Snelgrove 2016, Parmar et al. 2016, Munroe et al. 2018) and fish assemblages have been used to assess the impacts of fishing and climate change (Benoit et al. 2013, Benoit and Swain 2008). Particular groups of organisms can be used as indicators for different elements of ecosystem health; 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 EBFM (Long et al. 2015). Here, the use of both towed and BRUVs data together will provide a unique assessment ranging across a large portion of the benthic ecosystem, 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 to assess the taxonomic and functional diversity across Lyme Bay over 10 years:

1. Number of Taxa and Functional Richness increase over time in the MPA, relative to the Open Controls.
2. Functional Divergence and Functional Evenness decrease 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.

4.2 Materials and Methods

4.2.1 Survey Design

Location

Lyme Bay is a moderate energy, south facing area of the south west coast of the UK (Fig. 4.1). The Lyme Bay MPA (50.67 N, -2.95 E), is 206km² 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 et al. 2013b). Since designation, the MPA has acquired additional layers of protection, such as a Special Area of Conservation. However, the focus of this study is on the reef habitat that was protected from mobile demersal fishing, employing the whole-site approach in 2008.

Sample Design

To identify suitable sites for monitoring, spatial analyses were conducted combining historical fishing effort, benthic substrate and depth (Stevens et al. 2014, Sheehan et al. 2013b). Sites were selected within the MPA as well as Open Controls (OC) sites that remain open to mobile demersal fishing. Annual towed video surveys were undertaken at 11 sites in the MPA and 6 OC, totalling 46 video transects in 2008 to 2010 (28 MPA and 18 OC) and 51 in 2011 to 2018 (33 MPA and 18 OC). At each area three replicate towed video transects were carried out (Fig. 4.1). For the BRUVs surveys, sites of three replicate BRUVs, spaced ~ 100m apart, were deployed, to depths ranging from 15m to 32m, before being recovered after 45 minutes. Twelve sites were inside the MPA and six were in the OC (Fig. 4.1). To avoid confusion between the two methods,

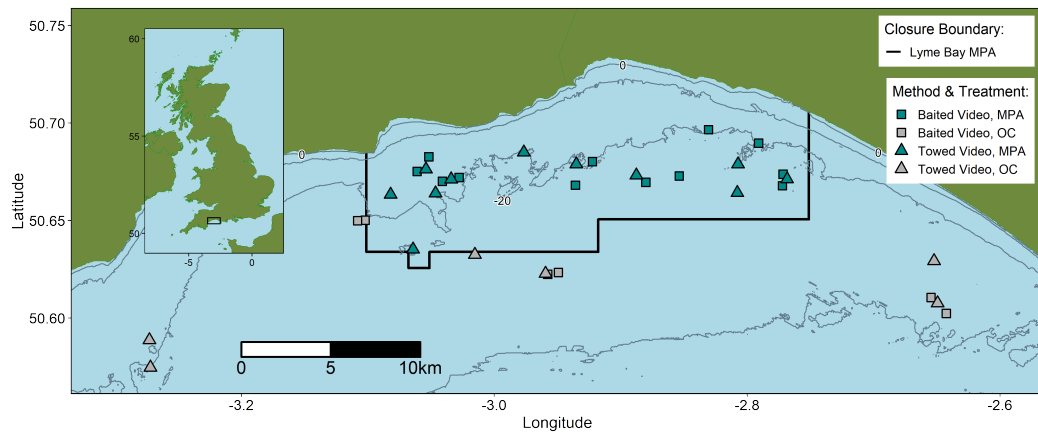


Fig. 4.1: Towed Video (triangles) and Baited Remote Underwater Video system (squares) locations within Lyme Bay MPA (blue) and Open Controls (grey). Each point represents an area of three replicate sites.

each video will be referred to as a site, with a group of three replicate sites within each area.

4.2.2 Towed Flying Array

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.

Video Analysis

An overall Site x Species matrix ([S]) was created by combining relative abundance information from two separate methods. 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 m² quadrat overlaid. Frames were selected and analysed if they met certain criteria of habitat, focus of camera, laser placement and visibility. 30 frames per transect was shown to give equivalent results to assessing the entire transect, while saving significant amounts of time (Sheehan et al. 2013a, 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.

4.2.3 Baited Remote Underwater Video Systems (BRUVs)

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, one meter from the camera, filled with ~ 100 g of Atlantic mackerel *Scomber scombrus* cut into segments. Fresh bait was replenished for each deployment. Videos from BRUVs were assessed *in situ* to ensure that the camera had landed and recorded a viable sample (Chapters 2 & 3). Failed attempts were repeated to ensure that all samples were suitable.

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 or high levels of plankton); 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 minutes across the recording. Videos which did not meet these requirements were omitted from analysis. Videos which did meet the requirements were watched at normal speed for 30 minutes, after a preliminary 5 minute settling period. For every minute all mobile fauna were identified to the highest taxonomic resolution possible and counted. Mobile species were categorised as taxa which were deemed able to continuously move, either in response to the bait or in response to other taxa, which are themselves reacting to the bait. Thus, benthic taxa such as *Pecten maximus*, *Aequipecten opercularis* and *Ophiothrix fragilis* were not included. For every 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 one minute, within the 30 minutes 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).

4.2.4 Combining Baited and Towed

Towed and Baited video data were combined by converting all abundance, cover and MaxN values into relative values (proportion of individuals of a given species at a given site) using the 'make_relative' function within the 'funrar' package in R (Grenié et al. 2020, Matthias Grenié et al. 2017). Relative data sets were then joined by year, treatment and geographically similar areas, cre-

ating a combined site by species matrix of relative abundances.

4.2.5 Functional Metrics

Trait Acquisition

In total, 10 functional traits (e.g. feeding habit) were used with a cumulative 60 modalities (e.g. predator or filter feeder) (Table 4.1). They were selected for importance for the benthic environment and its coupling with other environments in the ecosystem (e.g. Pelagic/Neritic), as well as availability of information. Trait data were taken from multiple different sources: MarLIN BIOTIC; Fishbase and Seallifebase (MarLIN 2006, Shojaei et al. 2015, Beauchard et al. 2017, Froese and Pauly 2019, Palomares and Pauly 2019). 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 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). 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 and Legendre 2010). This created a Species x Trait matrix ([T]) for the species sampled by the towed flying array and the BRUVs.

Table 4.1: All the traits and their constituent modalities used for Biological Trait Analysis.

Traits and Modalities	
<u>Feeding Habit</u>	<u>Age at Maturity</u>
Surface Deposit	< 1 Years
Subsurface Deposit	1-2 Years

Suspension/Filter	2-4 Years
Interface	4-8 Years
Predator	8-15 Years
SandLicker	> 15 Years
Grazer	<u>Fecundity</u>
Parasite	0-10 Eggs
Predatory Scavenger	10-100 Eggs
Photosynthesiser	100-1,000 Eggs
<u>Motility</u>	1,000-10,000 Eggs
Swimmer	10,000-1,000,000 Eggs
Crawler	> 1,000,000 Eggs
Burrower	
Sessile	
<u>Larval Development</u>	<u>Environmental Position</u>
Direct	Epifauna
Lecithotrophic	Infauna
Planktitrophic	Epizoic
<u>Sexual Differentiation</u>	Demersal
Gonochoric	Pelagic
Synchronous Hermaphrodite	<u>Adult Dispersal Potential</u>
Sequential Hermaphrodite	<1 m
<u>Adult Longevity</u>	1-10 m
< 1 Years	10-100 m
1-2 Years	100-1,000 m
2-10 Years	1,000-10,000 m
10-15 Years	>10,000 m

15- 20 Years	<u>Maximum Size</u>
> 20 Years	<1 cm
<u>Diet Type</u>	1-10 cm
Omnivore	10-20 cm
Carnivore	20-50 cm
Herbivore	50-100 cm
Detritivore	> 100 cm
Photosynthesiser	

Metric Calculation

Number of taxa was calculated as the total number of different taxa present within each site. Functional richness, functional divergence, functional evenness and functional distinctiveness, which are unaffected by difference in the type of abundance values used (e.g. biomass, count, percentage cover or density; [Villegger et al. 2008](#)), were calculated for each site. Functional richness, functional divergence and functional evenness were calculated using the R package 'FD' and functional distinctiveness from the 'funrar' package ([Laliberté and Legendre 2010](#), [Grenié et al. 2020](#)). Functional richness represents the number of different functional traits within the community, functional evenness and functional divergence describe how the abundance is distributed across the traits within the community. 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 (O) was calculated as one minus functional distinctiveness (U), meaning values close to one imply high redundancy ([Ricotta et al. 2016](#), [Biggs et al. 2020](#)).

Community-level Weighted Means

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

4.2.6 Statistical Analysis

To assess changes in metrics and CWM of *a priori* selected traits, mixed effect modelling was carried out from the 'glmmADMB' and 'lme4' package within R (Fournier et al. 2012a, Skaug et al. 2016, Bates et al. 2020). Generalised Linear Mixed Effect models were applied using: a Poisson distribution for the count variable, number of taxa; a Gamma distribution for the continuous positive variable, functional richness, and Beta distributions for all proportional variables (functional divergence, functional evenness, functional redundancy and all CWM of *a priori* selected traits). A marginal transformation was applied to the CWM data to fit the assumptions of the Beta distribution following Smithson and Verkuilen (2006) to account for the presence of zeros and ones in the data. All variables were modelled as a function of Year (2009:2018) and Treatment (MPA and OC) as fixed factors and Area (Area 1:16) as a random factor, where model selection utilised pairwise assessment of AIC to progressively establish the most parsimonious models (Zuur and Ieno 2016, Appendix C Tables C.1 & C.2). Stated values are GLMM estimates \pm standard errors.

4.3 Results

4.3.1 Functional Metrics

The number of taxa was significantly greater inside the MPA than the OC and significantly increased over time (from 35.3 ± 1.41 in 2009 to 47.6 ± 2.23 in 2018: a 34.7% increase), while this metric for the OC was significantly lower than the MPA and decreased over time (from 28.9 ± 1.65 in 2009 to 26.1 ± 1.49 in 2018: a 9.66% decrease: Table 4.2 & Fig. 4.2a). The functional richness inside the MPA was significantly greater than the Open Controls (OC) and increased significantly over time (from 0.00028 ± 0.0000888 in 2009 to 0.000426 ± 0.000155 in 2018: a 52.1% increase), while the OC showed no significant change over time (from 0.000236 ± 0.000101 in 2009 to 0.000188 ± 0.0000764 in 2018: a 20.1% decrease: Table 4.2 & Fig. 4.2b). Functional Divergence was significantly lower in the MPA compared to the OC across all years, with both the MPA and OC significantly decreasing over time (the MPA changed from 0.876 ± 0.0165 in 2009 to 0.848 ± 0.0231 in 2018: a 3.24% decrease, while the OC changed from 0.923 ± 0.00803 in 2009 to 0.905 ± 0.0127 in 2018: a 2.03% decrease: Table 4.2 & Fig. 4.2c). However, there was no Year x Treatment interaction, and thus the change over time was not significantly different between treatments (Table 4.2). There were no significant differences between treatments in functional evenness (both the MPA and OC had a functional evenness of 0.457 ± 0.00913 throughout: Table 4.2 & Fig. 4.2d). There was significantly higher functional redundancy in the MPA, with a significant increase in the MPA and decrease in the OC over time (the MPA changed from 0.728 ± 0.012 in 2009 to 0.737 ± 0.0198 in 2018: a 1.28% increase, while the OC changed from 0.721 ± 0.00759 in 2009 to 0.706 ± 0.0133 in 2018: a 2.17% decrease: Table 4.2 & Fig. 4.2e).

Table 4.2: General 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. Year and Treatment are abbreviated throughout to Yr and Tr.

Term	Estimate (SE)	z/t value	p value
<u>Number of Taxa</u>			
Intercept	3.37 (0.0654)	51.6	<0.0001***
Yr	-0.0113 (0.00856)	-1.32	0.19
Tr	0.157 (0.0801)	1.96	0.05
YrxTr	0.0444 (0.0101)	4.38	<0.0001***
<u>Functional Richness</u>			
Intercept	-8.33 (0.132)	-63.3	<0.0001***
Yr	-0.025 (0.018)	-1.39	0.17
Tr	0.101 (0.167)	0.606	0.54
YrxTr	0.0716 (0.0228)	3.14	0.0017**
<u>Functional Divergence</u>			
Intercept	2.51 (0.119)	21.2	<0.0001***
Yr	-0.0265 (0.0108)	-2.47	0.014*
Tr	-0.533 (0.125)	-4.27	<0.0001***
YrxTr			
<u>Functional Evenness</u>			
Intercept	-0.1704 (0.0367)	-4.65	<0.0001***
Yr			
Tr			
YrxTr			

Table 4.2: General Linear Mixed Effects Model outputs for diversity metrics (continued)

Term	Estimate (SE)	z/t value	p value
Functional Redundancy			
Intercept	0.959 (0.0329)	29.1	<0.0001***
Yr	-0.00849 (0.00494)	-1.72	0.085
Tr	0.0182 (0.0418)	0.436	0.66
YrxTr	0.0138 (0.00629)	2.19	0.029*

4.3.2 Functional Trait Modalities

Feeding Type

The change over time in the relative proportion of the filter feeding modality, within the feeding type trait, was significantly different between the two treatments, with a significant increase over time in the MPA and a significant decrease over time in the OC (the MPA changed from 0.542 ± 0.677 in 2009 to 0.666 ± 0.828 in 2018: a 23% increase, while the OC changed from 0.499 ± 0.586 in 2009 to 0.402 ± 0.535 in 2018: a 19.4% decrease: Table 4.3 & Fig. 4.3a). The scavenger feeding modality showed a significant increase in both the OC and MPA over time, with the OC significantly greater than the MPA (the MPA changed from 0.0362 ± 0.0551 in 2009 to 0.0596 ± 0.0976 in 2018: a 64.4% increase, while the OC changed from 0.0687 ± 0.0903 in 2009 to 0.11 ± 0.161 in 2018: a 60.9% increase: Table 4.3 & Fig. 4.3b).

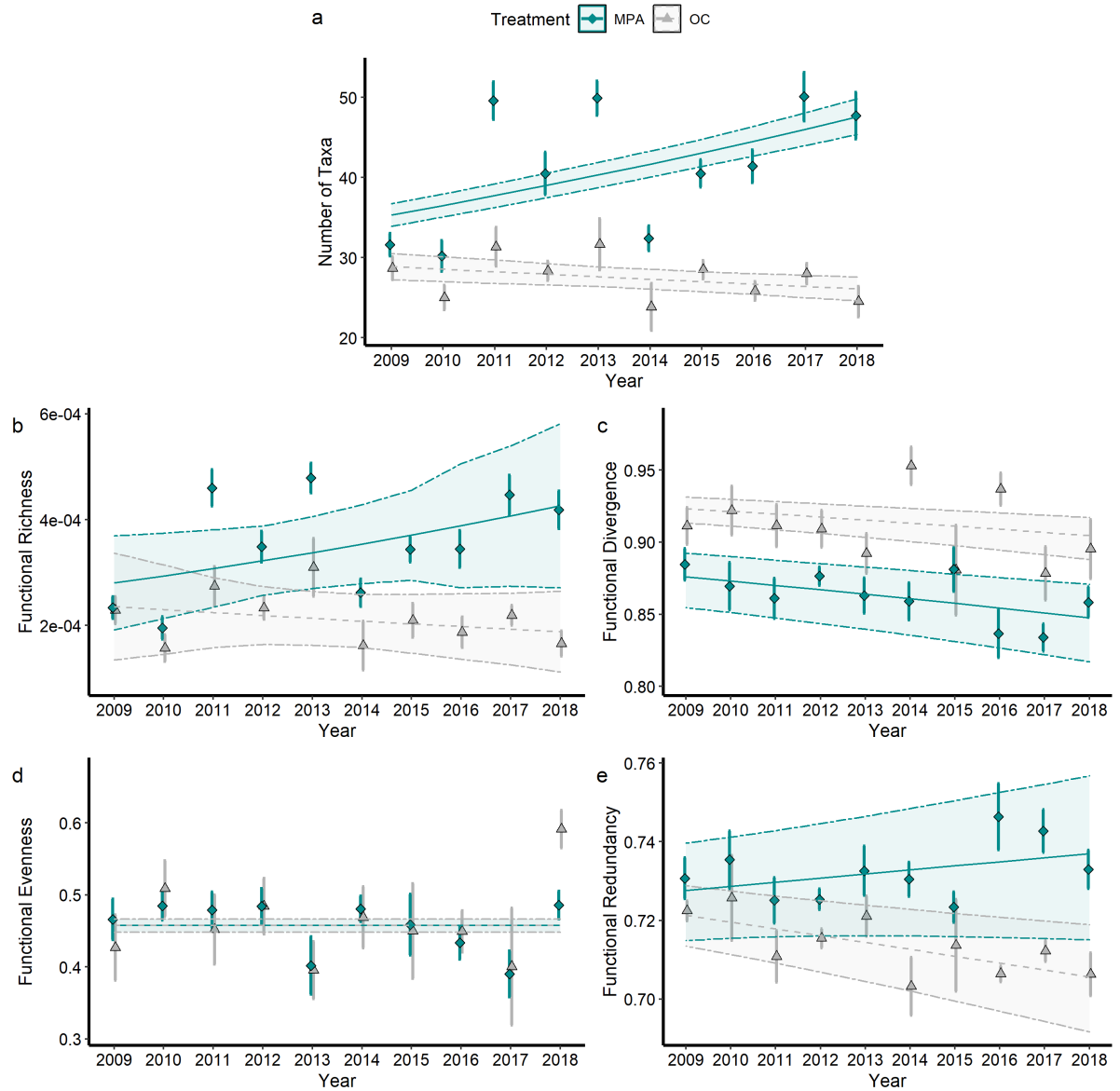


Fig. 4.2: Temporal changes in diversity metrics from combined towed underwater video and Baited Remote Underwater Video Systems data (Number of Taxa (a), Functional Richness (b), Functional Divergence (c), Functional Evenness (d) and Functional Redundancy (e)). Lines show GLMM estimates with shading showing standard error. Points with errors bars show mean values and standard errors.

