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Removal of bottom-towed fishing from whole-site Marine Protected Areas promotes mobile species biodiversity



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ABSTRACT

Marine habitats are being altered by anthropogenic pressures, influencing the diversity and distribution of species. Marine Protected Areas (MPAs) are increasingly used as spatial management tools to mitigate these human impacts on marine systems, but levels of protection vary. MPAs that exclude bottom-towed fishing activities from all habitats within their boundaries while still allowing static gear fishing, taking a "whole-site approach", have shown benefits in terms of increasing biodiversity and biomass on reef habitat. In this study we use Baited Remote Underwater Videos (BRUVs) to quantify differences in mobile species assemblage composition, diversity and abundance on mixed sediment habitats inside and outside three MPAs adopting this whole-site approach within Jersey's territorial waters. Greater numbers of taxa were recorded within all three MPAs compared to nearby unprotected areas, with an average of 4.9 \pm 1.8 taxa observed per deployment inside the MPAs compared to 3.9 \pm 1.7 taxa outside the MPAs. No significant difference was observed in the overall abundance. The proportion of presence of two indicator species (Labridae Spp. and juvenile bream Spondyliosoma cantharus) was greater within the MPAs than the nearby unprotected areas. IUCN threatened and vulnerable shark species were observed on more BRUVs inside the MPAs, while IUCN threatened and vulnerable ray species were present on fewer BRUVs in the MPAs, but both occurred in too few numbers to statistically assess. Not all species responded positively to the MPAs, with scavenging species such as spider crab (Maja brachydactyla) recorded in lower numbers in two out of the three MPAs compared to the nearby unprotected areas. BRUV surveys that have been used to survey MPAs that exclude bottom-towed fishing in Europe are sparse and have primarily focussed on reef habitat. This study provides the first account of how this whole-site approach for mixed sediment habitats in three MPAs affects mobile species. These results evidence the merit of an ecosystembased approach to MPA management for species of both conservation and commercial importance.

1. Introduction

The oceans face a number of threats in an increasingly populated world, with greater anthropogenic pressure being put on ecosystems through fishing, climate change, pollution and habitat loss (Pauly et al., 1998; Hughes et al., 2003; Pauly et al., 2005; Worm et al., 2006; Halpern et al., 2008, 2020; Sumaila et al., 2016). Fisheries are an economically valuable resource as well as an important food source across the globe (FAO, 2020). Underpinning fisheries, are multiple and interlinked food webs, cross cutting with the processes and functions of the ecosystem. (Dobson et al., 2006; Staples and Funge-Smith 2009). Despite this

dependency, the activity of fishing itself poses one of the largest threats to the sustainability of this food resource (Pauly et al., 2005), through direct physical impacts to marine habitats (Hall-Spencer and Moore, 2000; Thrush and Dayton, 2002). The fragmentation and loss of habitats is contributing to biodiversity loss in the oceans (Dobson et al., 2006; Haddad et al., 2015). Some of the most damaging fishing methods include bottom-towed fishing gears such as dredges and trawls that drag along the seabed. They reduce habitat complexity through habitat fragmentation and homogenisation (Veale et al., 2000; Thrush and Dayton, 2002) and physically damage mobile species such as crustaceans (Kaiser and Spencer, 1995; Beukers-Stewart et al., 2001), leading

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to decreases in densities of species that are commercially valuable (Veale et al., 2000). Despite both national and international management measures in place to protect benthic ecosystems to support fisheries, there are still global declines in habitat condition (Dobson et al., 2006; Klein et al., 2013), biodiversity (Worm et al., 2006; Sala et al., 2021) and fish stocks (Claudet et al., 2020; Halpern et al., 2008).

Marine Protected Areas (MPAs) are a common management tool employed to conserve habitats and species of conservation importance, but the level of protection afforded to an MPA varies greatly (Day et al., 2012). Approximately 8.1% of the world's oceans are currently within MPAs, but only 2.4% are highly protected (Marine Conservation Institute, 2022). Research suggests that highly protected MPAs that exclude the most destructive human activities are the most beneficial for biodiversity (Lester and Halpern, 2008; Edgar et al., 2014; Sala and Giakoumi, 2018), but it may not always be possible to achieve this level of protection due to societal constraints (Halpern et al., 2008). It has been argued that increasing the size and number of MPAs needs to align with an agenda for sustainable lives and livelihoods (Rees et al., 2020). In this framing, only fishing methods deemed to negatively impact the conservation goals of the MPA are prohibited. In the UK, many MPAs have been designated with the intention to conserve a single species or marine feature, but this management approach has been shown to be less effective in the recovery of marine biodiversity than an ecosystem-based approach (Solandt et al., 2014; Davies et al., 2022). The feature based approach leaves mixed sedimentary habitats that are not considered part of the reef feature unprotected and still open to destructive fishing practices within the MPA (Rees et al., 2020; Solandt et al., 2020). Currently in UK waters, MPAs cover 294,807 km², of which 124,443 km² comprises sedimentary habitats (mixed sediments (51,849 km²), mud (16,197 km²), sand (56,375 km²) and seagrass (22 km²)) that are not protected from bottom towed fishing (MPA Reality Check, 2022), but these habitats have the potential to contribute to the recovery of MPA biodiversity for species of both conservation and commercial interest. There is increasing pressure on governments to protect existing MPAs in the UK from bottom-towed fishing and there is a need for further evidence to effect this change (MMO, 2022).

MPAs that adopt the "whole-site approach" are those in which the protection afforded is consistent across the full suite of habitats within its boundary (HM Government, 2018; Department for Environment Food and Rural Affairs, 2019; Rees et al., 2020; Solandt et al., 2020). For example, Lyme Bay MPA, southwest UK, where the "whole-site approach" was first described, excluded bottom-towed fishing while allowing static gear fishing to continue (Sheehan et al., 2013). The "whole-site approach" can also be used to describe No Take Zones in which all forms of extraction are prohibited from within the MPA boundary. However, in this paper the "whole-site approach" refers to the former and are hereafter referred to as whole-site MPAs. The exclusion of bottom-towed fishing gears from all features within an MPA, protects seabed integrity and ecosystem function (Davies et al., 2022), which can support greater fish biomass including commercial species (Willis et al., 2003; Beukers-Stewart et al., 2005; Brown et al., 2010a). This will benefit some species more than others depending on their life histories (Tillin et al., 2006; Kaplan et al., 2009), and will improve the connectivity of life stages for species that use multiple habitats in their life cycle.