Table 4.3: Generalised Linear Mixed Effect model outputs for the Cumulative Weighted Means of *a priori* selected Trait Modalities (Filter Feeder, Scavenger Feeder, 20 Years Plus Longevity, Sessile Motility, Crawler Motility and Swimmer Motility) as functions of Year and Treatment. Year and Treatment are abbreviated to Yr and Tr.

Term	Estimate (SE)	z/t value	p value
<u>Filter Feeder</u>			
Intercept	0.038 (0.179)	0.21	0.83
Yr	-0.044 (0.021)	-2.11	0.035*
Tr	0.072 (0.228)	0.315	0.75
YrxTr	0.102 (0.026)	3.87	<0.0001***
<u>Scavenger Feeder</u>			
Intercept	-2.665 (0.153)	-17.410	<0.0001***
Yr	0.058 (0.018)	3.196	0.0014**
Tr	-0.673 (0.146)	-4.599	<0.0001***
YrxTr			
<u>Longevity</u>			
Intercept	-0.170 (0.097)	-1.756	0.079
Yr			
Tr			
YrxTr			
<u>Sessile Motility</u>			
Intercept	1.413 (0.256)	5.524	<0.0001***
Yr	-0.171 (0.033)	-5.187	<0.0001***
Tr	-0.009 (0.322)	-0.027	0.98
YrxTr	0.166 (0.042)	3.913	<0.0001***

Table 4.3: General Linear Mixed Effects Model outputs for diversity metrics (continued)

Term	Estimate (SE)	z/t value	p value
Crawler Motility			
Intercept	-2.191 (0.236)	-9.281	<0.0001***
Yr	0.140 (0.030)	4.719	<0.0001***
Tr	-0.527 (0.305)	-1.727	0.084
YrxTr	-0.112 (0.041)	-2.76	0.0058**
Swimmer Motility			
Intercept	-2.276 (0.230)	-9.882	<0.0001***
Yr	0.091 (0.032)	2.856	0.0043**
Tr	0.290 (0.289)	1.004	0.32
YrxTr	-0.110 (0.041)	-2.678	0.0074**

Longevity

As an ordinal trait, the relative proportion of longevity shows the weighting of different lifespans in the community, with a greater proportion meaning a tendency towards longer-lived organisms. However, there was no significant difference in the relative proportion of the longevity trait, inside the MPA compared to the OC or over time (0.458 ± 0.505 : Table 4.3 & Fig. 4.3c).

Motility

The relative proportion of the sessile modality, within the motility trait, changed significantly across the treatments over time, the decrease over time was not significant in the MPA but was in the OC (the MPA changed from 0.802 ± 0.903

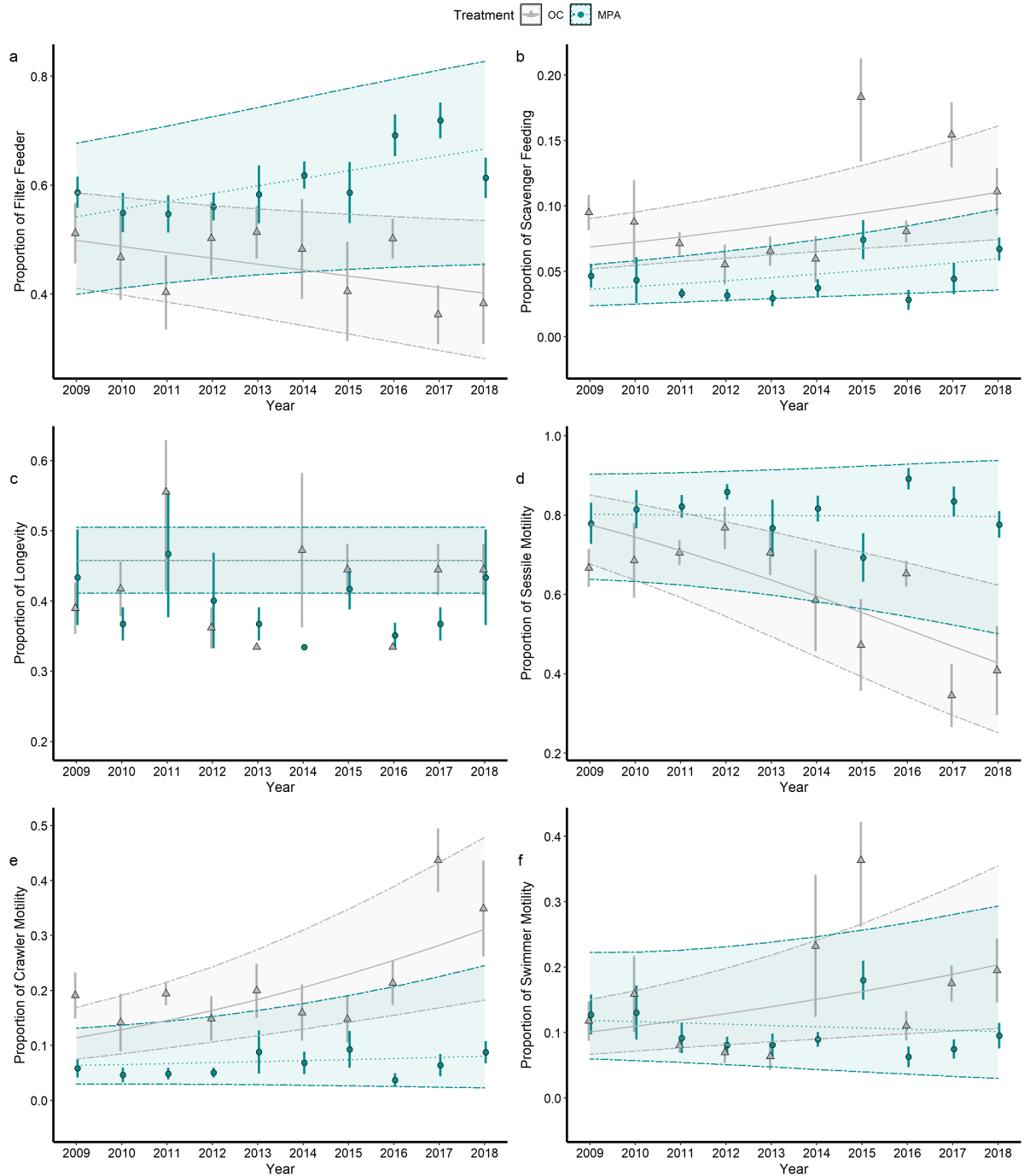


Fig. 4.3: Temporal change in Functional Trait Modalities (Filter Feeder (a), Scavenger Feeder (b), Longevity (c), Sessile Motility (d), Crawler Motility (e) and Swimmer Motility (f)) from combined towed underwater video and Baited Remote Underwater Video Systems data based on GLMM model estimates. Shaded extent shows standard error. Points with errors bars show mean values and standard errors.

in 2009 to 0.796 ± 0.938 in 2018: a 0.793% decrease, while the OC changed from 0.776 ± 0.851 in 2009 to 0.427 ± 0.624 in 2018: a 44.9% decrease: Table 4.3 & Fig. 4.3d). Between the two treatments, the relative proportion of the crawler modality changed differently, with a significant increase over time in the OC (the MPA changed from 0.0635 ± 0.132 in 2009 to 0.0802 ± 0.245 in 2018: a 26.2% increase, while the OC changed from 0.114 ± 0.169 in 2009 to 0.312 ± 0.478 in 2018: a 173% increase: Table 4.3 & Fig. 4.3e). Similar to the crawler modality, the relative proportion of the swimmer modality significantly increased in the OC over time, while showing a slight decrease over time in the MPA (the MPA changed from 0.119 ± 0.222 in 2009 to 0.101 ± 0.294 in 2018: a 14.6% decrease, while the OC changed from 0.101 ± 0.151 in 2009 to 0.204 ± 0.355 in 2018: a 101% increase: Table 4.3 & Fig. 4.3f).

4.4 Discussion

The functional changes in Lyme Bay MPA were assessed over 10 years since protection, using a combination of video survey methods (Towed Flying Array and Baited Remote Underwater Video Systems). Ecosystem function has been linked to the services provided by an ecosystem. Therefore, the taxonomic and functional changes of the MPA were assessed following protection. Hypothesis 1 was accepted as both the number of taxa and functional richness were highest in the MPA, and increased significantly over time, compared to the Open Controls (OC), with a 34.7% and 52.1% increase in the number of taxa and functional richness respectively. In contrast, the functional divergence showed significant decrease over time in the MPA and the OC (a decrease of 3.24% & 2.03% in the MPA and OC respectively), but was lowest in the MPA. Functional evenness showed no significant change over time or significant difference between treatments. This meant that hypothesis 2 could not be accepted.

Functional redundancy, like the functional richness, was highest in the MPA, increasing over time (1.28% increase) and decreased significantly over time in the OC (2.17% decrease), meaning hypothesis 3 could be accepted. Filter feeders increased by 23% in the protected area compared to the OC, where swimmers and crawlers increased over time (increases of 101% & 173% respectively). There was 44.9% increase in the MPA and a 44.9% decrease in the OC over time 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. This meant hypothesis 4 could not be fully accepted.

As expected, there was an increase in the level of both the number of taxa and the functional richness over time inside the MPA. Although it has had many definitions, functional richness has consistently been shown to be an important driver for ecosystem stability, resilience and services (Wahl et al. 2011, Törnroos et al. 2015, Canning-Clode et al. 2010). Functional and taxonomic richness are closely related, regardless of how functional richness is defined: the volume of the functional trait space (used in the present study: Villeger et al. 2008, Boyé et al. 2019), the species richness within functional groupings (Wahl et al. 2011, Canning-Clode et al. 2010) or species richness of functionally unique species (Canning-Clode et al. 2009). Here, the exclusion of mobile demersal fishing inside the MPA has allowed the functional traits to proliferate. This increase will have likely altered ecosystem-wide processes, with positive effects to productivity and regulation of biogeochemical fluxes (Vačkář et al. 2012, Perović et al. 2018, Ricotta et al. 2016).

Pressures imposed by high levels of demersal towed fishing can impact communities in varying ways. Strong disturbance regimes will continually reset

communities to small initial successional stage assemblages (Song and Saavedra 2018). This introduces 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, which allow them to persist (Boyé et al. 2019). This was likely the driver for the observed decrease over time in functional divergence in the MPA and decrease in functional redundancy seen in the OC (Table 4.2).

In this study, functional evenness stayed consistent over time. Assuming that resource availability was even across the system, this implies that as the number of different traits (functional richness) increased, the relative abundance across those traits was not evenly distributed. Hence, the community was becoming less effective at utilising the available resources (Mason et al. 2005). This lack of change in evenness in the MPA, even though the functional richness increased over time, may be due to increases in abundance of species with locally rarer traits. This was further supported by the decrease over time in the functional divergence across both treatments (Fig. 4.2c).

Communities containing high levels of trait overlap, functional redundancy, provide a higher resilience to environmental impacts, such as fishing, storms or biological invasions (Mason et al. 2005, Tillin et al. 2006, McLean et al. 2019). When a species becomes regionally extinct, its suite of traits is less likely to become regionally extinct when there is high trait overlap. The higher levels of functional redundancy witnessed in the MPA compared to the OC shows a higher resilience to perturbations (Rincón-Díaz et al. 2018). Furthermore, the MPA showed a significant increase in functional redundancy over time, meaning the area became more resilient over time to such impact effects. The increase

in functional redundancy in the MPA in relation to the OC happened alongside a significant increase in the number of taxa and the functional richness inside the MPA. This 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 that when there is an increase in functional richness, the functional trait space increases and thus the likelihood of overlap in traits decreases. However, it may also be an artefact of studying narrower functional ranges (one taxonomic group: i.e. fish). 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.

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). As shown here, the area protected from demersal mobile fishing showed increases in filter feeding organisms, with the OC showing decreases in the proportion of sessile organisms and increases in the proportion of swimmers and crawlers. In 2008, the first surveys of the MPA showed limited sessile life growing on the boulders and cobbles (Sheehan et al. 2013b). The Lyme Bay MPA was designated to protect the rocky reef habitat, which in turn is characterised by sessile fauna species, such as pink sea fans *Eunicella verrucosa* and ross corals *Pen-
tapora foliacea* (Sheehan et al. 2013b). Thus, the decrease in sessile traits

in the OC compared to the MPA alongside increases in the MPA compared to the OC of filter feeding organisms shows the protection is being effective and is protecting the sessile filter feeding rocky reef species. These changes will likely have led to alterations in ecosystem-wide processes, such as productivity and regulation of biogeochemical fluxes (Perović et al. 2018, Ricotta et al. 2016).

The relatively novel methodology of combining two survey methods (Towed flying array and BRUVs) to assess a broad range of the benthic ecosystem could be a useful tool for management, with functional assessment already being advocated for management (Tillin et al. 2006, Wiedmann et al. 2014, Rijnsdorp et al. 2016). Assessing the 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. Primarily, the number of different traits used needs to be consistent to allow comparison but also the maximum number of potential species assessed, as the functional richness quantifies an absolute volume filled (Villegger et al. 2008). Therefore, increases in repositories of biological trait information for a wide range of species are highly important to allow comparison between locations, nationally and internationally.

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 protected area decreased in functional divergence, while the OC decreased in functional redundancy. The increase in the number of different taxa, and the subsequent increase in functional traits, will lead to more potential ecosystem services throughout the bay. This increase of traits in the MPA was accompanied by uneven distribution of

abundance across traits and a decrease in trait overlap in the OC. Thus, the protected area was enabling the increase in trait overlap and the accompanied resilience to perturbations, while the OC became less resilient. 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 of the reef, especially without data of before-fishing levels. However, it does show a trend towards a more biologically and functionally diverse, and resilient rocky reef habitat.

"Protect the natural systems as if your life depends on it because it does!"

Sylvia Earle

5

An Assessment of a 'Feature' Based Protection and Comparison with a Whole-Site Approach Marine Protected Area.

Status: To Be Submitted

Authors' Contributions

EVS and MJA conceived the ideas and monitoring design; EVS, LH and BFRD collected data; LH and BFRD organized and analysed data; BFRD, EVS and LH led the writing of the manuscript.

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Bede F. R. Davies	University of Plymouth	80
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Emma V. Sheehan	University of Plymouth	10

Abstract

Globally, nations are designating Marine Protected Areas to recover and protect habitats and species of conservation and commercial importance. With targets to protect 30% by 2030, it is important to assess the effectiveness of MPAs to protect the designated space that is being reported. Many MPAs are multi-use and only exclude the most destructive fishing activities from specific areas where conservation features have been evidenced: ‘feature based’ management. Alternatively, a more ambitious management practice, known as the whole-site approach applies consistent management throughout an MPA allowing the recovery and expansion of habitats and species’ populations. In Lyme Bay two co-located MPAs exist that have each adopted one of these management styles to exclude mobile demersal fishing. To assess the effectiveness of the ‘feature based’ approach and compare it to the whole-site approach, and to areas that remain open to all fishing, underwater video was used to enumerate change overtime of reef species in three treatments (2008-2019). Firstly, a BACI approach showed that the ‘feature based’ MPA increased in diversity (taxonomic and functional) of sessile and sedentary taxa from before to after designation compared to open controls. Overtime, both management styles resulted in increases in sessile and sedentary taxa diversity (taxonomic and functional) relative to open controls, with increases in total abundance of 15% and 95% in the ‘feature based’ and whole-site MPAs respectively. However, the mobile taxa in the whole-site MPA showed levels of functional redundancy 7% greater than the ‘feature based’ MPA, indicative of a greater community resilience inside the whole-site MPA to perturbations, such as storms or biological invasions. It was expected that the increases seen in the diversity of sessile taxa would only be in areas where mobile demersal fishing is excluded. As seen in the whole-site

MPA previously, protection of the whole extent of an MPA can lead to increases in functional extent of reef area. Therefore, it was expected that if the whole 'feature based' MPA was consistently protected it would see similar levels of increase in functional extent of reef.

5.1 Introduction

The use of Marine Protected Areas (MPAs) as a tool to protect habitats and species is increasing globally (Edgar and Stuart-Smith 2014, Sala and Giakoumi 2018, Lubchenco and Grorud-Colvert 2015). MPAs have been shown to recover benthic ecosystems (Sheehan et al. 2013a) with evidenced positive outcomes for species' biomass, catch per unit effort, diversity, density and community stability (Mellin et al. 2016, Sciberras et al. 2013, Lester et al. 2009, Sheehan et al. 2013b) 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 (Rees et al. 2020, Waldron et al. 2020, O'Leary et al. 2016, Brander 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, has been shown to be dependent on being a combination of no take, large, old, isolated and well enforced (Kerr et al. 2019, Lubchenco et al. 2003, Carpenter et al. 2001, Roberts et al. 2017, Edgar and Stuart-Smith 2014). Where MPAs have been designated but not managed appropriately, they have been shown to be ineffective and in some cases have resulted in effects counter to their objectives (Claudet 2018, Edgar et al. 2004, Devillers et al. 2015, Rife et al. 2013a).

In the UK, there are a number of MPA designations, such 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) ([Solandt et al. 2020](#), [Sheehan et al. 2016](#), [Rees et al. 2020](#), [2021b](#), [Stewart et al. 2020](#), [Gall and Rodwell 2016](#)). SACs, SPAs and MCZs are all types of partially protected area, 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 evidenced within the MPA boundary. This type of protection has been termed ‘feature based’ as only the feature of interest is specifically protected within the confines of the area 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 ([Pikitch et al. 2004a](#), [Costanza et al. 1998](#)). Therefore, MPAs which 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,b, 2016](#), [Rees et al. 2020](#), [Solandt et al. 2020](#)).