Juveniles, including those of commercial species, use several habitats but tend to show selectivity (Elliott et al., 2017), and loss of particular habitats through bottom-towed fishing will reduce the survivability of such habitat specialists (Clavel et al., 2011; Berger, 2021). Further, habitats such as seagrass have greater abundances of juvenile fish than surrounding sand and mud habitats (Jackson et al., 2002; Lilley and Unsworth, 2014). Other complex habitats with relatively high epifaunal diversity or structural complexity, such as maerl, have been shown to support higher abundances of commercially targeted organisms, such as commercially exploited scallop species (Kamenos et al., 2004; Howarth et al., 2011). Further, post-settlement survival of some benthic species, such as crustaceans and bivalves, are thought to be higher in more complex habitats (Palma et al., 1998; Stevens and Kittaka, 1998; Robinson and Tully, 2000; Howarth et al., 2011; Tonk and Rozemeijer, 2019). Therefore, the exclusion of bottom-towed fishing may improve larval recruitment of certain species as benthic habitats recover, allowing the growth of more complex habitat structures (Wahle and Steneck, 1991; Howarth et al., 2011).

Monitoring changes in biological communities following the designation of protection measures can provide important information on the effectiveness of MPAs (Pomeroy et al., 2005) and their ability to protect certain species (White et al., 2013). Change is likely to be most observable in benthic and demersal species as they rely on benthic habitats for a combination of life stages (Kritzer et al., 2016). The abundance and diversity of sessile, sedentary and mobile species continue to recover inside the Lyme Bay whole-site MPA, relative to open control areas and areas that adopted the feature-based approach (Davies et al., 2021, 2022; Sheehan et al., 2021). However the first most notable sign of recovery was sessile reef-associated species growing in areas of sediment veneers, where they were not expected to occur (Sheehan et al., 2013). The long-term effects of fishing on sediments had removed these species from inter-reef sediment habitats giving a false impression of where these species naturally occur. This is known as shifting baselines, where human impact has modified our perception of the natural environment (Collie et al., 2000; Jackson et al., 2011; Braeckman et al., 2014). The occurrence of reef-associated species on sediment veneers also demonstrated that the whole-site approach has the potential to expand current reef features when managed appropriately (Sheehan et al., 2013; Rees et al., 2020). By protecting whole areas of seafloor habitats from bottom-towed fishing, habitat stability and structural complexity can improve biodiversity, primary productivity and overall ecosystem functioning (Worm and Duffy, 2003). Recovery of sessile reef-associated species that create habitat structural complexity then supports higher trophic level, mobile species (Hunt and McKinnell, 2006; Davies et al., 2021).

There are a variety of scientific sampling methods to monitor the recovery of demersal, mobile species within MPAs including: Underwater Visual Census (UVC) (Edgar and Samson, 2004; Russ et al., 2004), extractive sampling methods, such as trawls (Jackson et al., 2002; Day et al., 2020), and both baited and un-baited remote video surveys (Cappo et al., 2006; Langlois et al., 2012; Sheaves et al., 2016; Bradley et al., 2017). Baited Remote Underwater Videos (BRUVs) provide a non-extractive way of assessing the mobile fauna associated with a habitat or location over short time periods. While BRUVs cannot be used to measure absolute abundance, they can provide a way of understanding relative differences in mobile species assemblages (Cappo, Speare and De'ath, 2004). While the use of bait may bias results towards predators and scavengers, BRUVs have been compared to non-baited set ups and the use of bait increased attraction of all species and made for a clearer distinction between fish assemblages (Watson et al., 2005).

BRUVs have primarily been used on hard reef habitat in MPAs, especially in tropical systems where biotic reef has been the focus (Goetze et al., 2021). In northern Europe this has generally been the case (Davies et al., 2021) and those that have considered non-reef habitat have done so in relation to fully protected marine reserves (Howarth et al., 2015) or not in relation to MPAs (Unsworth et al., 2014; Elliott et al., 2017; Rhodes et al., 2020). Here we use BRUVs to assess the effectiveness of three whole-site MPAs to support more diverse mobile assemblages by surveying across a range of sedimentary habitats inside each MPA and outside in nearby fished controls. This research aims to assess the following hypotheses:

- Mobile species diversity, overall abundance and the abundance of preselected indicator species is greater in MPAs compared to Open Controls.
- 2) Assemblage composition differs between MPAs and Open Controls.

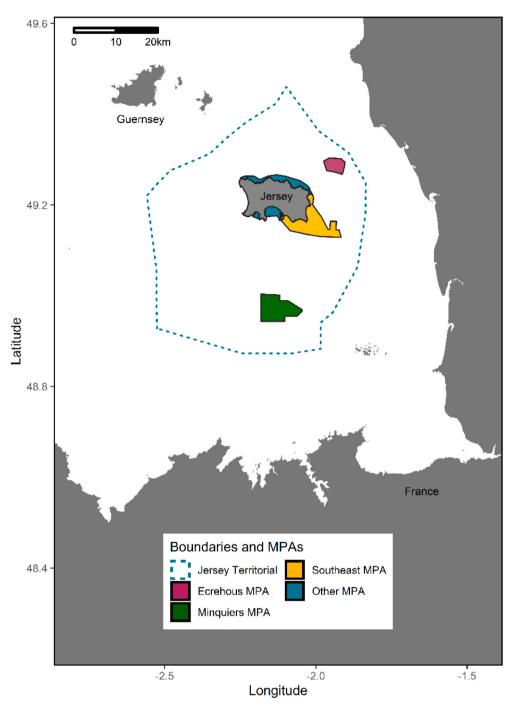


Fig. 1. Location of Jersey in the Normano-Breton Gulf and the location of MPAs within Jersey's territorial waters.

2. Methods

2.1. Case study

Jersey is a self-governing dependency of the United Kingdom situated in the Normano-Breton Gulf off the north coast of Brittany, with a marine territorial area of approximately 2,500 km². Jersey's marine environment is primarily shallow water coastal seascape consisting of rocky reef, boulders, cobbles, gravel, sand and biogenic habitats such as maerl and seagrass (Marine Resources, 2019). The large tidal range (up to 12.2 m) experienced in Jersey also creates a vast intertidal area, contributing to a diverse habitat composition supporting a wide array of species. Maerl and seagrass are habitats of international importance, both of which are IUCN red list species and OSPAR (Convention for the Protection of the Marine Environment of the North East Atlantic) threatened habitats (OSPAR, 2002). As a signatory to OSPAR, The Bern Convention (Convention on the Conservation of European Wildlife and Natural Habitats), Convention on Biological Diversity, Ramsar (Convention on Wetlands of International Importance), and ASCOBANS (Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas), Jersey is committed to protecting its marine habitats (Government of Jersey, 2013).

The majority of Jersey's territorial waters (78%) are subject to shared fishing access with French commercial vessels, and there are several habitats of international importance that are located within these shared fishing grounds. As a result of this shared access, the politics and laws surrounding the conservation of these habitats is complex, making them a challenge to manage effectively (Fleury, 2011; Fleury

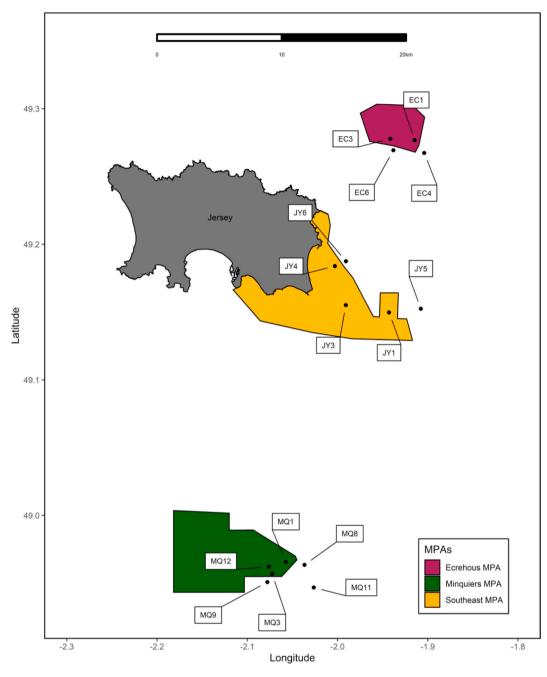


Fig. 2. Survey sites in relation to Jersey and the three MPAs (the Ecrehous, the Minquiers and the Southeast).

and Johnson, 2015; Chambers et al., 2020). While the primary fishing method by Jersey vessels is potting for crab and lobster, vessels from both Jersey and France employ bottom-towed fishing methods in the form of dredges and trawls (Marine Resources, 2019). Spatial fishing effort information is unavailable for the majority of the French and Jersey fleet as the under 12 m vessels are not monitored and the over 12 m vessels' VMS (Vessel Monitoring Systems) data are not publicly available. Conflict over management between nations can result in measures that are politically driven rather than evidence based, which could lead to unsustainable fisheries. To protect areas of fragile habitat and high biodiversity associated with two offshore reefs in Jersey's territorial waters, two Marine Protected Areas (MPAs) which excluded mobile fishing gear, including bottom towed, were designated in 2017 (Chambers et al., 2020) (Fig. 1).

These two MPAs, along with several other previously established inshore MPAs, resulted in 6.5% of Jersey's territorial waters protected

from mobile fishing gear. These MPAs are considered to follow the whole-site approach to marine management as all habitats within their boundary are afforded the same level of protection from bottom-towed fishing (Solandt et al., 2020), while allowing lower impact fisheries such as potting and angling to continue. In addition to the MPAs at the Minquiers and the Ecrehous, Jersey also has several inshore whole-site MPAs, which have been established over a longer period than the two recent offshore MPAs. Of these, the Southeast (SE) Corner MPA (Fig. 1) has been included as a comparison site for the two recent MPAs. The SE Corner was first established in 2010, with an extension to the east in 2014. The Minquiers, Ecrehous and Southeast are all shallow reefs with subtidal habitats ranging from 0 to 15 m below chart datum within the MPA boundaries. All are exposed to strong tidal currents, caused by the large tidal range experienced around Jersey.

The habitats assessed were the mixed sedimentary habitats between the rocky reefs that would typically continue to be fished in a feature-



Fig. 3. a) Profile of a BRUV and b) view of bait pole and attached bait cage within the field of view of the camera, with two cuttlefish (*Sepia officinalis*) observed on a sandy substrate.

based approach. Indicator taxa were selected based on their association with complex habitats and their likelihood of being sampled using BRUVs. High trophic level species, such as sharks, are indicators of ecosystem health (Yagnesh et al., 2020) and BRUVs provide useful information for helping design conservation strategies for rare or threatened elasmobranchs (White et al., 2013). Therefore, shark and ray species listed as threatened by the IUCN were investigated, as the ability of MPAs to support these species is not well known in temperate waters.

2.2. Survey design

Three MPAs, two designated in 2017 (Ecrehous and Minquiers) and one in 2010 that was later extended to the east in 2014 (Southeast), were selected as survey locations. Comparable sites, consisting of similar mixed sediments and depth ranges between 5 and 15 m (Below Chart Datum), were selected both inside the MPAs and outside in Open Controls. BRUVs were deployed in July and August in 2019 and 2020. Eight sites were inside the MPAs: two at the Ecrehous, three at the Southeast and three at the Minquiers. Seven sites were Open Controls within 0.4–2.5 km from the MPA boundaries, with two at the Ecrehous, two at the Southeast and three at the Minquiers (Fig. 2). Between two and six BRUV replicates were deployed at each site each year.