Lyme Bay, in the southwest 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 (Wildlife and Countryside Act 1981). The reefs support many species of conservation and commercial importance, for example 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 the biogenic reef species and the mudstone reef habitat. For this reason, the area has been the focus of debate between conservationists and fishers since the early 1990s. Since this time, areas of the reefs have been protected under voluntary agreements (7 km² from 2001 and 41 km² from 2006 Jones 2012, Fig. 5.1); a Statutory Instrument (whole-site exclusion of mobile demersal fishing of 206 km² from 2008, Fig. 5.1); local byelaws set by Devon IFCA and Southern IFCA, and a 'feature based' SAC that encompassed the SI (a 312 km² Site of Community Importance from November 2011: Rees et al. 2012a, and then a SAC from 2017, Fig. 5.1). This co-location of management approaches provides the rare opportunity to assess the comparative effectiveness of feature vs whole site management. The aim of this study was to first assess the effect of the SAC in comparison to Open Controls (OC), which continue to be open to mobile demersal fishing, on benthic and demersal fauna. Secondly, the recovery trajectory of taxa over 5 years since protection was compared between the SAC ('feature' based SAC: Year 1=2012), the SI MPA (whole-site MPA: Year 1=2008) and the Open Controls (areas open to mobile demersal fishing: Year 1=2012).

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, 2016](#), [Stevens et al. 2014](#), & chapter 3). 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, 1992, 1994](#)). This assessment style is advocated globally, yet the necessary 'before' data for MPA assessment are rarely available ([Osio et al. 2007](#), [Fraschetti et al. 2002](#), [Solandt et al. 2020](#)).

To assess changes in biodiversity the following response metrics were used: assemblage composition, number of taxa and total abundance. To assess the changes in ecosystem service provision and the resilience of the community to perturbations (storms, invasive species and destructive fishing [Tillin et al. 2006](#)) the following response metrics were used: functional richness, which quantifies the number of different functional traits in a community, and functional redundancy, which quantifies the overlap of functional traits between different species in the community. It was expected that there would be a shift in assemblage composition in the SAC 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, it was expected that there would be significant changes in assemblage composition 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, yet that the whole-site MPA would increase more rapidly than the 'feature' based SAC. The OC data were sampled to align with the SAC treatment age of protection. The towed flying array surveys all conspicuous sessile and sedentary taxa, while the BRUVs survey all conspicuous mobile taxa. Each hypothesis was tested twice. Firstly using the sessile and sedentary fauna data

collected by the towed flying array ('sessile taxa' henceforth, [Sheehan et al. 2013a](#), & chapter 4) and secondly using the mobile taxa data sampled by the BRUVs ('mobile taxa' henceforth, chapters 3 & 4).

The hypotheses for the BACI assessment were:

- Number of taxa, total abundance, functional richness and functional redundancy increase from before to after in the SAC, relative to the Open Controls.
- Assemblage composition significantly changes from before to after in the SAC, becoming less similar to the OC.

The hypotheses for the Age of Protection assessment were:

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

5.2 Methods

5.2.1 Location

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 km². The Lyme Bay element of the SAC, under study here, encompasses ~270 km² of seabed, including a 206 km² area, which prohibited mobile demersal fishing from 2008 under a Statutory Instrument (SI) (Fig. 5.1). The area designated under the SI (whole-site MPA henceforth) ranges in depths from 15 to 35m and allows less destructive fishing activities, such as 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 evidenced (Natural-England 2015). Consequently, ~33.9 km² of other habitats, including pebbly sand veneers that can be colonised by reef associated species (Sheehan et al. 2013b), are reported as "protected" but can be legally dredged or trawled.

5.2.2 Survey Design

Annual underwater video surveys were carried out across Lyme Bay (Fig. 5.1), within three treatments: Within the feature based "SAC" but outside the whole-site MPA in areas identified as Sensitive Areas that are protected from mobile demersal fishing (evidenced Annex I reef habitat) ('SAC' henceforth); inside the whole-site MPA ('whole-site MPA' henceforth), and 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 (Stevens et al. 2014). Areas were sampled annually using the towed flying array and Baited Remote Underwater Videos (BRUVs) from 2008 and 2009 respectively. Surveys were carried out during the summer for four years prior (Before) and seven years post designation of the SAC (After). All SAC areas were on Annex I reef habitats and therefore protected from mobile demersal

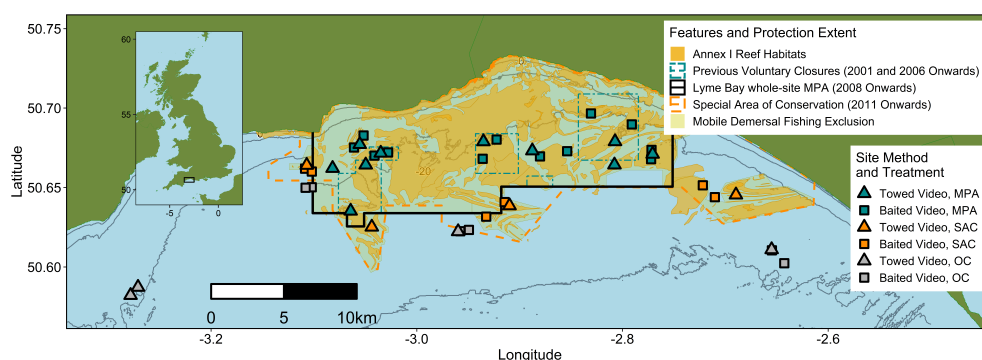


Fig. 5.1: Towed flying array (triangles) and Baited Remote Underwater Video system (squares) locations in the SAC (orange), whole-site MPA (blue) and Open Controls (grey), and Closure Boundaries within Lyme Bay. Each location represents three replicates.

fishing. No areas within the SAC that are open to mobile demersal fishing were surveyed as 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.

Towed Flying Array

From 2008, 18 areas, comprising 3 sites each, were surveyed annually (1 x 200m transect) by the towed flying array across the treatments (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, from 2011, 19 areas were surveyed across the treatments (10 whole-site MPA, 4 SAC and 5 OC; Fig. 5.1).

Baited Remote Underwater Video systems (BRUVs)

From 2009, 19 areas were surveyed annually, comprising 3 BRUV deployments (12 whole-site MPA and 6 OC). After SAC designation all OC areas became SAC, leading to the addition of 6 new OC areas. Therefore, from 2011 to 2019, 24 areas were surveyed in total (12 whole-site MPA, 6 OC and 6 SAC; Fig. 5.1).

5.2.3 Data Collection

Towed Flying Array

The Towed Flying Array was used to record High Definition (HD) video transects ($\sim 200 \text{ m} \times 0.5 \text{ m}$) 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). The array (consisting of camera, lights, lasers and CTD profiler) 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. To analyse the video transects, firstly, each entire transect was watched at normal speed and all conspicuous taxa that pass through the gap between the lasers were enumerated. Secondly, to quantify abundance and cover of all remaining visible taxa, each video transect was extracted into frame-grabs, separated by 5 seconds. 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. (See Sheehan et al. 2010, 2016, Chapter 4 for further details of equipment and video analysis methods). Densities of taxa per transect were calculated for video transects by dividing taxa counts by the area of the transect ($300 \text{ mm} \times \text{Transect length}$) and for frames by dividing the taxa counts by the known quadrat area. As each taxa was only recorded by one method, the abundances from both these methods were then combined.

Baited Remote Underwater Video Systems (BRUVs)

Baited Remote Underwater Video Systems (BRUVs) were used to collect 30 minute videos of mobile benthic taxa. 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 minutes, videos were watched for 30 minutes, recording the maximum number of individuals of all mobile benthic taxa seen every minute. The MaxN or relative abundance of each taxon was calculated as the maximum value recorded in any one minute segment for that taxon over the 30 minute video, (See [Bicknell et al. 2019](#), chapters 2, 3 & 4 for further details of equipment and analytical methods).

5.2.4 Univariate Metric Calculation

For both the towed flying array and BRUVs data, number of taxa and total abundance were calculated using the ‘vegan’ package within R ([Oksanen et al. 2020](#)). The R packages ‘FD’ and ‘funrar’ were used to calculate the multivariate metrics functional richness and functional distinctiveness respectively using Euclidean and Gower distances ([Laliberté and Legendre 2010](#), [Laliberté et al. 2014](#), [Grenié et al. 2020](#), [Matthias Grenié et al. 2017](#)). Both functional metrics are unaffected by difference in the type of abundance values used (e.g. biomass, count, percentage cover or density: [Villegger et al. 2008](#)). Functional richness represents the number of different functional trait modalities found within a community and functional distinctiveness calculates how functionally rare each species is per survey. Here, functional redundancy (O) was calculated as one minus functional distinctiveness (U), meaning values close to one imply high redundancy ([Ricotta et al. 2016](#), [Biggs et al. 2020](#)).

5.2.5 Statistical Analysis

Diversity

To investigate changes in the univariate metrics for taxonomic and functional diversity, mixed effects models were carried out from the ‘lme4’, ‘lmerTest’ and ‘glmmADMB’ packages within R (R Core Team 2019, Bates et al. 2020, Kuznetsova et al. 2020, Fournier et al. 2012b). Generalised Linear Mixed Effect 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 distributions were used for continuous positive variables (Total Abundance for sessile taxa and Functional Richness for both sessile and mobile taxa) and Beta distributions were used for all 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 Treatment (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 (Appendix D Table D.1). As the whole-site MPA was protected but no ‘before’ data was available, it was not included in the BACI assessment. For the Age of Protection 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) and Treatment (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 (Appendix D Table D.2). Model selection was carried out by step-wise deletion of terms and pairwise comparison of models by AIC (Appendix D Tables D.3 & D.4). The most parsimonious models were applied and the highest

order interactions evaluated. Sample vs fitted residuals, quartile-quartile and autocorrelation of temporally sequential samples were assessed visually, to fit assumptions of the models used. Stated values are GLMM model estimate means per video \pm standard error.

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). For the BACI assessment, Time Frame (BA) and Treatment (Tr) were fixed factors with two levels each (BA: Before-After; Tr: SAC and Open Control). Year (11 levels for both sessile and mobile taxa) and Site (14 and 18 levels for sessile and mobile taxa respectively) were random factors. Year was nested within BA and Site was nested within Tr. For the Age of Protection assessment, Treatment was a fixed factor with three levels (SAC, whole-site MPA and OC) and age of protection was a continuous covariate (Years since 2008 for whole-site MPA Years since 2011 for SAC and OC). Year and Site were random factors with 11 and 14 levels for sessile taxa and 11 and 18 levels for mobile taxa. Year was nested within age of protection and Site was nested within Treatment. The statistical significance of the variance components were tested using 9999 permutations under a reduced model (Anderson 2001a, Anderson and ter Braak 2002). PERMANOVA was selected as it 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. Distance to centroid was calculated for Year and Tr and then ordinated using non-metric multidimensional scaling (MDS).

5.3 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 treatments and years were: Hydroids, *Stolonica socialis* and *Cellaria fistulosa* for the towed flying array and *Pagurus* spp., *Trachurus trachurus* and *Tritia reticulata* for the BRUVs.

5.3.1 Before After Control Impact (BACI) Assessment

Diversity

The number of sessile taxa was significantly greater within the SAC compared to the OC and both treatments from before to after designation (from 19 ± 1.17 before to 21.8 ± 1.22 after in the SAC and 15.7 ± 1 before to 18 ± 0.861 after in the OC: Table 5.1 & Fig. 5.2a). Similarly, the total abundance was significantly greater within the SAC compared to the OC but showed no significant change before vs after designation (74.2 ± 22.9 in the SAC and 38 ± 14.8 in the OC: Table 5.1 & Fig 5.2b). Functional richness significantly increased within both treatments from before to after designation (From 0.000964 ± 0.00021 before to 0.00137 ± 0.000292 after in the SAC and 0.000964 ± 0.00021 before to 0.00137 ± 0.000292 after in the OC: Table 5.1 & Fig. 5.2c), whereas the functional redundancy showed a significant BACI interaction, with an increase from before to after in the SAC and a decrease from before to after in the OC (From 0.747 ± 0.0122 before to 0.758 ± 0.0162 after in the SAC and 0.743 ± 0.00792

before to 0.731 ± 0.0116 after in the OC: Table 5.1 & Fig. 5.2d).

Table 5.1, Mixed effects model results for Before After Control Impact Assessment of SAC vs OC with Number of Taxa, Total Abundance, Functional Richness, Functional Distinctiveness and 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.

Terms	Sessile Taxa				Mobile Taxa			
	Estimate	SE	t/z value	p value	Estimate	SE	t/z value	p value
Taxonomic Diversity								
Number of Taxa								
Intercept	2.75	0.0687	40.1	<0.0001***	1.79	0.0444	40.2	<0.0001***
BA	0.136	0.0637	2.13	0.033*				
Tr	0.192	0.0666	2.88	0.004**				
BAxTr								
Total Abundance								
Intercept	3.64	0.00139	2620	<0.0001***	3.12	0.154	20.2	<0.0001***
BA								
Tr	0.67	0.00143	467	<0.0001***				
BAxTr								
Functional Diversity								
Functional Richness								
Intercept	-6.94	0.15	-46.3	<0.0001***	-2.85	0.00186	-1530	<0.0001***
BA	0.354	0.151	2.34	0.019*				
Tr								
BAxTr								
Functional Redundancy								
Intercept	1.06	0.0414	25.6	<0.0001***	0.944	0.0224	42.2	<0.0001***
BA	-0.0591	0.0405	-1.46	0.14				
Tr	0.0221	0.0513	0.43	0.67				
BAxTr	0.119	0.0454	2.61	0.009**				

Table 5.2, PERMANOVA results for Before After Control Impact Assessment of SAC vs OC with Number of Taxa, Total Abundance, Functional Richness, Functional Distinctiveness and 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.

Terms	Sessile Taxa				Mobile Taxa			
	Estimate	SE	t/z value	p value	Estimate	SE	t/z value	p value
Assemblage Composition								
BA	1	18600	4.02	<0.0001***	1	7710	1.55	0.16
Tr	1	8210	1.6	0.06	1	2880	0.73	0.77
Yr(BA)	9	54500	5.94	<0.0001***	9	81300	6.8	<0.0001***
Si(Tr)	6	35900	5.88	<0.0001***	10	51000	3.8	<0.0001***
BAXTr	1	3380	2.24	0.0033**	1	1100	0.598	0.89
BAXSi(Tr)	6	6570	1.08	0.32	10	21700	1.61	0.0048**
TrxYr(BA)	9	12100	1.31	0.037*	7	13200	1.42	0.041*
Si(Tr)xYr(BA)	48	49600	2.08	<0.0001***	78	104000	2.06	<0.0001***
Res	180	89200			232	150000		

Unlike the sessile taxa, there was no change in mobile taxa with time frame or treatment in any of the univariate diversity metrics (Table 5.1 & Fig. 5.3).

Assemblage Composition

The Assemblage composition of the sessile taxa (surveyed by the towed flying array) showed a significant BACI interaction (BAXTr; Table 5.2). Assemblages were similar between SAC and OC treatments from 2008 until 2012, where they diverged until 2015 when they became more similar again, and finally diverged from 2016 until 2018 (Fig. 5.4a). The assemblage composition of mobile taxa (surveyed by the BRUVs) showed no significant BACI effect with only the interaction of random effects being significant (Si(Tr)xYr(BA) Table 5.2). This is

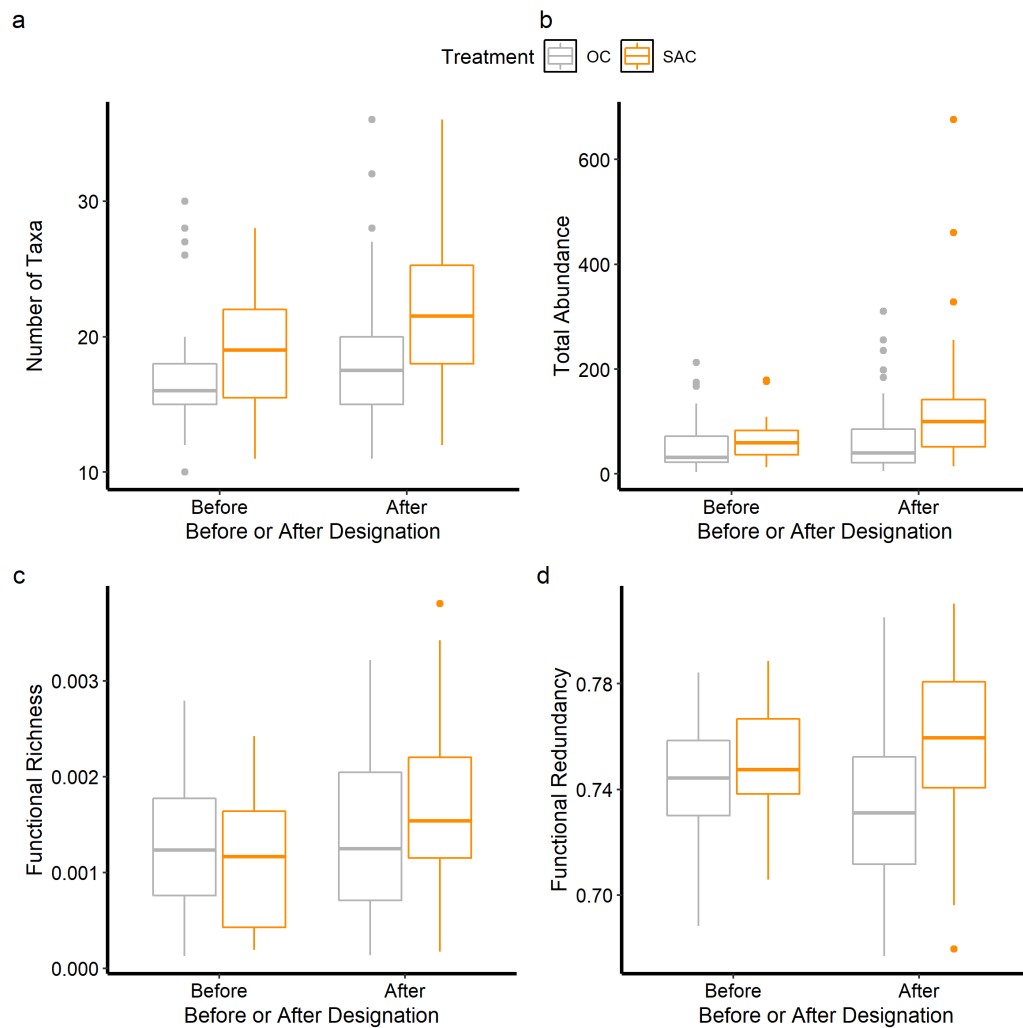


Fig. 5.2: Metrics (a: Number of Taxa, b: Total Abundance, c: Functional Richness and d: Functional redundancy) of sessile taxa, Before and After designation inside (orange) and outside (grey) the SAC.