2.3. Site selection

To select sites, spatial analyses using a combination of benthic substrate, depth, historical fishing information, and the boundaries of the MPAs were used. The habitat structure differs between the locations: with seagrass found in the Southeast and Minquiers MPAs but not the Ecrehous; and maerl found at the Southeast MPA and Ecrehous MPA but not the Minquiers. Coarse sediment without maerl or seagrass was also surveyed at all locations. Benthic substrate was determined from towed videos that were conducted in 2018 so that only mixed sediments, such as those that are targeted by bottom-towed fishing, were sampled. Towed video data was obtained from a PhD study (Blampied, 2022), where a towed video array, adapted from Stevens (2003) and Sheehan et al. (2010), was used to survey 100 m video transects of the seabed and record the dominant substrate type in the areas surveyed. Depth was obtained from admiralty charts. Historical fishing information was determined from Vessel Monitoring System (VMS) data between 2014 and 2018 that was supplied by the Government of Jersey Marine Resources team. VMS was only available for boats over 12 m in length and so complete spatial fishing information was unknown, but areas where bottom-towed fishing had previously occurred could be identified. The boundaries of the MPAs define areas where bottom-towed fishing gear is excluded and were used to define the boundary between impacted and unimpacted sites. All selected sites were located on mixed sediments

(gravel, sand, shell and cobbles), between 5 and 15 m below chart datum.

2.4. Data collection and equipment

BRUV units consisted of a 0.8 m (8 mm diameter) fiberglass bait pole attached at a 90-degree angle to a 0.5 m (10 mm diameter) fiberglass base pole with weights attached to one end of the base pole (2 kg) and a float attached to the other to ensure the correct orientation of the unit (Fig. 3a). A metal bait cage was attached at the end of the bait pole (Fig. 3b). A GoPro (Hero 4 or 6) was attached to the base pole underneath the bait pole, with the field of view angled at the bait cage. Each unit was attached to ~ 20 kgs of lead weight via a leading rope (~ 5 m) and a marker buoy attached to the lead weight with 20 m of leaded line. The bait cage was filled with ~100 g of Atlantic mackerel (Scomber scombrus); after each deployment, left over bait was discarded and replaced with fresh bait. Tidal currents may confound interpretation of BRUV data as the sampled area increases with increasing current velocity (Taylor et al., 2013). Strong tidal currents are experienced in the survey location of Jersey, and current speed is known to influence the number of species observed on BRUVs in Jersey's waters (Plaster, 2017). To account for the large tidal range in Jersey and the effect of current speed on bait plume size, all BRUVs were deployed on neap tides within a 2-h period around slack water. BRUVs were left to 'soak' for 40 min before being recovered and were spaced a minimum of 300 m from one another to ensure bait plumes were independent.

2.5. Video analysis

Videos were assessed for quality and were not analysed if the camera was out of focus, the seabed was not in view, or the view of the bait box was obscured. Videos were analysed for 40 min from the moment the BRUV was stationary on the seafloor. The number of individuals of each mobile species on screen were recorded every minute, to the highest taxonomic resolution possible. For every minute recorded, the greatest count of each species was taken as the MaxN (maximum number of individuals on screen), and the largest value over the 40 min period was used. MaxN was used to decrease the chance of an individual being recorded more than once, giving an estimate of relative abundance rather than absolute abundance (Cappo, Speare and De'ath, 2004). Small and cryptic benthic species, such as hermit crabs (*Pagurus* spp.), dog whelk (*Tritia reticulata*), and dragonet (*Callionymus* spp.), were not recorded as it was not possible to accurately record these species in high algal or high seagrass cover sites.

S.R. Blampied et al.

Table 1

List of the recorded taxa in all Locations and Treatments.

Actinopterygii	Elasmobranchii		
Labrus bergylta	Scyliorhinus canicula		
Symphodus melops	Scyliorhinus stellaris		
Ctenolabrus rupestris	Galeorhinus galeus		
Labridae spp.	Dasyatis pastinaca		
Dicentrarchus labrax	Raja undulata		
Mullus surmuletus	Raja brachyura		
Diplodus vulgaris	Mustelus spp.		
Trisopterus luscus			
Trisopterus minutus			
Conger conger	Gastropoda		
Trachurus trachurus	Buccinum undatum		
Sparus aurata			
Chelon spp.			
Chelidonichthys lucerna	Malacostraca		
Tripterygion delaisi	Maja brachydactyla		
Centrolabrus exoletus	Cancer pagurus		
Gobiusculus flavescens	Homarus gammarus		
Spondyliosoma cantharus	Liocarcinus spp.		
Pollachius pollachius	Necora puber		
	Inachus spp.		
Cephalopoda	Decapoda spp.		
Sepia officinalis	Ebalia spp (see Table 1).		

2.6. Data analysis

Generalised Linear Mixed Effects Models (GLMMs) were used to assess the response of taxa diversity and abundance (MaxN) in R (Wickham et al., 2019). Response variables were modelled as a function of Treatment (MPA and Open Control) and Location (Ecrehous, Southeast and Minquiers) with Year (2019 and 2020) and Site (n = 15) as random effects. Counts of species and individuals were modelled using a Poisson distribution. When counts of individuals showed overdispersion, a negative binomial distribution was used. To assess the presence/absence of low abundance indicator taxa, a binomial distribution was used and the results from this are reported as the proportion of presence. Optimal models were determined using the Akaike Information Criterion (AIC) in which an iterative process was used, where predictor variables were sequentially added and then dropped from the model, to determine variable contribution to model fit. Data manipulation and visualisation was carried out in the statistical program R (R Core Team, 2021) using the packages in the tidyverse (Wickham et al., 2019). Values stated in the text are means \pm standard error.