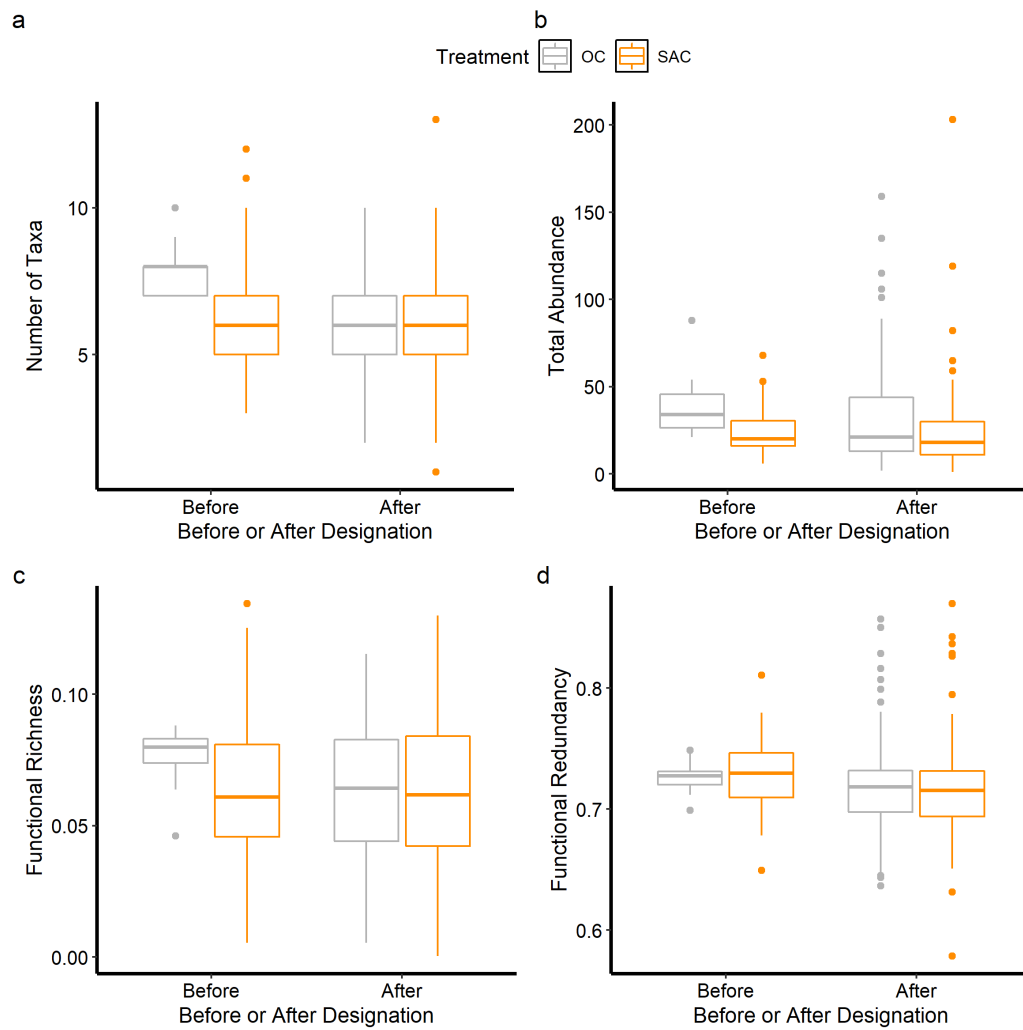


Fig. 5.3: Metrics (a: Number of Taxa, b: Total Abundance, c: Functional Richness and d: Functional Redundancy) of mobile taxa, Before and After designation inside (orange) and outside (grey) the SAC.

represented by assemblage compositions being similar across treatments every year, with no trend from before (2009, 2010 and 2011) to after (2012:2019) designation (Fig. 5.4b).

5.3.2 Age of Protection Assessment

Diversity

There was a significant difference between the change with age of protection and the different treatments for the number of sessile taxa (Table 5.3). This was shown by a significant increase with age of protection of the SAC (From 18.3 ± 1.55 at age 1 to 26.3 ± 2.66 at age 8: Table 5.3 & Fig. 5.5a) towards the greater levels of the whole-site MPA which did not change with age of protection (24.4 ± 2.18 at age 1 to 24.8 ± 1.93 at age 8: Table 5.3 & Fig. 5.5a). There was a significant difference between the change in total abundance with age of protection between the whole-site MPA and OC but not between the SAC and whole-site MPA (Table 5.3 & Fig. 5.5b). Total abundance in the whole-site MPA and SAC increased with age of protection (From 85 ± 65.7 at age 1 to 97.8 ± 83.1 at age 8 in the SAC and 72.6 ± 34.7 at age 1 to 142 ± 93.9 at age 8 in the MPA: Fig. 5.5b) whereas the OC decreased (63.3 ± 41.2 at age 1 to 23.9 ± 14.2 : Table 5.3 & Fig 5b). The functional richness showed no significant change with protection age or between treatments (Table 5.3 & Fig. 5.5c). The functional redundancy showed no significant change with age of protection from the whole-site MPA (0.768 ± 0.00737 at age 1 to 0.777 ± 0.012 at age 7: Table 5.3 & Fig. 5.5d), but showed a small increase with age of protection in the SAC (From 0.752 ± 0.0152 at age 1 to 0.764 ± 0.0245 at age 7: Table 5.3 & Fig. 5.5d) and a significant decrease with age of protection in the OC (0.754 ± 0.0151 at age 1 to 0.708 ± 0.0275 at age 7: Table 5.3 & Fig. 5.5d).

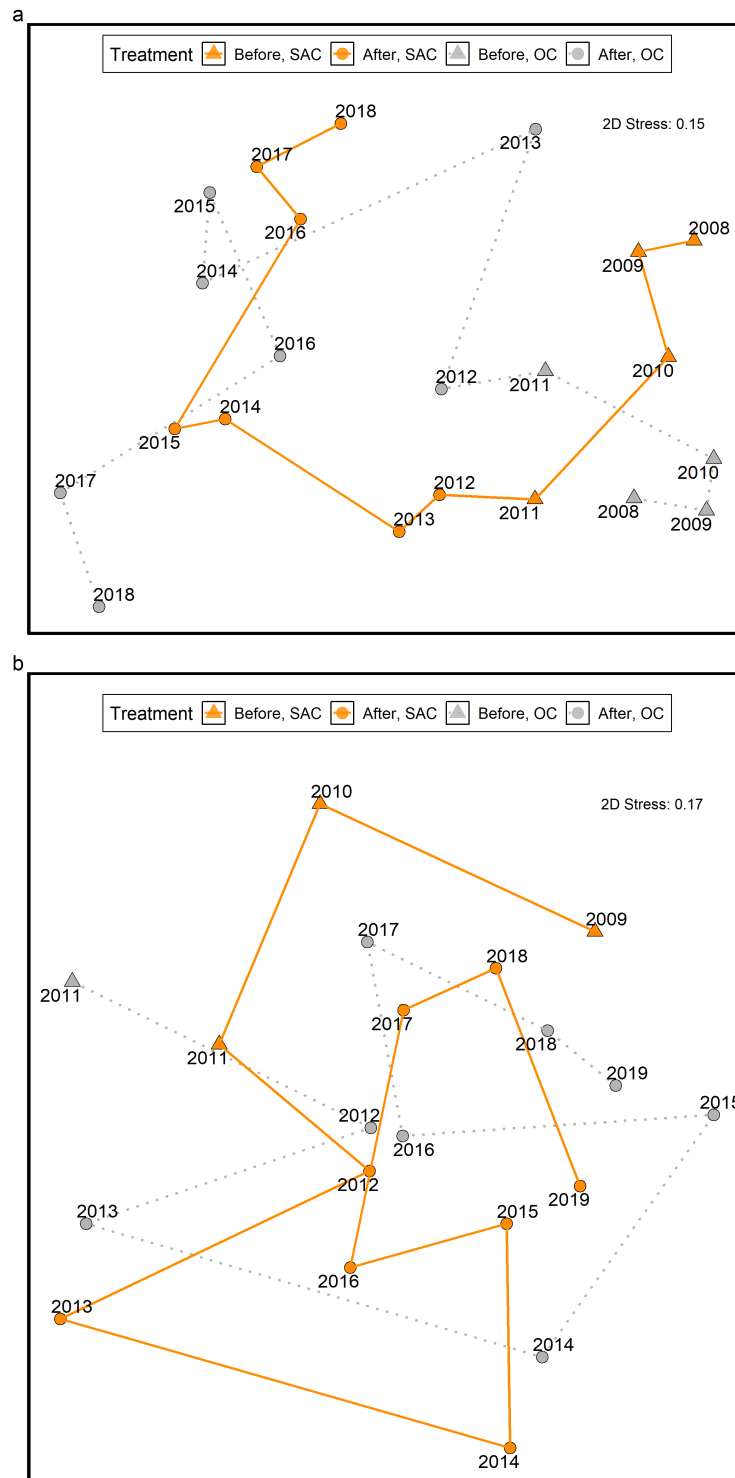


Fig. 5.4: Assemblage Change over time Before (Triangles) and After (Circles) for Inside the SAC (orange) and Outside Controls (Grey) for sessile (a) and mobile (b) taxa. Derived from distance to centroid values based on Bray-Curtis similarity of fourth root transformed abundances.

Table 5.3, Mixed effects model and PERMANOVA results for Age of Protection Assessment of SAC, whole-site MPA and OC with Number of Taxa, Total Abundance, Functional Richness, Functional Distinctiveness and Assemblage Composition as response variables measured from Baited and Towed Videos. Terms are shortened with Age of Protection as Age, Year as Yr, Site as Si and Treatment as Tr.

Terms	Sessile Taxa				Mobile Species			
	Estimate	SE	t/z value	p value	Estimate	SE	t/z value	p value
Taxonomic Diversity								
	Number of Taxa							
Intercept	3.19	0.115	27.8	<0.0001***	1.79	0.0563	31.8	<0.0001***
Age	0.00217	0.0225	0.0964	0.92				
MPA-OC	-0.382	0.163	-2.34	0.019*				
MPA-SAC	-0.347	0.164	-2.12	0.034*				
AgexMPA-OC	0.0116	0.0355	0.328	0.74				
AgexMPA-SAC	0.0581	0.0356	1.63	0.1				
	Total Abundance							
Intercept	4.17	0.237	17.6	<0.0001***	2.75	0.148	18.5	<0.0001***
Age	0.112	0.0477	2.35	0.019*				
MPA-OC	0.137	0.378	0.363	0.72	0.51	0.187	2.73	0.0063**
MPA-SAC	0.245	0.38	0.645	0.52	0.174	0.187	0.933	0.35
AgexMPA-OC	-0.275	0.0799	-3.44	<0.0001***				
AgexMPA-SAC	-0.0885	0.0805	-1.1	0.27				
Functional Diversity								
	Functional Richness							
Intercept	-6.74	0.137	-49.1	<0.0001***	-3	0.116	-25.9	<0.0001***
Age	0.0289	0.025	1.16	0.25				
MPA-OC								
MPA-SAC								
AgexMPA-OC								
AgexMPA-SAC								

Table 5.3, Mixed effects model and PERMANOVA results for Age of Protection Assessment of SAC, whole-site MPA and OC (*continued*)

Terms	Sessile Taxa				Mobile Species			
	Estimate	SE	t/z value	p value	Estimate	SE	t/z value	p value
Functional Redundancy								
Intercept	1.19	0.0405	29.3	<0.0001***	1.2	0.0494	24.2	<0.0001***
Age	0.00836	0.00795	1.05	0.29				
MPA-OC	-0.0308	0.0661	-0.466	0.64	-0.259	0.085	-3.04	0.0024**
MPA-SAC	-0.0896	0.0669	-1.34	0.18	-0.266	0.085	-3.13	0.0018**
AgexMPA-OC	-0.0468	0.0131	-3.56	<0.0001***				
AgexMPA-SAC	0.003	0.0134	0.224	0.82				
Source	df	SS	Pseudo F	p value	df	SS	Pseudo F	p value
Assemblage Composition								
Age	1	13000	2.01	0.0086**	1	19900	2.16	0.026*
Tr	2	108000	5.29	<0.0001***	2	120000	4.55	<0.0001***
Yr(Age)	10	72200	7.16	<0.0001***	10	110000	6.29	<0.0001***
Si(Tr)	15	86100	6.06	<0.0001***	21	160000	4.37	<0.0001***
AgexTr	2	5780	2.39	0.004**	2	10000	2.41	0.033*
AgexSi(Tr)	15	16300	1.02	0.42	21	47200	1.11	0.18
Yr(Age)xTr	5	5510	1.21	0.15	5	9430	1.18	0.22
Yr(Age)xSi(Tr)	75	63400	1.7	<0.0001***	104	167000	1.97	<0.0001***
Res	238	118000			327	266000		

There was no change with age of protection of treatment in the number of mobile taxa (Table 5.3). There was lower total abundance of mobile taxa inside the whole-site MPA (15.6 ± 2.03 : Table 5.3 & Fig. 5.6a) compared to the OC but no change with age of protection (18.6 ± 3.37 in the SAC and 26 ± 4.68 in the OC: Table 5.3 & Fig. 5.6b). Like number of taxa, there was no significant change with age of protection or treatment in the functional richness

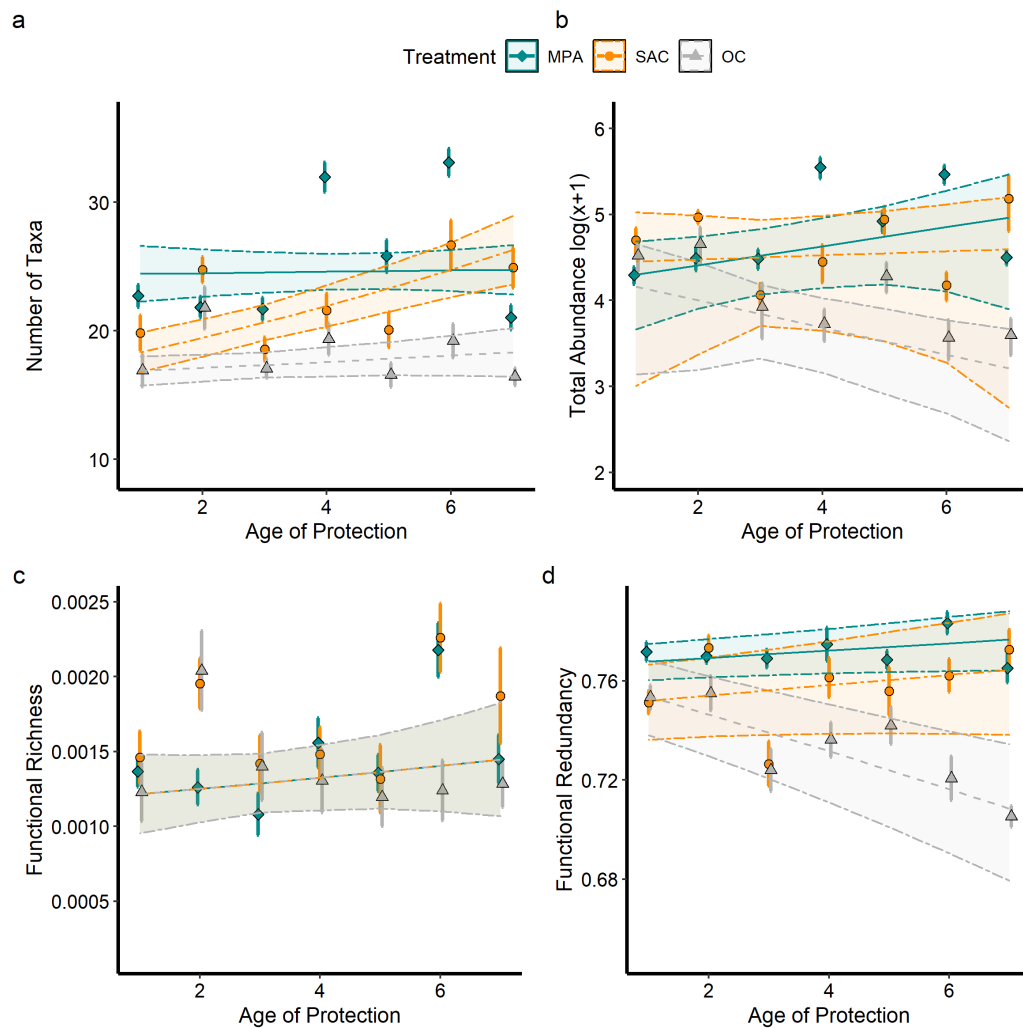


Fig. 5.5: Change in metrics (a: Number of Taxa, b: Total Abundance, c: Functional Richness and d: Functional redundancy) of sessile taxa, with age of protection of the whole-site MPA (blue), SAC (orange) and OC (grey; 'age of protection' based off of SAC age). Lines with shading show GLMM estimates and standard errors. Points with error bars show mean values and standard errors.

of mobile taxa (Table 5.3). However, there was a significantly greater functional redundancy in the whole-site MPA (from 0.768 ± 0.0088) than the SAC and OC (0.717 ± 0.0199 in the SAC and 0.719 ± 0.0198 in the OC: Table 5.3 & Fig. 5.6d).

Assemblage Composition

The Assemblage composition of the sessile and mobile taxa showed significant Age of protection:Treatment interactions (Table 5.3). The assemblages were highly distinct between the whole-site MPA and the other two treatments (Fig. 5.7a & 5.7b). With age of protection, the sessile and mobile taxa assemblages within the SAC became more similar to the whole-site MPA and less similar to the OC, although this was more pronounced in the sessile taxa (Fig. 5.7a & 5.7b).

5.4 Discussion

Eleven years of sessile and mobile benthic taxa monitoring were assessed, quantifying changes in assemblage composition, number of taxa, total abundance, functional richness and functional redundancy. Firstly, these metrics were used to assess the effect of a Special Area of Conservation (SAC) compared to nearby Open Controls (OC). The number of sessile taxa and their functional richness both increased from before to after (14.6% and 42.5% increase in the number of taxa and functional richness in both the SAC and OC), with the number of taxa, like the total abundance, being consistently greater in the SAC than the OC (Fig. 5.2). The sessile benthic taxa showed a shift in the assemblage composition in the SAC compared to the OC (Fig. 5.4a) and a modest increase in functional redundancy in the SAC (1.48% increase) compared to a decrease in the OC (1.54% decrease) from before SAC designation to after

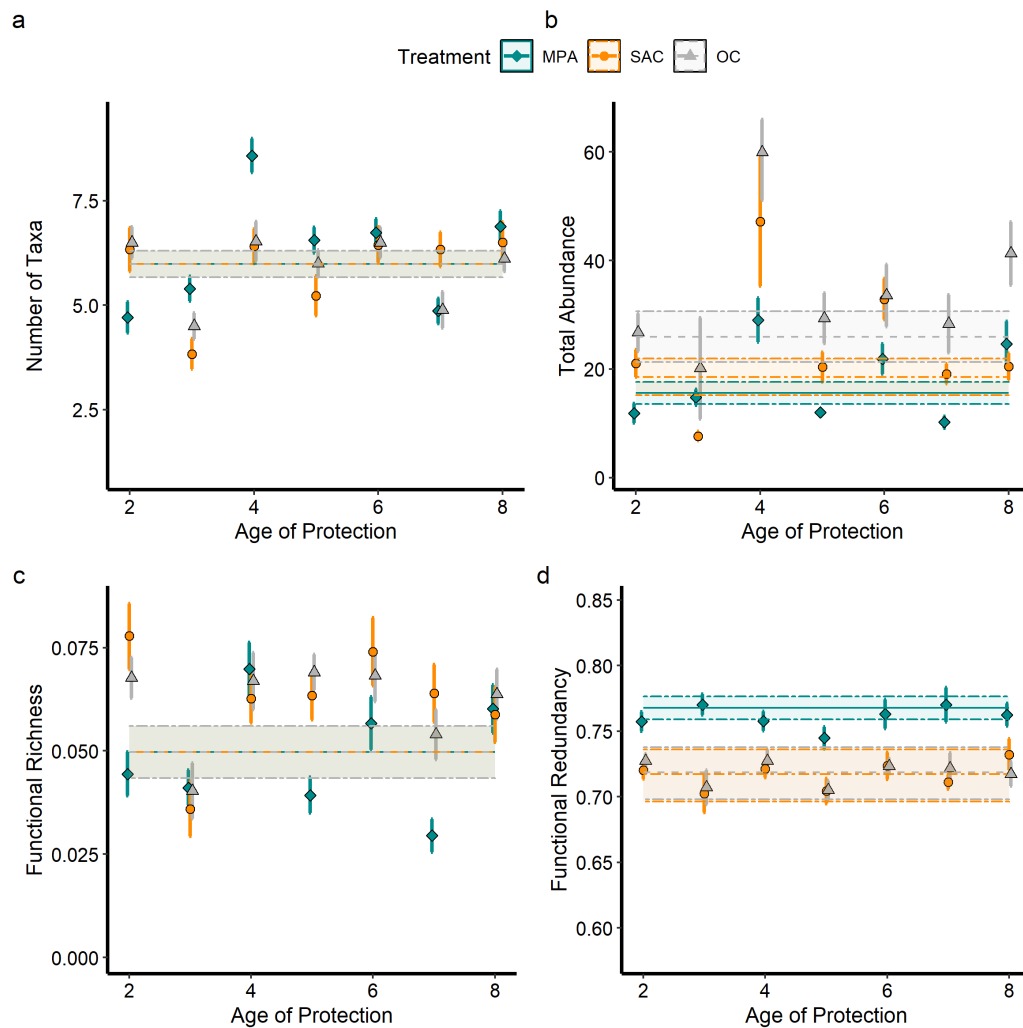


Fig. 5.6: Change in metrics (Number of Taxa, Total Abundance, Functional Richness and Functional redundancy) of mobile taxa, with age of protection of the whole-site MPA (blue), SAC (orange) and OC (grey; age based off of SAC age). Lines with shading show GLMM estimates and standard errors. Points with error bars show mean values and standard errors.

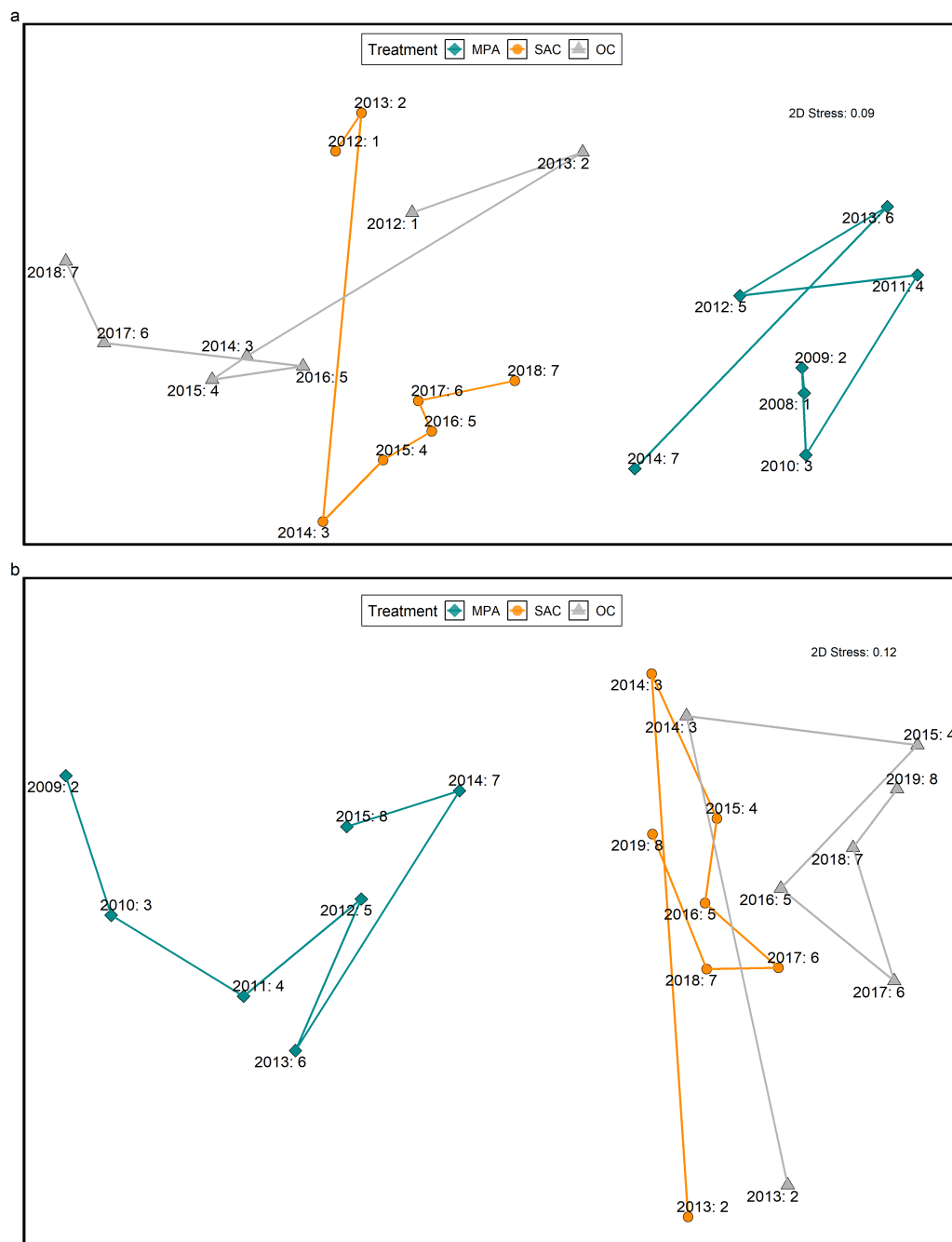


Fig. 5.7: Assemblage Change with age of protection for inside the SAC (orange), inside the whole-site whole-site MPA (blue) and OC sites (grey; age based off of SAC age) for sessile (a) and mobile (b) taxa. Derived from distance to centroid values based on Bray-Curtis similarity of fourth root transformed abundances.

(Fig. 5.2d). The mobile taxa showed no such trends, where only a shift in assemblage composition from before to after was found (Fig. 5.4b). Secondly, the metrics were used to assess the change with age of protection between the SAC and the whole-site Marine Protected Area (MPA), alongside unprotected comparison sites (where years since SAC protection was used as 'age' for the unprotected OC). The sessile fauna showed shifts in the assemblage composition with age of protection; the SAC became more like the whole-site MPA and less like the OC (Fig. 5.7a). This was seen with an increase in the number of sessile taxa with age of protection in the SAC (a 43.5% increase) but not in the OC (Fig. 5.5). Likewise, the total abundance and functional redundancy increased in the SAC (15.1% increase in total abundance and 1.66% increase in functional redundancy) and whole-site MPA (95.8% increase in total abundance and 1.15% increase in functional redundancy) with age of protection, and decreased in the OC (Fig. 5.5). The differences seen in the mobile taxa were: a shift in the assemblage composition in the SAC, which became more similar to the whole-site MPA with age of protection (Fig. 5.7b); greater abundance in the whole-site MPA than the OC (Fig. 5.6), and greater functional redundancy in the whole-site MPA compared to both the SAC and OC (Fig. 5.6). Regardless of treatment, functional richness of sessile and mobile taxa did not change with age of protection (Fig. 5.5 & 5.6).

Once protected, the SAC in Lyme Bay showed a trend of becoming more similar to the older and successful whole-site MPA already within the bay (See for example: [Sheehan et al. 2013a](#), [Rees et al. 2010a](#)). There were significant BACI effects found for the functional redundancy and assemblage composition measured within the SAC designation in Lyme Bay and, with increasing age of protection, the SAC became more similar to the whole-site MPA in comparison

to the OC. These trends were almost exclusively within the sessile taxa surveyed by the towed flying array. As the protections in both the whole-site MPA and SAC are aimed at protecting the Annex I reef habitats, it was expected that the sessile taxa would respond to these protections. This was witnessed after three years of protection in the whole-site MPA (Sheehan et al. 2013a). Yet, bottom-up recovery of reef associated mobile taxa is likely to happen over much longer time scales (Kaplan et al. 2019). However, it has been shown that over 12 years of exclusion of mobile demersal fishing, exploited fish taxa responded positively to the protection in the whole-site MPA (chapter 3). Further, the functional extent of the reef habitats inside the whole-site MPA increased over time, with the growth of reef associated species in previously non-reef protected areas (Sheehan et al. 2013a). The protection of these non-reef areas as well as the reef habitats allowed this increase. It is likely that the ecological response seen in the SAC will only extend to the areas of protected features and 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, it would be expected that the same increase in functional reef habitat extent would occur.

A simultaneous increase in the number and functional redundancy of sessile taxa alongside no change in functional richness suggests that the traits of the novel species appearing, due to the SAC protection, were not novel to the community. This in turn increases the level of overlap of functional traits in these protected sites. This would imply that mobile demersal fishing is removing benthic species with a wide variety of functional traits; thus displaying functionally 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). As biological invasions, storm events and other perturbations to benthic ecosystems increase in magnitude and frequency with climate change (Hettiarachchi et al. 2018, Diez et al. 2012), the 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 the ecosystem services, which humans rely on so heavily (Tillin et al. 2006). The combination of multiple functional and taxonomic univariate metrics will better describe the complex suite of ecosystem interactions that drive ecosystem function and health than a single univariate metric (Perović et al. 2018, Ricotta et al. 2016). Therefore, the 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, Mouchet et al. 2019, Howarth et al. 2018). However, inter-site comparison by the functional metrics used here, calculated with biological trait analysis, will require consistent numbers of traits and modalities (Villegger et al. 2008) as well as equivalent coverage of the ecosystem being assessed for their values 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 the effects of a MPA and effectively adapt management based on this assessment is very important for both fisheries and conservation (Claudet et al. 2020). This can be highly challenging to achieve, especially when the area is subject to many different pressures and protections. Thus, the application of spatially and temporally appropriate monitoring programs alongside rigorous statistical assessment of these monitoring projects are critical, not only to best protect the specific area itself but also 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, the decisions leading to many MPA designations were politically driven or altered, leading to the MPAs being unable to attain their objectives (Rife et al. 2013a, Devillers et al. 2015). Other protection regimes may have fully attainable objectives but due to the level of protection offered by the management policies in place they struggle to succeed as expected (feature vs whole-site Solandt et al. 2020). Hence, to appropriately plan and designate future MPAs, the assessment of MPA impacts, both positive and negative, needs to be analysed.

In conclusion, the designation of the 'feature' based SAC has led to increases in the diversity (both taxonomic and functional) of sessile taxa in Lyme Bay. These results are specific to areas inside the SAC outside of the whole-site MPA, where Annex I reef habitats have been evidenced. The protected feature, Annex I reef habitats, within the SAC are being protected and are showing increases in the potential to provide ecosystem services and increases in resilience to perturbations from storms, destructive fishing or biological invasions. The areas that have been protected are increasingly resembling areas within the whole-site MPA, meaning with age of protection, the increases in exploited mobile species found inside the whole-site MPA are likely to be seen in the SAC. As with the other metrics here, it would be expected if more than the extent of the visible reef was protected within the SAC, like the whole-site MPA, the extent of the biogenic reef habitats would increase. Therefore, to fully ensure protection of the Annex I reef habitats, their functional extent should be protected not just their visible extent.

“When you have oceans, you have hope.”

Jacques Cousteau

6

Discussion

6.1 Rationale

Direct and indirect human impacts to the oceans have increased over the last century and are predicted to continue increasing (Armour et al. 2016, Trossman et al. 2016). This has and will lead to decreased resilience to the effects of climate change (Halpern et al. 2015, Frölicher and Laufkötter 2018). One of the most globally important anthropogenic impacts to the oceans is overfishing (Jones et al. 1992, Ding et al. 2017). As over 3 billion people rely on fisheries

for food security and health, overfishing has been assessed by the United Nations with specific goals on moving towards sustainable fisheries globally (UN News Centre 2015, FAO 2016). To manage fisheries, Marine Protected Areas (MPAs) have been used extensively with varying results (Claudet 2018). However, the use of Ecosystem Approach to Fisheries Management (EAFM), where the whole ecosystem is managed not just the target species, has been advocated for a framework for successful MPAs (Katsanevakis et al. 2011). Designation rate of MPAs is increasing greatly, as nations commit to the sustainability goal of 30% by 2030 (Rees et al. 2020, Waldron et al. 2020, O'Leary et al. 2016). To achieve sustainability of fisheries through MPAs, three different techniques have been employed globally: protecting a specific species; protecting an environment or protecting the biodiversity found in the environment (Rees et al. 2012b). The most common of these techniques is protecting a specific species or 'feature' (Solandt et al. 2020). However, it has been argued that to follow an EAFM framework, an MPA should protect the whole ecosystem of the target species. Yet, protecting a whole ecosystem consistently is rare and the assessment of the ecological effect of this management over time is rarer still.

Here, a unique example of a UK MPA, which has protected the whole ecosystem consistently from mobile demersal fishing, has been studied over 12 years in Lyme Bay by the University of Plymouth. The towed flying array has been used to carry out 665 transects, with ~230 hours of transect video analysed and ~39,900 m² of seabed covered, counting 160 different taxa across 8 phyla. Baited Remote Underwater Video systems (BRUVs) have recorded 743 videos, with 371 hours analysed, counting 74 different taxa across 4 phyla. Passive Acoustic Monitoring (PAM) was used to record 3,645 fifteen second record-

ings; 16.2 hours in total. These data spanned three different treatments: the whole-site MPA, which excluded all forms of mobile demersal fishing; a Special Area of Conservation (SAC) designation, where 'reef' habitat features only were protected from mobile demersal fishing, and Open Controls where mobile demersal fishing is still permitted. The towed flying array assesses all sedentary and sessile benthic epifauna, while the BRUVs enumerates all visible mobile benthic taxa. These two methods together survey a large proportion of the benthic ecosystem. The whole-site MPA and the subsequent SAC were both designated to protect and allow recovery of the Annex I reef habitats and associated species. Therefore, the combination of these two methods effectively sample the species that the MPA was designated to protect (Anon 2008).

6.2 Assessing Biodiversity with Passive Acoustic Monitoring

Across five years of the MPA's protection, 2014 to 2018, the use of PAM was assessed alongside BRUVs (Chapter 2). The complexity of underwater acoustics (ACI) was expected to reflect the level of mobile benthic biodiversity present in the system. This expectation was influenced by studies assessing PAM in different reef systems. The potential advantages of using PAM make them a prime candidate for regular MPA surveys. PAM can provide a vast quantity of information with minimal user input and has been demonstrated to be able to predict benthic biodiversity (Picciulin et al. 2013, Harris et al. 2016, Peck et al. 2021). The use of ACI in this MPA did not show the direct relationship with the benthic biodiversity observed through BRUVs. However, the assemblage composition showed significant covariance with the ACI. For this, or another, acoustic index to be used as a fast and low cost monitoring tool, the elements that it samples need to be further understood, as simple biodiversity showed changeable relationships depending on the year of sampling. Therefore, thorough experimental

(empirical and theoretical) assessments of the algorithm, which calculates ACI from a recording, will be needed, with robust spatial and temporal coverage. This is necessary, as in specific years of this data set (e.g. 2014 or 2018) the ACI followed expected trends of positive correlation with species richness, yet in other years showed opposing trends. The Acoustic Complexity Index is not, as yet, ready to be used as a marine diversity monitoring tool, even in conjunction with other methods, such as BRUVs, which effectively demonstrated the recovery and increased diversity within the Lyme Bay MPA. However, this acoustic index showed potential to enumerate patterns of shifting benthic assemblage compositions but this had no consistency alongside univariate measures of diversity. This implies that the metric is quantifying elements of the ecosystem not directly quantified by the univariate diversity metrics enumerated here. For it to be used as a monitoring tool, the information it provides, regarding these shifting compositions and associated taxa, need to be fully researched and understood.