Permutational Multivariate Analysis of Variance (PERMANOVA) in PRIMER v7 statistical software package (Clarke and Warwick, 2001), was used to test for species assemblage composition differences between Locations and Treatments. The fixed factors were Location and Treatment, and the random factors were Site and Year. Site was nested within Location and Treatment. There were three levels within the factor Location (Ecrehous, Minquiers, Southeast) and two levels within Treatment (MPA and Open Control), and abundances were pooled at the Site (n = 15) and Year (2019 and 2020) levels for analysis. To test the species assemblage compositions between Locations and Treatments, the multivariate data (MaxN derived from BRUVs) were square root transformed and a dummy species with an abundance of 1 was added to ensure that samples that are similarly devoid of species were considered as being similar (Clarke et al., 2006; Sheehan et al., 2013). Bray-Curtis dissimilarity indices (Bray and Curtis, 1957) were used to enumerate difference in assemblage compositions between Location and Treatment. Analyses used 9999 permutations (Anderson and Ter Braak, 2003). Non-metric Multidimensional Scaling ordinations (nMDS) were used to visualise the differences in similarity of assemblage composition between locations and treatments.

2.7. Results

A total of 36 taxa were identified (Table 1) across the 101 BRUVs that were retained for analysis following the removal of low quality videos and failed BRUVs (total 153 deployed). Actinopterygii were the most represented with 19 taxa, the most common of which was black seabream (*Spondyliosoma cantharus*). Malacostraca were represented by eight taxa, most commonly spider crab (*Maja brachydactyla*), and Elasmobranchii by seven taxa, with catshark (*Scyliorhinus canicula*) the most observed species. There was only one species of Gastropoda (*Bucinum undatum*) and one species of Cephalopoda (*Sepia officinalis*) (Table. SPP).

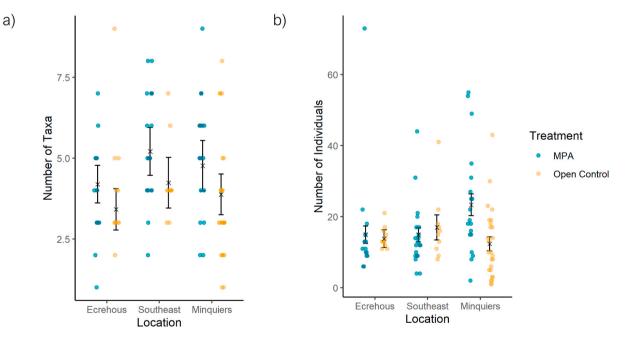


Fig. 4. Total numbers of a) taxa and b) individuals for Location and Treatment. Black crosses and error bars show fitted GLMM means and standard errors of individual abundance predicted using GLMMs with Treatment (MPA and Open Control) and Location (Ecrehous, Southeast and Minquiers) as fixed effects and Year (2019 and 2020) and Site (n = 15) as random effects.

General Linear Mixed Effects Model outputs for BRUV taxa and abundance as a function of Location and Treatment with Year and Site as random effects. Figures in bold denote a significant result.

Terms	Estimate	Std. Error	Z value	Р
Таха				
Intercept	1.65	0.157	10.5	< 0.0001***
MPA - Open	-0.206	0.0984	-2.09	0.036*
Southeast - Ecrehous	-0.217	0.129	-1.68	0.092
Southeast - Minquiers	-0.0891	0.111	-0.801	0.42
Ecrehous - Minquiers	0.127	0.123	1.04	0.3
Abundance				
Intercept	2.91	0.142	20.5	< 0.0001***
MPA - Open	-0.283	0.208	-1.36	0.26
Southeast - Ecrehous	_	-	_	-
Southeast - Minquiers	_	-	_	-
Ecrehous - Minquiers	-	-	-	-

2.8. Total diversity (taxa)

There was a significant treatment effect on the mean number of taxa, which was greatest in the MPAs (4.9 \pm 1.8) compared to the Open Controls (3.9 \pm 1.7) (Fig. 4a, Table 2). There was no treatment effect on the number of taxa between Locations.

2.9. Total abundance

There was no significant treatment effect on mean abundance (Table 2). While the mean number of individuals at the Minquiers was greater inside the MPA (23.8 ± 15.2) compared to Open Controls (12.4 ± 10), this was not significant. The same pattern was seen at the Ecrehous and Southeast, where there was no significant difference in the mean number of individuals between the MPA and Open Controls (Fig. 4b, Table 2).

2.10. Total assemblage

A significant Treatment x Location interaction indicated that species assemblage composition differences between treatments varied across locations (p = 0.009, Table 3; Fig. 5). This was driven by the significant difference in assemblage composition between the MPA and Open Controls at the Minquiers (p = 0.0002). While there was a difference in the assemblage compositions between the MPA and the Open Control at the Southeast, this was not significant (p = 0.0525) (see Table 4).

2.11. SIMPER analysis

The average abundance of *S. cantharus, Maja brachydactyla* and *Scyliorhinus canicula* were high in all treatments and locations (Table 4). There was also a relatively high average abundance of *Trisopterus luscus* in both the MPA and Open Control treatments at the Southeast. *Mullus surmuletus* had higher abundances within MPAs compared to Open Controls at all locations. *Sepia officinalis* and *Inachus* spp. both had higher contributions to the Open Control assemblage compositions than the MPA at the Ecrehous; similar trends were seen at the Minquiers and

Southeast for these two species, but contributed less overall to assemblage composition. Two Labridae species (*Labrus bergylta* and *Symphodus melops*) were found to contribute to the average abundance in the assemblage compositions within the MPAs at both the Minquiers and Southeast compared to Open Controls (Table 4).

2.12. Indicator taxa

Indicator taxa were selected based on their association with complex habitats and their likelihood of being sampled using BRUVs, these included: spider crab (*Maja brachydactyla*), wrasse (Labridae spp.), bream (*Spondyliosoma cantharus*), juvenile bream (juvenile *S. cantharus*) and sharks and rays listed as threatened on the IUCN red list (Nieto et al., 2015; Walker et al., 2020) (Fig. 6).

2.13. Maja brachydactyla

Maja brachydactyla (Fig. 6a) was the only species of the five key commercial species that could be assessed using BRUV data and was recorded in high enough numbers to assess differences in mean relative abundance. *M. brachydactyla* was recorded in greater abundance in Open Controls (2.5 ± 1.8) compared to MPAs (1.9 ± 2.4), except for at the Minquiers where there was marginally greater abundance inside the MPA (3 ± 2.9) compared to Open Controls (2.7 ± 2) (Fig. 7, Table 5). Abundance of *M. brachydactyla* was greater at the Minquiers compared to both the Ecrehous and Southeast, suggesting there was an effect of geographical location.

2.13.1. Labridae species

There was a significant treatment effect on the presence of Labridae spp., with a greater proportion of presence of Labridae within the MPAs compared to the Open Controls (Fig. 8, Table 6). While there was no location effect on the proportion of presence of Labridae spp., they were

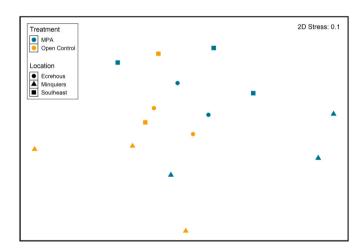


Fig. 5. nMDS illustrating the dissimilarities in assemblage composition between Locations and Treatments. Each point represents a replicate site.

Table 3

PERMANOVA of assemblage based on Bray-Curtis dissimilarities. a) Main test and b) Pairwise tests for the interactions Location (Lo) and Treatment (Tr). Data were square root transformed. Figures in bold denote a significant result.

a) PERMANOVA					b) Pairwise					
Source	df	SS	MS	Pseudo-F	р	perms	Groups	t	р	Unique perms
Tr	1	5031.6	5031.60	5.075	< 0.0001***	9929	Minquiers Open Control - MPA	2.5254	0.0002***	9944
Lo	2	5861.1	2930.50	2.956	< 0.0001***	9921	Ecrehous Open Control - MPA	1.2882	0.1171	9933
TrxLo Pooled Total	2 95 100	4203.8 94180.0 111940.0	2101.90 991.37	2.120	0.009**	9923	Southeast Open Control - MPA	1.408	0.0525	9934

SIMPER analysis results showing the differences in average abundance (Av. Abund) and dissimilarity (Av.Diss) between MPA and Open Control treatments at each Location (Ecrehous, Southeast and Minquiers). Species contribution cutoff was set at 95%.

Species	MPA Av.	Open Control	Av. Diss	Diss/ SD	Contrib %	Cum. %
	Abund	Av.Abund				
Ecrehous						
Spondyliosoma cantharus	2.34	2.47	6.84	1.23	19.5	19.5
Maja brachydactyla	0.79	1.36	5.71	1.17	16.28	35.78
Scyliorhinus canicula	1.74	1.82	4.17	0.93	11.88	47.66
Sepia officinalis	0.13	0.4	2.97	0.8	8.47	56.13
Inachus spp.	0	0.48	2.93	0.57	8.35	64.49
Trisopterus minutus	0.52	0	2.27	0.27	6.46	70.94
Mullus surmuletus	0.23	0	1.68	0.49	4.78	75.72
Homarus gammarus	0.13	0.09	1.3	0.49	3.71	79.43
Cancer pagurus	0.2	0	1.23	0.48	3.51	82.94
Necora puber	0.13	0	0.74	0.38	2.1	85.04
Labrus bergylta	0.09	0	0.69	0.26	1.98	87.02
Liocarcinus spp.	0	0.13	0.67	0.31	1.92	88.93
Raja brachyura	0	0.09	0.66	0.31	1.87	90.8
Ctenolabrus rupestris	0.07	0	0.51	0.26	1.46	92.27
Dasyatis pastinaca	0.07	0	0.51	0.26	1.46	93.73
Trisopterus luscus Southeast	0.07	0	0.51	0.26	1.46	95.19
Spondyliosoma cantharus	2.1	2.08	5.79	0.97	13.13	13.13
Trisopterus luscus	0.54	0.65	5.66	0.6	12.81	25.94
Maja brachydactyla	1.01	1.46	5.54	1.26	12.55	38.49
Scyliorhinus canicula	1.71	2.09	3.77	1.26	8.55	47.04
Mullus surmuletus	0.49	0.17	3.71	0.87	8.41	55.44
Sepia officinalis	0.25	0.34	2.78	0.78	6.29	61.73
Trachurus trachurus	0	0.42	2.68	0.57	6.06	67.8
Labrus bergylta	0.32	0.17	2.51	0.72	5.68	73.48
Symphodus melops	0.35	0	2.16	0.72	4.9	78.39
Pollachius pollachius	0.22	0	1.36	0.47	3.08	81.46
Scyliorhinus stellaris	0.2	0	1.34	0.49	3.04	84.5
Buccinum undatum	0.05	0.1	0.91	0.39	2.05	86.56
Galeorhinus galeus	0.12	0	0.89	0.33	2.01	88.57
Trisopterus minutus	0	0.14	0.73	0.33	1.66	90.23
Conger conger	0.1	0	0.66	0.33	1.5	91.73
Inachus spp.	0	0.1	0.6	0.33	1.36	93.09
Raja brachyura	0	0.1	0.54	0.33	1.23	94.32
Dicentrarchus labrax	0.09	0	0.44	0.23	1.01	95.33
Minquiers						
Spondyliosoma cantharus	3.03	1.28	16.05	1.35	25.54	25.54
Scyliorhinus canicula	0.98	1.43	7.24	1.18	11.53	37.07
Maja brachydactyla	1.49	1.5	6.66	0.98	10.6	47.67
Mullus surmuletus	0.73	0	4.61	0.79	7.33	55
Labrus bergylta	0.5	0.04	3.42	0.88	5.44	60.45
Inachus spp.	0.11	0.49	3.14	0.66	4.99	65.43

Table 4 (continued)

Species	MPA Av. Abund	Open Control Av.Abund	Av. Diss	Diss/ SD	Contrib %	Cum. %
	Abuliu	Av.Abuliu				
Liocarcinus spp.	0.51	0.08	2.88	0.44	4.58	70.01
Chelon spp.	0.38	0	2.8	0.4	4.46	74.47
Symphodus melops	0.38	0.04	2.54	0.64	4.04	78.51
Trachurus trachurus	0.2	0.24	2.48	0.44	3.94	82.45
Sepia officinalis	0.23	0.19	2.05	0.67	3.26	85.71
Trisopterus luscus	0.18	0.12	1.64	0.4	2.62	88.33
Scyliorhinus stellaris	0.11	0.13	1.4	0.46	2.22	90.56
Trisopterus minutus	0.05	0.15	1.01	0.29	1.61	92.16
Dasyatis pastinaca	0.05	0.08	0.9	0.35	1.43	93.59
Cancer pagurus	0.11	0.08	0.87	0.43	1.38	94.97
Pollachius pollachius	0.07	0	0.5	0.23	0.79	95.76

present on fewer BRUVs at the Ecrehous compared to the other two locations (Table 6).