6.3 Can Ecosystem Approach to Fisheries Management benefit both exploited and non-exploited organisms?

After three years of protection, evidence showed that sessile benthic taxa within Lyme Bay MPA had started to recover from the exclusion of mobile demersal fishing (Sheehan et al. 2013b), with the functional extent of the reef habitat increasing into previously non-reef areas (Sheehan et al. 2013a). These sessile taxa were the main reason for the MPA designation but the majority of fisheries by weight and value in Lyme Bay (Mangi et al. 2011), and globally (FAO 2016), rely on mobile taxa. Therefore, assessing the effect of the MPA on these taxa will be important to illustrate any bottom-up benefit the MPA is having to the

nearby fisheries, by protecting the habitats that support these taxa. However, the timescales to detect a positive response from protection can be over 10 years (Kaplan et al. 2019). Yet, in chapter 3, as elsewhere (Speed et al. 2018), increasing trends in exploited fish diversity and abundance were seen over a shorter timescale than expected.

From 2009, BRUVs were deployed throughout Lyme Bay MPA and surrounding areas. The effects over time on the assemblage composition, total diversity and abundance, and diversity and abundance of exploited groups of taxa were assessed. This analysis showed a positive temporal response in the number and total abundance of exploited fish taxa (~400% increase over 11 years), these taxa inside the MPA increased at a rate twice that of the OC. This showed that the protection and enforcement have provided benefits to conservation and potentially fisheries alike. The main target taxa by value, Whelks *Buccinum undatum*, Brown Crab *Cancer pagurus* and Lobster *Homarus gammarus*, require further assessment, as they showed no temporal changes in diversity or abundance. Potting for these species within the MPA increased once mobile demersal fishing was prohibited (Mangi et al. 2011, Rees et al. 2021b,a), yet this increase in effort did not decrease the abundance of the targeted species. This further supports the idea that the current levels of static fishing in Lyme Bay MPA are allowing sustainable populations of these species to be maintained. However, the analysis of landings data, which include spatial capture information, alongside surveyed population data would give a better picture of the sustainability of the fishing that continues within the MPA. Regardless, this provides further evidence of the capabilities of well enforced and monitored partial protection, and how the compromise between conservation and fisheries management can benefit benthic ecosystems when the whole-site approach is

employed, as opposed to individual feature protection.

6.4 How was the Functional Diversity affected by applying the Ecosystem Approach to Fisheries Management?

Within frameworks of EAFM, the protection of ecosystem services is of increasing importance (Halpern et al. 2010). Ecosystem services are driven by the suite of functional traits present within a community, with links between functions and ecosystem wide processes. For example: feeding habit has been linked to benthic-pelagic coupling and trophic linkage (Beauchard et al. 2017); environmental position (benthic, pelagic etc) has been linked to sensitivity to destructive fishing, and longevity, maturation age and reproductive strategy have all been linked to recovery from destructive fishing (Rijnsdorp et al. 2016). Further, the overlap of functional traits, or functional redundancy, will lead to more resilience to perturbations such as storms, biological invasions or destructive fishing (Tillin et al. 2006, McLean et al. 2019). Therefore, assessment of functional trait abundance and any changes over time, in relation to different protection strategies, will allow the potential level of ecosystem services to be monitored.

Diversity (Taxonomic and Functional), number of taxa and the combination of functional richness, functional divergence and functional evenness, showed positive increases within the MPA since designation (Chapter 4). Number of taxa and the functional richness increased significantly over time in the MPA compared to the OC, meaning an increase in the number of different traits. In contrast, the functional divergence was significantly lower and decreased over time in the MPA, showing that the abundance of rarer traits decreased in the MPA over time. The functional evenness, how evenly abundant traits are in the

system, did not show significant patterns with treatment. Finally, the functional redundancy, the amount of trait overlap in the system, increased over time in the MPA while it decreased in the OC. Together this shows that, functionally, the number of traits is increasing over time in the MPA when compared to areas that continue to be open to mobile demersal fishing, alongside increases in trait overlap, increasing the potential for ecosystem services to be provided.

The goal of many MPAs is not just to protect biodiversity but the ecosystem processes, which provide key services (Coleman et al. 2015). The responses expected in traditional biodiversity metrics following protection, which are often driven by ecosystem wide functional and trophic changes (Babcock et al. 2010), can take long time periods to manifest (Kaplan et al. 2019). By assessing the change in metrics that drive biodiversity change, functional assessment can more rapidly provide information on the effects of MPA management. However, as functional metrics will be affected by many ecosystem wide processes, some of which may not lead to increased biodiversity, it is suggested that functional metric assessment is added to the suite of MPA monitoring tools alongside traditional biodiversity to provide a more complete assessment of the system under investigation. Furthermore, comparison between sites using these metrics requires consistency in the maximum number of taxa assessed and the number of biological traits used to assess them (Villegger et al. 2008). Therefore, as available biological trait information increases and becomes more accessible this approach becomes more widely applicable and will provide a useful tool for MPA management.

As expected, the cessation of mobile demersal fishing also had an impact on the proportion of specific traits within the MPA. There were increases in sessile filter feeders in the MPA with simultaneous increases in mobile (crawling

and swimming) scavengers in the OC. This demonstrates that the functions within the MPA are changing towards more sessile reef communities, while the OC displays traits associated with low successional communities. These low successional communities are often under chronic pressure, which mobile scavenging taxa are adept at enduring.

6.5 Does ‘feature’ protection provide similar benefits to the whole-site approach?

The introduction of a SAC, which increased the total area where mobile demersal fishing was prohibited within Lyme Bay, gave two unique opportunities: the ability to assess the effects of the SAC compared to nearby controls, using both before and after data, and the ability to assess the difference between a whole-site MPA (the original designation) to a feature based MPA (the new SAC). The sessile and sedentary and mobile benthic communities were used to assess these changes (Chapter 5). The SAC significantly altered the assemblage composition of both the mobile and the sessile and sedentary benthic fauna (derived from BRUVs and towed flying array data respectively). The positive impact of the SAC was most clearly shown in the sessile benthic fauna, where there was a significant increase in the number of taxa from before to after designation across both treatments, although the SAC was higher throughout. There was also higher total abundance of sessile and sedentary benthic fauna in the SAC than the nearby controls. However, functional redundancy was the only univariate metric that showed a significant increase in the SAC in comparison to the OC where it decreased. This showed that the sessile and sedentary benthic fauna increased in biodiversity generally throughout the treatments, while the assemblage within the SAC became more resilient to perturbations than the

OC. There was also a general increase in the number of sessile benthic taxa with age of protection in both the MPA and the SAC, but no difference between the two treatments. The only difference between the treatments with age was found in the assemblage composition of both the sessile and mobile benthic fauna. As before, the functional redundancy of the mobile benthic fauna was significantly higher inside the MPA compared to the SAC and did not change with age of protection. Thus, the MPA consistently showed higher resilience to perturbations in the mobile portion of the assemblage, displayed by a greater functional redundancy. However, no change over time in this metrics was seen across the treatments in the mobile taxa.

Protection of the reef habitats inside the SAC has led to a significant increase in sessile taxa, similar to that of the MPA over time. However, non-reef areas within the SAC were not assessed but as these non-reef SAC areas were subjected to the same regulations on mobile demersal fishing as the OC, it was expected they would respond in a similar way. If true, this would mean that ~46% of the SAC outside the whole-site MPA would have seen negative trends in total abundance and functional redundancy, and lower numbers of sessile taxa. By definition, these areas within the SAC that have no legislation attributed to them can be considered as 'paper parks'. Therefore, any future analyses, which assess or monitor these protections that are spatially limited to a 'feature', will need to account for this treatment dissimilarity when planning sample designs. These unprotected areas within MPAs could be erroneously included within calculations of attaining sustainability targets.

6.6 Implications of Lyme Bay Research

This thesis is the culmination of a project, which in its entirety provides the largest, longest and highest temporal resolution study of a whole-site MPA in temperate seas. As such, it has allowed the assessment of multiple monitoring methodologies: taxonomic diversity, acoustic complexity, functional diversity and assemblage composition through the simultaneous use of BRUVs, PAM and towed flying array. As governments around the world, and especially in Europe, are increasing their inclusion of policy emphasising the use of Ecosystem Approach to Fisheries Management, Lyme Bay MPA stands as the most complete and comprehensive guide for how to best: instigate management, which addresses key ecological issues at their source; adaptively manage a marine area, by inclusion of as many stakeholders as possible; utilise appropriate sampling methods, which non-destructively, non-invasively and non-extractively sample the protected ecosystem, and utilise the data produced, to inform other management and monitoring frameworks elsewhere. The cumulative work from Lyme Bay has come at an opportune moment to influence 'best' practise throughout the UK and Europe. Specifically in the UK, fisheries policy is looking towards using an EBFM approach ([Anon 2018](#)), which this work can directly influence.

6.7 Recommendations for Future Research

Here the acoustic complexity index (ACI) was used, as it is a relative value of underwater acoustic noise as opposed to an absolute value of acoustic energy. As the equipment used here was encased within resin it was impossible to carry out regular validations of instrument performance. Therefore, the true specification of the equipment was likely to shift over time. This limited the ability to

assess nuances within different frequencies of the underwater soundscape and how those alterations within the different frequency bands were changing over time. Further, it meant the total acoustic energy produced could not be calculated and analysed alongside BRUVs surveys. In the future, when assessing PAM as a tool for MPA monitoring, the whole soundscape should be assessed, with the total acoustic energy across multiple frequency bands being compared to simultaneous BRUVs.

The values created from these BRUV surveys are a measure of relative abundance, and therefore may not sample a consistent portion of the whole population. Likewise, as a relative abundance they cannot be explicitly compared or combined with other methods, which calculate absolute abundance, but the integration of the BRUV and towed Flying array data was possible when analysing functional trait metrics, as these are calculated either without abundances or using relative abundances. However, to fully integrate the BRUV data with other forms of survey, the relative abundance values need to be converted into absolute abundances. This will be highly reliant on the local conditions during BRUV deployment, the behaviour of the species, and the type and surface area of the bait used (Dunlop et al. 2015, Bicknell et al. 2019). Throughout this work the surface area and type of bait was maintained consistently, but the local conditions were not. Therefore, measuring local current velocities and taking into account the specific behaviour of certain species will help estimate the true abundance of those species.

To carry out functional assessment, online repositories, peer reviewed literature and expert opinion was used to assign traits to species. However, for many species and groups of taxa the data were unavailable, meaning these taxa were assigned values found for nearest taxonomic neighbours. Yet, especially within

some taxonomic families, there can be huge variation in function and traits. Therefore, this lack of consistency in available functional trait information may have decreased the accuracy of the methods used, or at least decreased the possible variation within the community. Understanding the changes in ecosystem function is likely to become more important because ecosystem functions heavily affect ecosystem wide processes, influencing the services that humans derive from the ecosystem (Perović et al. 2018, Ricotta et al. 2016, Rees et al. 2020). Therefore, further efforts will be needed to create complete understanding of the functional traits of all species and increase the availability of this information.

The functional diversity assessments used in chapter 4 and 5 assessed a large portion of the benthic ecosystem and has been advocated to aid future MPA adaptive management (Tillin et al. 2006, Wiedmann et al. 2014, Rijnsdorp et al. 2016). However, as shown by the order of magnitude differences in functional richness between chapter 4 and 5, consistency needs to be kept for the total number of taxa, as well as the number of functional traits, if comparing two different sites. This occurs as the functional richness is an absolute volume at that site, which fills the potential absolute volume of all taxa and traits within the data being assessed. By combining the towed flying array and BRUV data in chapter 4 the maximum total volume is far larger than if the towed flying array or BRUV were assessed separately (Chapter 5). Therefore, to be a useful and appropriate tool for adaptive MPA management, functional metrics such as these need to also specify the maximum number of species possible, as well as the number of traits/modalities used as suggested by Villegger et al. (2008). As the number of traits and taxa are stored within the trait by taxa matrix, it could be useful for authors to quote the dimensions of this matrix when report-

ing functional metric values or setting future goals. This further emphasises the need for increased trait availability of data. If this trait information were available for all possible taxa within a region, practitioners could use an open access trait by taxa matrix that includes all possible taxa and traits, allowing consistent comparison between research groups and sites. To achieve this, the first objective would be to create a complete an exhaustive taxa list of organisms that could potentially occur during a specific survey type (BRUVs, Towed Underwater Video, Grabs etc.) within a study region (e.g. North Atlantic Coastal seas), then produce biological trait information for all taxa. This would require large quantities of resources, both time and money, while also relying on extensive international cooperation and collaboration. There would, for example, need to be consensus on the number and identity of traits of importance. Realistically, specific studies with specific aims would be more interested in different subsets or groups of traits. Therefore, transparency and consistency in reporting of number of taxa and number of traits within methods should be advocated.

The effectiveness of a 'feature' based protection method was assessed alongside a whole-site MPA. The 'feature' based SAC had higher numbers of taxa, total abundance and functional redundancy of sessile benthic fauna than the nearby control sites, and showed similar patterns with age of protection as the whole-site MPA. However, the SAC sites sampled were all located on reef habitats. Therefore, the potential differences between the two protection types were not seen in the data. The protection of SAC only encompasses the evidenced extent of the protected feature, the reef habitat. Yet, after four years within the whole-site MPA, where a mosaic of reef and non-reef habitats were protected, there was an increase in the functional extent of the reef into previously non-reef areas ([Sheehan et al. 2013a](#)). Surveying habitats adjacent to the reef

habitats would highlight the overall effect to the ecosystem of these protection types and likely provide further evidence supporting this type of EAFM.

The Lyme Bay monitoring project has already provided many different research opportunities covering ecological, social and economic effects of the MPA (Sheehan et al. 2013a,b, Rees et al. 2010b,a, 2012b, 2015, 2020, 2021b,a, Gall et al. 2020). However, the data it generates and will generate as it progresses into the future will allow more vital research, whether monitoring the effects of vulnerable or highly exploited fisheries species, such as sharks, rays, wrasse and whelks, or assessing the life history effects of anthropogenic and natural perturbations (storms, fishing pressure etc.) to nationally important species such as Pink Sea Fans *Eunicella verrucosa* and Ross Corals *Pentapora foliacea*. Simulations of bait plumes with stochastic models of species responses could be employed to convert BRUV relative abundance data to absolute abundance. These calculations could be tested at first on simple behaviour species, such as whelk, and ground-truthed using field experiments with BRUV deployments in known densities of whelks verified by towed flying array footage.

Lyme Bay has also highlighted the importance of carrying out effective sample designs to be able to accurately assess the effects of different management regimes. However, it has also highlighted the fact that management strategies change over time meaning that sample designs need to have high levels of redundancy to be useful and continue to provide evidence bases that can inform 'best' practice when it comes to management. Moving forward there should be a roll-out of the Lyme methodology (BRUVs and towed flying array) across UK and Europe, with continued updating of the methods through experience, while, also supplementing BRUVs and the towed flying array with other methods to provide a more complete assessment of the ecosystem, such as

infaunal survey and drifting BRUVs or Floating Aggregation Devices. As shown by [Sheehan et al. \(2013a\)](#), the functional extent of reef increased within Lyme Bay over 4 years; 12 years on, the reef extent data available could be updated at higher resolution and accuracy using the towed flying array.

6.8 Where Lyme Bay fits

Creation of MPAs will proliferate, with government targets aiming to protect 30% of the oceans by 2030 ([Brander et al. 2020](#), [Waldron et al. 2020](#)). These targets require extensive planning and appropriate goals to achieve their overarching aim of protecting and increasing biodiversity and the associated ecosystem services. If an inappropriate level of planning and use of scientific knowledge is applied, the 30% goal may be met but not the overarching goals themselves, leading to disengagement. Therefore, before protected areas are instigated, appropriate research should be consulted relating to the management practices to be applied. Thus, the need for more evidence on how best to protect these areas becomes more prominent but so does the importance of monitoring the protected system over appropriate temporal and spatial scales as well as the necessity for high quality baseline data. Like the species within them, ecosystems can be highly diverse and changeable, meaning the tools used to protect, monitor and manage them need to be equally as diverse and flexible.

This work can directly impact these management decisions, but should also instigate further research over similar temporal and geographical scales. The wealth of data and conclusions from 12 years of monitoring this site relates to local fisheries and the species they exploit, as well as the other ecosystem services they gain from the area. Currently, Lyme Bay stands alone in the UK as the largest example of a MPA with partial protection, where the whole-site

approach has been applied over long temporal scales. When aiming towards protecting 30% of the oceans by 2030, the quality and effectiveness of the protection is of great importance, arguably more so than the total area combined within one state's waters. Therefore, the inclusion of a whole-site approach to defining protected areas within marine management legislation should be advocated and employed.

This MPA, its' monitoring and research is unique in Northern Europe especially when considering: size of protected area; consistency of protection and monitoring; temporal scale of protection and stakeholder engagement. However, there are other successful examples of MPAs across the british isles that have some, if not all, of these traits, namely; Port Erin Closed Area in the Isle of Man and Lamlash Bay NTZ in the Isle of Arran in Scotland. These protections all include exclusions of mobile demersal fishing to protect seabed integrity with the aim of boosting or recovering local scallop fisheries. Port Erin was protected in 1989 and has shown positive outcomes with increases in adult scallop density by 7 times as well as inceases in exploitable and reproductive biomass by 11 and 12.5 times respectively after 14 years of protection (Beukers-Stewart et al. 2005). Lamlash Bay NTZ protected an area of seabed from all forms of extractive activity in 2008. This lead to increases in king scallop abundance by 1.8 times, and exploitable and reproducity biomass of 2 and 2.5 times respectively after 5 years of protection (Howarth et al. 2015). As successful as these examples are, they are highly specific to the local fisheries (scallops) and they also cover far smaller areas than Lyme Bay MPA: Port Erin is $\sim 2\text{km}^2$ and Lamlash Bay NTZ is $\sim 2.7\text{km}^2$.

The changes seen in Lyme Bay, increases in diversity (taxonomic and functional) and abundance of both sessile and mobile species, indicates a trend

towards recovery. However, it also highlights that the Bay was recovering from a heavily denuded system. The diversity, specifically of mobile species, is comparable to studies from elsewhere across the UK. [Jones et al. \(2021, 2020, 2019\)](#), [Peters et al. \(2015\)](#), [Griffin et al. \(2016\)](#) all utilised BRUV systems across areas of the UK finding ranges of number of taxa from 2 up to 12. This shows that although Lyme Bay is recovering from a very low level of diversity (~4 different species in 2009) it is increasing to similar levels to other areas of the UK (~7 different species in 2019). Assuming a continued increase in diversity of mobile species, Lyme Bay will be supporting high numbers of commercial species and thus, more able to support a wide range of fisheries.

6.9 Implications of Brexit

MPA legislation in the UK is a relatively novel concept, starting in the 1980's ([Jones 2008](#)). Yet, since then European-wide legislation has driven the majority of MPA designation across Europe, including the UK ([Gall and Rodwell 2016](#), [European Commission 1992](#)). The majority of UK MPAs have been 'feature' based, relying on evidenced extent of Annex species and habitats, and the impacts specific practices have on these species and habitats ([Solandt et al. 2020](#)). However, as shown here and in other literature, protection of a whole site, taking into account as many habitats and species within an ecosystem as possible, will increase ecosystem health and lead to benefits in local and global fisheries, biodiversity and ecosystem services ([Elliott et al. 2017](#)). As the UK moves away from the EU legal framework, much of the legislation governing MPAs is likely to be updated or reassessed, providing a perfect opportunity to use the best available research to drive legislation, with indications from a White Paper that the government will be focusing more on the whole-site approach ([Anon 2018](#)). This is, to a certain degree, already taking place, with the

proposal to protect whole-site areas to mobile demersal fishing, such as Dogger Bank Special Area of Conservation; Inner Dowsing, Race Bank and North Ridge Special Area of Conservation; South Dorset Marine Conservation Zone, and The Canyons Marine Conservation Zone ([Formal MMO Consultation on MPA](#)). However, the establishment of these areas must also be combined with monitoring efforts that not only encompasses the protected areas and their sensitive habitats but the whole ecosystems they interact with. Finally, these management methods must adapt to the outcomes of this monitoring to maximise the positive effect that these protections can have.

6.10 Conclusions

Across 12 years of whole-site protection, Lyme Bay MPA monitoring project has allowed the comparison of different management styles, the rapid assessment of the benthic environment to inform management and the critical assessment of MPA monitoring methods leading to ongoing practical development. It has shown the necessity of temporal and spatial extent when assessing emerging methods, and that theoretical and empirical understanding must corroborate over these extents to accept such methods (chapter 2). Chapter 3 showed that main exploited fish taxa increased in diversity and abundance. However, the major exploited group, invertebrates, showed no change over time, even though the MPA designation led to an increase in static fishing within the MPA ([Rees et al. 2021b](#)). The cessation of mobile demersal fishing in Lyme Bay allowed the proliferation of functional traits across mobile and sessile benthic taxa (chapter 4). As expected and predicted from other literature ([Tillin et al. 2006](#)), the proportion of filter feeders and sessile organisms increased in the MPA compared to the OC. This means the MPA increased over time in its ability to provide ecosystem services, while its resilience to perturbation events

increased with greater overlap of traits. This expands and extends the functional benefits that are being displayed by the MPA to the benthic communities in Lyme Bay. Finally, the effect of a 'feature' based MPA (SAC) was assessed in Lyme Bay (chapter 5). It displayed significant positive responses in diversity (taxonomic and functional) of sessile taxa from before to after designation, relative to open controls. Furthermore, the assemblage composition became more similar to the MPA and less similar to the OC with increased age of protection. Yet, it was expected that, to see an increase in mobile species, as seen in the whole-site MPA, the SAC would need to likewise protect areas of 'non-reef'. This protection would be expected to increase the functional extent of the 'reef' areas and thus increase the available Essential Fish Habitat. This work has tested approaches for MPA monitoring (chapter 2), displayed the benefits to the sessile benthic ecosystem of protecting fragile habitats from mobile demersal fishing (chapter 5) and shown how extending protection across a mosaic of habitats can benefit both the sessile and mobile benthic taxa. This led to higher resilience to perturbations, greater potential to provide ecosystem services and increases in commercially exploited taxa within Lyme Bay MPA (chapters 3 & 4).

The suite of methods used, both data collection and analysis, and their applications within MPA management have been assessed. These methods have highlighted their own value and the necessity for further research (chapters 2 & 4), while others have been used to test the management and protection strategies within Lyme Bay (Chapters 3 & 5). All methods used and assessed here have displayed research and knowledge gaps: chapter 2 highlighted the need for more empirical evidence of acoustic complexity enumerating biodiversity and what elements of the community are driving this complexity; chapter 3 showed

the complexities of defining ‘commercial’ taxa and the necessity for high resolution fisheries data to adequately assess recovery of taxa important to fisheries; chapter 4 highlighted the need for consistency of assessment using specific metrics and indices, especially when comparing between systems or regions, and chapter 5 highlighted the need to take into consideration the non-protected areas within MPAs when assessing their effects. This thesis assessed a unique dataset and showed the effects of a whole-site partially protected Marine Protected Area to the benthic ecosystem over 12 years with increases over that time in commercially exploited fish, diversity (taxonomic and functional) of benthic fauna (sessile, sedentary and mobile combined) and resilience to perturbations in comparison to nearby controls. Showing that the whole-site approach employed in Lyme Bay has benefited the benthic ecosystem substantially and should be considered for future management applications.

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“But I am very poorly today and very stupid, and hate everybody and everything.”

Charles Darwin



Appendix A

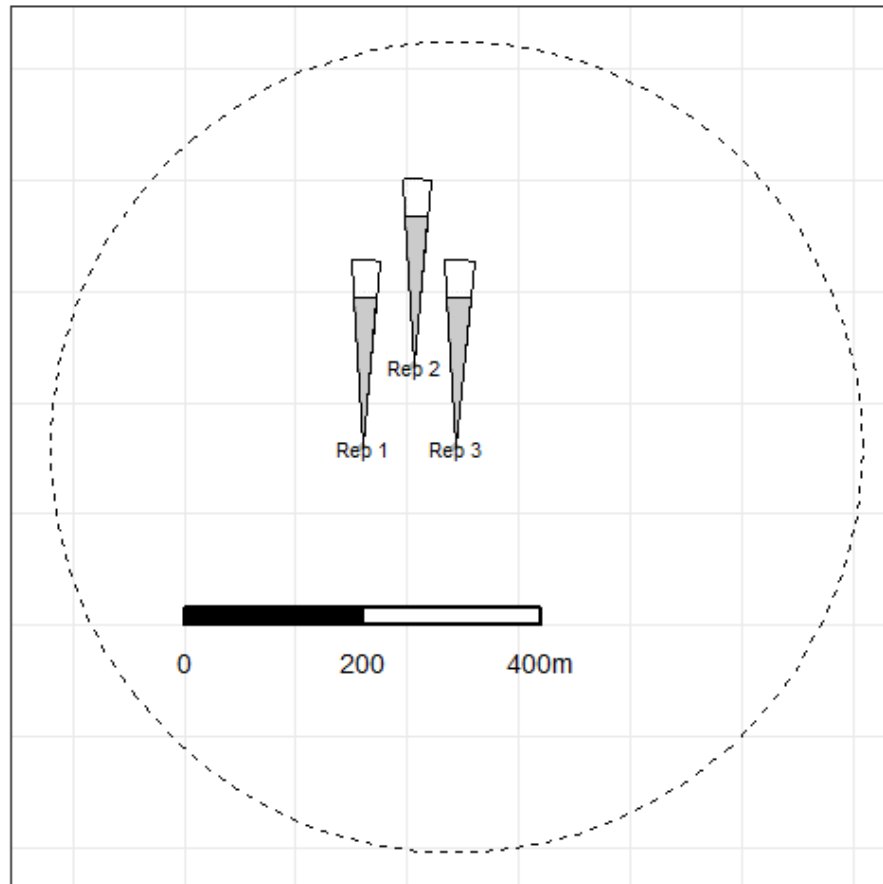


Fig. A.1: Schematic of three BRUVs replicates, their bait plumes and the acoustic recording array. Bait plume size (unfilled segment) from Dunlop et al. (2015), range of effective attraction (filled segment) from Cappo et al. (2004) and detection range of acoustic (dashed circle) DSG from Simard et al. (2015).

“Science makes people reach selflessly for truth and objectivity.”

Lise Meitner

B

Appendix B

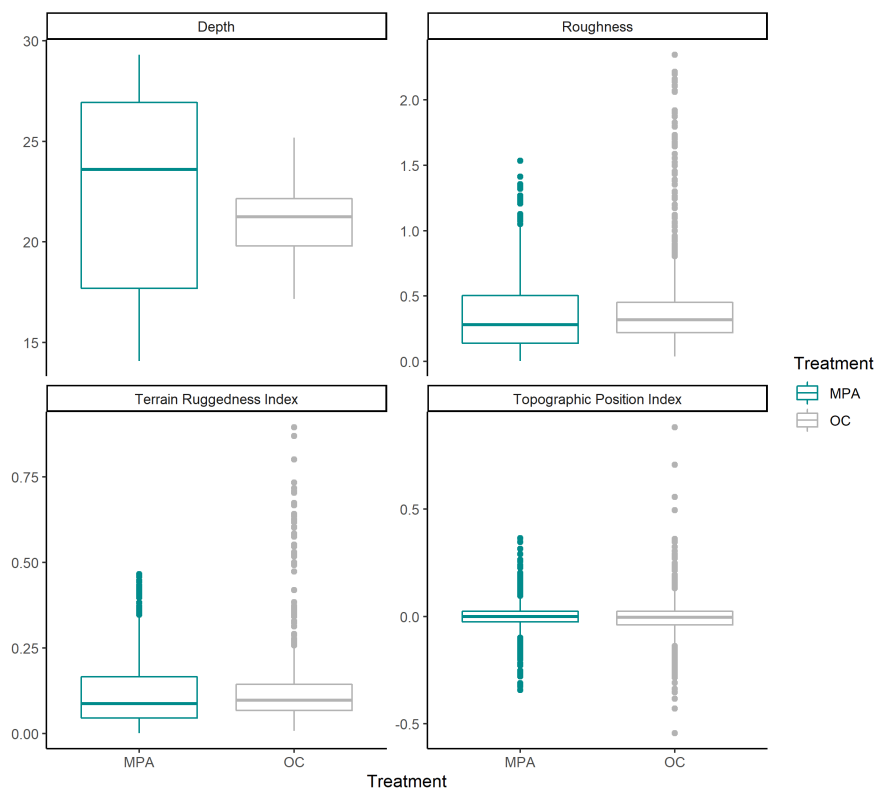


Fig. B.1: Bathymetry (Depth, Roughness, Terrain Ruggedness Index and Topographic Position Index) of 100m radius surrounding area of BRUVs camera drops inside the MPA and in the OCs.

Table B.1: Δ AIC (difference in the AIC and the minimum AIC model) values for all variations of the Count and Zero parts of the Zero Inflated Poisson models for exploited Invertebrates for Number of Taxa and Total Abundance. Bold values show the chosen models. Treatment and Year are abbreviated to Tr and Yr.

Formula	Number of Taxa	Total Abundance
	Δ AIC	Δ AIC
Value ~1 1	0.000	26.322
Value ~1 Tr	2.000	28.109
Value ~1 TrxYr	5.999	31.175
Value ~1 Tr+Yr	2.654	29.413
Value ~1 Yr	2.000	27.624
Value ~Tr 1	1.664	4.482
Value ~Tr Tr	3.665	0.000
Value ~Tr TrxYr	5.904	3.018
Value ~Tr Tr+Yr	3.904	1.505
Value ~Tr Yr	3.559	5.927
Value ~TrxYr 1	4.805	6.939
Value ~TrxYr Tr	6.809	2.367
Value ~TrxYr TrxYr	9.873	5.633
Value ~TrxYr Tr+Yr	7.873	3.861
Value ~TrxYr Yr	6.807	8.114
Value ~Tr+Yr 1	3.005	6.355
Value ~Tr+Yr Tr	5.007	1.934
Value ~Tr+Yr TrxYr	7.874	3.897
Value ~Tr+Yr Tr+Yr	5.875	2.985
Value ~Tr+Yr Yr	5.005	7.170

Value ~Yr 1	1.355	28.172
Value ~Yr Tr	3.355	29.952
Value ~Yr TrxYr	6.572	32.059
Value ~Yr Tr+Yr	4.599	30.366
Value ~Yr Yr	3.357	28.591

“All models are wrong, but some are useful.”

George E. P. Box

C

Appendix C

Table C.1: Δ AIC (difference in the AIC and the minimum AIC model) values for all variations of the GLMM models for the Diversity metrics (Number of Taxa, Functional Richness, Functional Divergence, Functional Evenness and Functional Redundancy). Bold values show the chosen models. Treatment, Year and Site are abbreviated to Tr, Yr and Si.

	Number of Taxa	Functional Richness	Functional Divergence	Functional Evenness	Functional Redundancy
Formula	AIC	AIC	AIC	AIC	AIC
Value ~TrxYr+ (1 Si)	0.000	0.000	1.666	3.878	0.000
Value ~Tr+Yr+ (1 Si)	2.792	7.548	0.000	3.688	17.190
Value ~Tr+ (1 Si)	0.792	8.540	3.948	1.940	35.068
Value ~Yr+ (1 Si)	11.912	16.620	10.246	1.748	38.048
Value ~1+ (1 Si)	9.912	17.788	14.344	0.000	55.926

Table C.2: Δ AIC (difference in the AIC and the minimum AIC model) values for all variations of the Beta models for Cumulative Weight Means for the trait modalities Longevity, Crawler, Sessile and Swimmer Motility and Scavenger and Filter feeders. Bold values show the chosen models.

	Longevity	Crawler	Sessile	Swimmer	Scavenger	Filter
Formula	Δ AIC	Δ AIC	Δ AIC	Δ AIC	Δ AIC	Δ AIC
Value ~TrxYr+ (1 Si)	4.031	0.000	0.000	0.000	0.000	0.000
Value ~Tr+Yr+ (1 Si)	2.055	5.484	12.896	5.056	0.206	12.316
Value ~Tr+ (1 Si)	1.819	17.408	21.978	4.540	8.024	12.444
Value ~Yr+ (1 Si)	0.235	23.790	24.394	6.346	11.650	19.780
Value ~1+ (1 Si)	0.000	36.774	33.251	5.506	19.388	19.934

"We forget that nature doesn't need us, we need nature."

Asha de Vos

D

Appendix D

Table D.1: Survey Effort in Videos taken by the Towed Flying Array and Baited Remote Underwater Video systems (BRUVs) from OC and SAC Sites Before and After SAC designation. Bold values show surveys utilised for the BACI Assessment.

Yr	Towed Flying Array		BRUVs	
	OC	SAC	OC	SAC
<u>Before</u>				
2008	9	9	0	0
2009	9	9	0	18
2010	9	9	0	12
2011	14	12	18	18
<u>After</u>				
2012	14	12	18	18
2013	14	12	18	18
2014	14	12	16	18
2015	14	12	17	17
2016	14	12	18	18
2017	14	12	18	18
2018	14	12	18	18
2019	0	0	18	18

Table D.2: Survey Effort in Videos taken by the Towed Flying Array and Baited Remote Underwater Video systems (BRUVs) from the MPA, SAC and OC at different Ages of Protection. OC 'age' is set as SAC age. Bold values show surveys utilised for the Age of Protection Assessment.

Age of Protection	Towed Flying Array			BRUVs		
	MPA	OC	SAC	MPA	OC	SAC
-3	0	9	9	0	0	0
-2	0	9	9	0	0	18
-1	0	9	9	0	0	12
0	0	14	12	0	18	18
1	25	14	12	0	18	18
2	25	14	12	34	18	18
3	25	14	12	33	16	18
4	27	14	12	36	17	17
5	26	14	12	36	18	18
6	27	14	12	35	18	18
7	27	14	12	36	18	18
8	27	0	0	36	18	18
9	27	0	0	35	0	0
10	27	0	0	35	0	0
11	27	0	0	36	0	0
12	0	0	0	35	0	0

Table D.3: Δ AIC values (difference in the AIC and the minimum AIC model) for Mixed effects models for Number of Taxa, Total Abundance, Functional Richness and Functional Redundancy derived from Towed Flying Array. Bold values indicate models used. BeforeAfter, Treatment, Year and Site are abbreviated to BA, Tr, Yr and Si.

Formula	Towed Flying Array			
	Number of Taxa	Total Abundance	Functional Richness	Functional Redundancy
	Δ AIC	Δ AIC	Δ AIC	Δ AIC
BACI Assessment				
Value ~BAxTr+(1 Yr:Si)+(1 Si)+(1 Yr)	0.000	0.000	0.737	0.000
Value ~BA+Tr+(1 Yr:Si)+(1 Si)+(1 Yr)	0.311	2.757	1.492	4.470
Value ~BA+(1 Yr:Si)+(1 Si)+(1 Yr)	4.083	4.072	0.000	7.586
Value ~Tr+(1 Yr:Si)+(1 Si)+(1 Yr)	2.245	1.543	4.129	2.472
Value ~1+(1 Yr:Si)+(1 Si)+(1 Yr)	6.047	2.832	2.609	5.586
Age of Protection Assessment				
Value ~AgexTr+(1 Yr:Si)+(1 Si)+(1 Yr)	0.000	0.000	6.544	0.000
Value ~Age+Tr+(1 Yr:Si)+(1 Si)+(1 Yr)	5.055	5.708	3.054	29.476
Value ~Age+(1 Yr:Si)+(1 Si)+(1 Yr)	15.393	9.368	0.694	43.918
Value ~Tr+(1 Yr:Si)+(1 Si)+(1 Yr)	5.071	3.924	2.409	28.142

Value $\sim 1+(1 Yr:Si)+(1 Si)+(1 Yr)$	21.999	9.088	0.000	41.978
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Table D.4: Δ AIC values (difference in the AIC and the minimum AIC model) for Mixed effects models for Number of Taxa, Total Abundance, Functional Richness and Functional Redundancy derived from Baited Remote Underwater Video systems (BRUVs). Bold values indicate models used.