2.13.2. Spondyliosoma cantharus

While there was a greater proportion of presence of adult *S. cantharus* within the MPAs compared to Open Controls, this was not significant (Fig. 9a, Table 7). This differed from the juveniles where a significantly greater proportion of presence within the MPAs compared to Open Controls (Fig. 9b, Table 7). There was no effect of location on the proportion of presence of adult or juvenile *S. cantharus*.

2.13.3. IUCN threatened shark species

Of the shark species observed on the BRUVs, three were included in the IUCN red list. These species were: nursehound *Scyliorhinus stellaris* (near threatened (Ellis et al., 2015a)), smoothhound *Mustelus* spp. (near threatened (Jabado et al., 2021) and vulnerable (Farrell et al., 2015)) and tope *Galeorhinus galeus* (critically endangered (Walker et al., 2020)). IUCN threatened shark species were only recorded on eight BRUVs within the MPAs over the two years, and on three BRUVs in the Open Controls. *G. galeus* is an IUCN critically endangered species as of 2020 (Walker et al., 2020) and was only recorded on one BRUV within the southeast MPA, where there were two individuals. While shark species were present on more BRUVs within the MPAs compared to Open Controls, it was not possible to statistically test this difference due to the small sample size.

2.13.4. IUCN threatened ray species

Of the ray species observed on the BRUVs, three were listed as threatened by the IUCN. These species were Blonde ray *Raja brachyura* (near threatened (Ellis et al., 2009)), Undulate ray *Raja undulata* (near threatened (Ellis et al., 2015b)) and Common stingray *Dasyatis pastinaca* (vulnerable (Serena et al., 2015)). These three ray species were recorded on four BRUVs within the MPAs over the two years, and on six BRUVs in the Open Controls. While ray species were present on more BRUVs in the Open Controls compared to the MPAs, it was not possible to statistically test this difference due to the small sample size.

3. Discussion

Between 2014 and 2017, three MPAs were designated in Jersey's territorial waters. These MPAs provide protection to all the habitats and species within the MPA boundary (rather than just the features of conservation interest) and provide a timely opportunity to undertake research to understand how this form of management can benefit biodiversity. The results from this study show that after three to six years

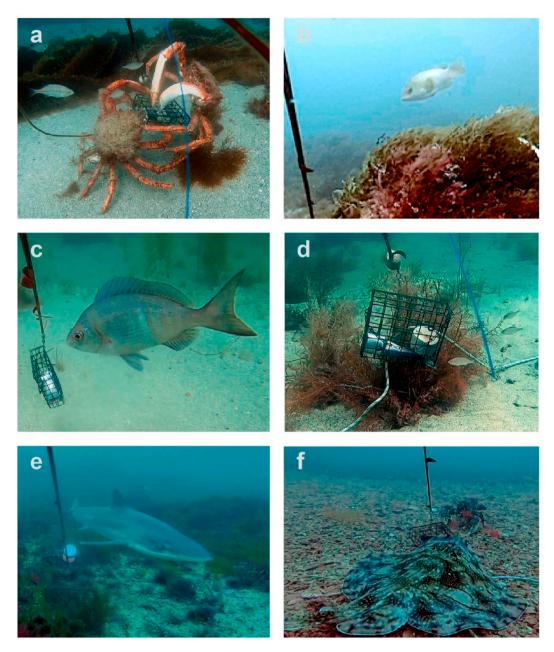


Fig. 6. Indicator taxa. a) Maja brachydactyla b) Labrus bergylta (example of Labridae spp.) c) Spondyliosoma cantharus d) Juvenile S. cantharus e) Galeorhinus galeus (example of shark species) f) Raja undulata (example of ray species).

of protection there appears to be significant differences in the number of mobile benthic species inside the MPAs compared to Open Controls. While there were some differences in assemblage composition, there was only a distinct difference between the MPA and Open Control at the Minquiers. The MPAs were characterised by greater proportions of wrasse (Labridae) species, red mullet (*M. surmuletus*) and juvenile bream (*S. cantharus*) compared to the Open Controls, which had greater proportions of brachyuran crabs (*Inachus* spp.) and cuttlefish (*S. officinalis*). However, as data was only collected post MPA designation, it is possible that the observed differences could have been pre-existing. This may be especially true of the two younger MPAs as they have not had long to develop different species assemblage compositions. Further surveys are needed to monitor future changes as the literature would suggest that this difference will strengthen over time as communities become established within the MPAs (Edgar et al., 2014; Davies et al., 2021).

The development of ecosystem-based management for fisheries and conservation that considers both target species and the habitats that they depend on can deliver both sustainable fisheries (Pikitch et al., 2004; Long et al., 2015) and improve broader societal benefits (e.g. recreational interest) (Thrush et al., 2016; Stewart et al., 2020). Understanding fish distributions is a key component of effective management to ensure that space and habitat requirements of species are accounted for. Results suggested that assemblage compositions varied across the treatments and this was most noticeable at the Minquiers where the mobile species assemblage composition was significantly different inside the MPA compared to Open Controls. While three species were found to dominate in all treatments and locations (S. cantharus, M. brachydactyla and S. canicula), there was a greater diversity of species contributing to the assemblage composition at the Minquiers. A previous BRUV survey also found these species to be dominant in inshore areas in Jersey (Plaster, 2017), suggesting they are prominent across the whole of Jersey's territorial waters. The Minquiers MPA is thought to have been the least affected by bottom-towed fishing prior to its designation due to the numerous unchartered reef heads which pose a hazard to

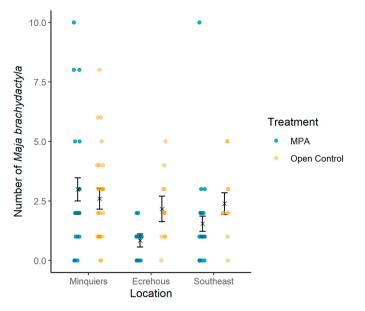


Fig. 7. Total numbers of *Maja brachydactyla* individuals for Location and Treatment. Black crosses and error bars show fitted GLMM means and standard errors of individual abundance predicted using GLMMs with Treatment (MPA and Open Control) and Location (Ecrehous, Southeast and Minquiers) as fixed effects and Year (2019 and 2020) and Site (n = 15) as random effects.