Formula	Baited Remote Underwater Video System			
	Number of Taxa	Total Abundance	Functional Richness	Functional Redundancy
	Δ AIC	Δ AIC	Δ AIC	Δ AIC
BACI Assessment				
Value ~BAxTr+(1 Yr:Si)+(1 Si)+(1 Yr)	4.082	3.613	5.189	3.906
Value ~BA+Tr+(1 Yr:Si)+(1 Si)+(1 Yr)	2.739	2.297	3.659	1.962
Value ~BA+(1 Yr:Si)+(1 Si)+(1 Yr)	1.175	1.885	1.917	0.000
Value ~Tr+(1 Yr:Si)+(1 Si)+(1 Yr)	1.732	0.442	1.774	3.150
Value ~1+(1 Yr:Si)+(1 Si)+(1 Yr)	0.000	0.000	0.000	1.156
Age of Protection Assessment				
Value ~AgexTr+(1 Yr:Si)+(1 Si)+(1 Yr)	6.143	2.281	6.230	2.242
Value ~Age+Tr+(1 Yr:Si)+(1 Si)+(1 Yr)	4.114	0.792	2.348	0.000
Value ~Age+(1 Yr:Si)+(1 Si)+(1 Yr)	0.257	4.631	1.685	3.320
Value ~Tr+(1 Yr:Si)+(1 Si)+(1 Yr)	2.788	0.000	0.539	1.868

Value $\sim 1 + (1 Yr:Si) + (1 Si) + (1 Yr)$	0.000	2.694	0.000	5.770
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“You have to first think about what you are going to do, then you have to describe what you want, precisely, and the computer will then hopefully go away and do it.”

Hadley Wickham



Appendix **E**: Ffinian Frame Extractor

v1.0

E.1 Background

An automated user interface (UI) for an image frame extractor was created to aid with towed video assessment. The task was to update and improve the software currently used in the team to take still images from the towed video transects and overlay a 0.25m^2 quadrat over the image. The previous software required continuous involvement of staff time, as only one folder of videos could be assessed at a time. Furthermore, the software was only available on specific desktop computers within the university. Due to the COVID-19 pandemic access to these specific computers was either unfeasible or undesirable, so the current work was produced to fit necessity. It also gave the opportunity to streamline a workflow that could save staff time.

The requirements for the UI were to be: user friendly for those with little to no coding experience; allow flexibility in the rate of image extraction, the input folder location within a directory, the video format type and image output type; utilise free, open source software; editable by other users, and easily transferable (small file sizes). These requirements drove the creation of a 'shinyApp' created within the r programming language.

E.2 Methods

E.2.1 User Interface (UI)

The UI utilises the r packages 'shiny', 'ggplot2', 'shinythemes', 'magick', 'shinyjs' and 'shinyFiles'. These create the actual user interface itself, its appearance, control widgets (buttons and any actionable items used by the user) and any images used for aesthetics. As the frame extractor would be accessing files, editing them and creating new ones within the users desktop, having the app

online would have introduced a high risk of cyber attack and decreases in cyber security. Therefore, the frame extractor was created and designed to be an app, saved and executed from the users computer.

E.2.2 Frame Extractor

The frame extractor itself utilises for loops with base r and 'dplyr', 'stringr', 'av' and 'magick' packages. These allow the creation of strings, which then locates the desired files, imports them, assesses the aspect ratio of the input, overlays a corresponding aspect ratio of quadrats and then saves the new image in a specific folder. Within the UI the user will select the folder location of the input, the rate of image extraction, the video file format of the input and image file format of the output. The app will then use these selections to apply the desired process.

E.2.3 Accessories

The app utilises a group of image files, which need to be in a folder named 'www' within the same directory as the app (called 'app.R'). These image files are the overlays to be combined with the frame grabs and images used within the UI to show the user when they haven't started the app, when the app is processing and when it is complete. The overlays currently cover the aspect ratios 1280x720, 1920x1080, 854x480, 1450x816, 1450x816, 1280x960 and 1920x1440.

E.2.4 Assumptions

The assumptions of the frame extractor are that the video itself is taken at or near a 45° angle to the seabed and that the image is not distorted near the edges (as with wide FOV gopro mode) for the overlay to be appropriate. Further, it assumes a specific file format and file naming system (used by the

Lyme Bay monitoring project). This assumes that the top level folder is one step above each ‘transect’ folders; within all transect folder there are 3 folder levels before the video folder. These videos are split into 5 minute maximum lengths. The naming style of each transect folder follows a numeric pattern of day, month, year, _ then the number of transect for that day, meaning the tenth transect of 15th of July 2018 would have a transect folder called ‘150718_10’.

E.2.5 Current Status

The frame extractor has utilised packages within R, Java and C++ to convert the R shiny app into a user desktop application. (FfinianFrameExtractor.exe)

E.2.6 Software Versions

Software versions used for this software were:

R version 4.0.3 (2020-10-10)

Platform: x86_64-w64-mingw32/x64 (64-bit)

Running under: Windows 10 x64 (build 18363)

Table E.1: Attached packages

grid	stats	graphics	grDevices	utils
datasets	methods	base	shinyFiles: 0.9.0	shinyjs: 2.0.0
jpeg: 0.1-8.1	av: 0.5.1	imager: 0.42.3	magrittr: 2.0.1	stringr: 1.4.0
magick: 2.6.0	shinythemes: 1.2.0	dplyr: 1.0.4	ggplot2: 3.3.3	shiny: 1.6.0

Table E.2: Packages loaded via a namespace (and not attached):

Rcpp: 1.0.4.6	pillar: 1.4.7	compiler: 4.0.3	later: 1.1.0.1	tools: 4.0.3
digest: 0.6.25	jsonlite: 1.7.2	lifecycle: 1.0.0	tibble: 3.0.1	gttable: 0.3.0
png: 0.1-7	pkgconfig: 2.0.3	rlang: 0.4.10	igraph: 1.2.6	DBI: 1.1.1
yaml: 2.2.1	bmp: 0.3	readbitmap: 0.1.5	fastmap: 1.1.0	withr: 2.4.1

fs: 1.5.0	generics: 0.1.0	vctrs: 0.3.6	tidyselect: 1.1.0	glue: 1.4.1
R6: 2.5.0	purrr: 0.3.4	scales: 1.1.1	promises: 1.2.0.1	ellipsis: 0.3.1
htmltools: 0.5.1.1	assertthat: 0.2.1	mime: 0.10	colorspace: 1.4-1	xtable: 1.8-4
tiff: 0.1-6	httpuv: 1.5.5	stringi: 1.4.6	munsell: 0.5.0	crayon: 1.4.1

E.3 Ffinian Frame Extractor v1.0

```
list.of.packages <- c("shiny",  
                      "ggplot2",  
                      "dplyr",  
                      "shinythemes",  
                      "magick",  
                      "stringr",  
                      "imager",  
                      "grid",  
                      "av",  
                      "jpeg",  
                      "shinyjs",  
                      "shinyFiles")  
  
new.packages <- list.of.packages[!(list.of.packages %in%  
                                  installed.packages()[,"Package"])]  
  
if (length(new.packages)) install.packages(new.packages)  
  
library(shiny)  
library(ggplot2)  
library(dplyr)
```

```
library(shinythemes)
library(magick)
library(stringr)
library(imager)
library(grid)
library(av)
library(jpeg)
library(shinyjs)
library(shinyFiles)
```

```
options(shiny.maxRequestSize = 10 * 1024^5)
```

```
image_ggplot_alt <- function (image, interpolate = FALSE) {
  info <- image_info(image)
  ggplot2::ggplot(data.frame(x = 0, y = 0),
    ggplot2::aes_string("x", "y")) +
  ggplot2::geom_blank() +
  ggplot2::theme_void() +
  ggplot2::scale_y_reverse() +
  ggplot2::coord_fixed(expand = FALSE,
    xlim = c(0, info$width),
    ylim = c(0, -info$height)) +
  ggplot2::annotation_raster(image, 0,
    info$width,
    info$height,
```

```

                                0,
                                interpolate = interpolate) +
  NULL
}

```

```
Overlay1280x720<-image_read("www/OverlayTowed.png")
```

```
Overlay1920x1080<-image_read("www/Overlay.png")
```

```
Overlay854x480<-image_read("www/OverlayGoPro - 480.png")
```

```
Overlay1450x816<-image_read("www/Overlay - resized.png")
```

```
Overlay1280x960<-image_read("www/Webp.net-resizeimage (1).png")
```

```
Overlay1920x1440<-image_read("www/Webp.net-resizeimage (1920_1440).png")
```

```
Start<-image_read('www/Start.jpg')
```

```
Half<-image_read('www/Half.jpg')
```

```
Complete<-image_read('www/Complete.jpg')
```

```
plot1<-image_ggplot_alt(Start)
```

```
plot2<-image_ggplot_alt ( Half )  
plot3<-image_ggplot_alt ( Complete )
```

```
Frames<-NULL
```

```
tmp<-NULL
```

```
VideoPaths<-NULL
```

```
VideoNames<-NULL
```

```
VideoLocations<-NULL
```

```
FrameOutput<-NULL
```

```
Counter<-0
```

```
Info<-0
```

```
VideoLength<-999
```

```
ui <- fluidPage ( theme = shinytheme ( "superhero" ) ,  
  titlePanel ( "Frame Extraction for Towed Video" ,  
    windowTitle = "Extraction" ) ,  
  sidebarLayout ( sidebarPanel (
```

```

fluidRow(
  column(12,
    wellPanel(shinyDirButton("dir",
      "Chose a directory", "Upload"))),
    verbatimTextOutput('rawInputValue'),
  fluidRow(
    column(6,radioButtons("fps",
      label = "Frame Rate Selection:",
      choices = c("1 Per Second",
        "1 Per 2 Seconds",
        "1 Per 5 Seconds",
        "1 Per 10 Seconds",
        "1 Per 15 Seconds",
        "1 Per 30 Seconds"),
      selected="1 Per 10 Seconds")),
    column(6,radioButtons("videoin",
      label = "Video Input Format:",
      choices = c(".avi",
        ".mp4",
        ".mov")),
    radioButtons("imageOut",
      label = "Frame Output format:",
      choices = c("png",
        "jpg")))),
    actionButton("run","Run")
  ),

```

```

mainPanel(column(2, textOutput("selected_var1")),
          column(10, plotOutput("plot1")),
          column(2, textOutput("selected_var2")),
          column(10, plotOutput("plot2")),
          column(2, textOutput("selected_var3")),
          column(10, plotOutput("plot3")),
          useShinyjs()
)
)
)

server <- function(input, output, session) {

  volumes = getVolumes()

  shinyDirChoose(input, "dir",
                 roots = volumes(),
                 session = session)

  output$plot1 <- renderPlot({
    print(plot1)
  })
}

```

```
output$plot1 <- renderPlot({  
  print(plot1)  
})
```

```
output$selected_var1 <- renderText({  
  paste0("Waiting ...")  
})  
hide("plot2")  
hide("selected_var2")
```

```
output$plot2 <- renderPlot({  
  print(plot2)  
})
```

```
output$selected_var2 <- renderText({  
  paste0("Processing ...")  
})
```

```
hide("plot3")  
hide("selected_var3")
```

```
output$plot3 <- renderPlot({  
  print(plot3)
```



```
})
```

```
output$selected_var3 <- renderText({  
  paste0("Completed!!!!")  
})
```

```
observe({
```

```
observeEvent(input$run, {
```

```
  hide("plot1")  
  hide("selected_var1")  
  show("plot2")  
  show("selected_var2")
```

```
  if (length(input$dir) != 1 ) {  
    dir.path <- parseDirPath(volumes,  
                             input$dir)  
    output$rawInputValue<-renderText({ dir.path})  
  }
```

```
FolderNames<-list.files(paste0(dir.path),
                        recursive=FALSE,
                        full.names = TRUE,
                        pattern= "[_]")
```

```
if (input$fps=="1 Per Second")      fps<-1
if (input$fps=="1 Per 2 Seconds")    fps<-1/2
if (input$fps=="1 Per 5 Seconds")    fps<-1/5
if (input$fps=="1 Per 10 Seconds")   fps<-1/10
if (input$fps=="1 Per 15 Seconds")   fps<-1/15
if (input$fps=="1 Per 30 Seconds")   fps<-1/30
```

```
if (input$videoin==".avi")          Movform<-"avi"
if (input$videoin==".mp4")          Movform<-"mp4"
if (input$videoin==".mov")          Movform<-"mov"
```

```
if (input$imageOut=="png")          Frameform<-"png"
if (input$imageOut=="jpg")          Frameform<-"jpg"
```

```
NumberVideos<-list.files(FolderNames,
                        recursive=TRUE,
                        full.names = TRUE,
                        pattern= paste0("*.",
```

```

Movform))

TotalFramesperVideo<-5*60*fps

NFrames<-length (NumberVideos)*TotalFramesperVideo

  withProgress (message = 'Extracting Frames:',
                value = Counter, {

    incProgress (1/NFrames,
                detail = paste0 (signif ((( Counter/NFrames)*100),2)
                "% Complete" ))

for(k in 1:length (FolderNames)){

  Counter<-Counter+1

  VideoLocations<-unique (sub (" / [^ / ]+$" , "" ,
    list . files (FolderNames [[ k]] ,
    recursive=TRUE,
    full.names = TRUE)))

  VideoLocations<-VideoLocations [ !grepl (" /ALLFrames" ,VideoLocations

for (t in 1:length (VideoLocations)){

```

```
VideoLocationswithSlash<-paste0(VideoLocations[[t]],"/")
```

```
VideoNames<-str_remove(  
  list.files(VideoLocationswithSlash,  
    recursive=TRUE,  
    pattern = paste0("*.","Movform"),  
    full.names = TRUE),  
pattern=VideoLocationswithSlash)
```

```
if (length(VideoNames>0)) {  
  VideoNames<-str_remove(VideoNames,  
    pattern=paste0(".",Movform))}
```

```
if (length(VideoNames>0)) {  
  VideoPaths<-list.files(VideoLocations[[t]],  
    pattern = paste0("*.","Movform"),  
    recursive=TRUE, full.names = TRUE)}
```

```
for (i in 1:length(VideoPaths)){
```

```
if (length(VideoNames>0) &  
  i%in%c(1,length(VideoPaths))) {  
  VideoLength<-length(image_read_video(VideoPaths[[i]],
```

```

        format='jpg'))}

if (length(VideoNames>0) & (1/VideoLength<fps)) {
  Frames<-image_read_video(VideoPaths[[i]],
    fps = fps ,format=Frameform)}

if (length(Frames)>0) {for (j in 1:length(Frames)){

  Info<-image_info(Frames[j])

  if (length(VideoNames>0) &
    Info$width==1280 &
    Info$height==720) {
    tmp<-image_mosaic(c(Frames[j], Overlay1280x720))
  }

  if (length(VideoNames>0) &
    Info$width==1920 &
    Info$height==1080) {
    tmp<-image_mosaic(c(Frames[j], Overlay1920x1080))
  }

  if (length(VideoNames>0) &
    Info$width==854 &
    Info$height==480) {
    tmp<-image_mosaic(c(Frames[j], Overlay854x480))
  }
}
}

```

```

}

if (length (VideoNames>0) &
    Info$width==1450 &
    Info$height==816) {
  tmp<-image_mosaic(c(Frames[j], Overlay1450x816))
}

if (length (VideoNames>0) &
    Info$width==1920 &
    Info$height==1440) {
  tmp<-image_mosaic(c(Frames[j], Overlay1920x1440))
}

if (length (VideoNames>0) &
    Info$width==1920 &
    Info$height==1440) {
  tmp<-image_mosaic(c(Frames[j], Overlay1920x1440))
}

if (length (VideoNames>0) &
    !Info$width%in%c(1280,1920,854,1450) &
    Info$height%in%c(720,1080,480,960,816,1440)) {
  tmp<-image_annotate(Frames[j], "Error: Unknown Aspect Ratio",
    size = 30, color = "red", boxcolor = "black",
    degrees = 45, location = "+50+100")
}

```

```

if (length (VideoNames>0)) {
  if (!dir . exists (paste0 (FolderNames [[ k]] , "/ALLFrames" ))) {
    dir . create (paste0 (FolderNames [[ k]] , "/ALLFrames" ))}}

if (length (VideoNames>0)) {

  if (!dir . exists (paste0 (FolderNames [[ k]] ,
                             "/ALLFrames/ " ,
                             VideoNames [[ i]] ,
                             "_" ,j , ".png" ))) {

    image_write (tmp , paste0 (FolderNames [[ k]] ,
                               "/ALLFrames/ " ,
                               VideoNames [[ i]] ,
                               "_" ,j , ".png" ))

    Counter<-Counter+1
  }}
  tmp<-NULL
  Info<-NULL
  incProgress (1 /NFrames ,
  detail = paste0 (signif ((( Counter /NFrames) * 100) ,2) ,
                   "% Complete" ))

}}
VideoLength<-999

```

```

Frames<-NULL

}
FrameOutput<-NULL
VideoNames<-NULL

VideoPaths<-NULL

}

VideoLocations<-NULL

}
hide("plot2")
hide("selected_var2")
show("plot3")
show("selected_var3")

})
})

})

```



```
}
```

```
shinyApp(ui , server)
```