General Linear Mixed Effects Model outputs for BRUV presence of Labridae spp. as a function of Treatment and Location with Year and Site as random effects. Figures in bold denote a significant result.

Terms	Estimate	Std. Error	Z value	Р
Labridae spp.				
Intercept	-1.490	0.685	-2.180	0.029*
MPA - Open	-2.580	0.720	-3.580	< 0.0001***
Ecrehous - Minquiers	1.580	0.812	1.940	0.052
Ecrehous - Southeast	1.500	0.819	1.840	0.066
Minquiers - Southeast	-0.071	0.639	-0.111	0.91

bottom-towed fishing gear (Pers. comm. Paul Chambers, Government of Jersey Marine Resources). It may be that the relatively unimpacted condition of this MPA contributes to greater habitat heterogeneity, complexity and integrity that is supporting a greater range of species. While the presence of seagrass at the Minquiers may be a factor in the species assemblage composition there, the fact that species assemblage composition at the Southeast MPA was not different to the Open Controls suggests the presence of seagrass is not the only driving factor, as seagrass is also present in the Southeast MPA. It may be that species assemblage compositions in the southern region of Jersey's territorial waters are distinct from those further north.

The response of a species to protection from bottom-towed fishing will vary depending on their life history and it was therefore appropriate to investigate indicator species which had been chosen for their predicted biological response to protection measures. Within three years of the MPAs being established, two of the five indicator taxa (Labridae spp. and juvenile *S. cantharus*) showed strong associations with the MPAs, one (*M. brachydactyla*) showed greater abundance in Open Controls and the other two indicator taxa (IUCN sharks and rays) were not detected in high enough numbers to assess. Of the five indicator taxa, only *M. brachydactyla* was recorded in high enough numbers to model abundance, which showed greater abundance in Open Controls except for at the Minquiers. *M. brachydactyla* was the only indicator species that experienced high levels of fishing pressure in the form of potting, with Landings Per Unit Effort (LPUE) known to be increasing in recent years (Marine Resources, 2019). As reported in other MPAs that have excluded

bottom-towed fishing (Mangi et al., 2011; Burton et al., 2016; Rees et al., 2021), there may have been increased potting effort within the MPA boundaries due reduced conflict with bottom-towed fishing. This may in part explain why *M. brachydactyla* abundance is lower in the MPAs overall compared to Open Controls. However, the observation of greater abundances in the southern MPA of the Minquiers, compared to the Ecrehous in the northeast, and the Southeast MPA, suggests there is a location effect. This could be due to a number of reasons, such as habitat composition, currents, exposure, or potting fishing effort.

Increased structural complexity of seafloor habitat promotes more productive and ecologically resilient assemblages that contribute to functional diversity, further increasing the diversity and abundance of species that are able to be supported by an ecosystem (Howarth et al., 2011; Graham and Nash, 2013). Pelagic-benthic coupling is stronger in coastal areas (Kopp et al., 2015) and systems with higher benthic primary productivity support higher trophic levels (Hunt and McKinnell, 2006; Brown et al., 2010b). Increased primary productivity will improve trophic links and provide prey for commercially important fishes such as bream (S. cantharus). Juvenile bream were identifiable from adults based on small size in relation to the bait box, a more pronounced black band on their tail and the presence of numerous broken vellow stripes running the length of the body. High densities of juveniles are indicative of nursery areas (Beck et al., 2001). S. cantharus is a species of commercial value and the greater proportion of presence of juveniles inside the MPA alongside no significant difference in adult bream indicates that there are areas within the MPAs that are important nursery areas for this species, not just that this species only occurs in the MPAs. Nursery areas tend to be highly productive (Heck et al., 1995; Beck et al., 2001; Howarth et al., 2015) and complex habitat structures improve the survivorship of juvenile species (Bradshaw et al., 2003), indicating that habitats within the MPAs may be more structurally complex. As this trend was seen across all locations, juvenile abundance is most likely driven by habitat integrity, rather than habitat type, as the habitats varied across the three MPAs. Juvenile pollack (Pollachius pollachius) and other unidentifiable juvenile fish were also recorded, but they were in two few numbers to assess. It may be that BRUVs are not an appropriate method to sample juveniles of many species as they may be deterred from BRUVs where larger individuals are congregated.

The success of marine reserves tends to be limited to sessile or sedentary species or those with high site fidelity (Kaplan, 2009; Klein et al., 2015). Labridae species, which are known to have strong site fidelity (Mucientes et al., 2019), were observed in greater proportion of presence in MPA sites than Open Control sites. Labridae species are relatively long lived: Symphodus melops and Labrus bergylta were the most commonly observed of the four species and they can live up to 9 and 29 years respectively (Treasurer, 1994; Skiftesvik et al., 2014). Reproductive success is lowered when populations are depleted and, particularly for long lived species, it will take time for larger species to be replenished (Lotze et al., 2011). No-take MPAs may favour large-sized, long-lived Labridae species (Coll et al., 2012), but considerable time-scales are needed for long-lived species to benefit from protection measures owing to their life-history traits (Lotze et al., 2011). While it was not significant, the proportion of presence of Labridae species was lower at the Ecrehous compared to the other two MPAs, suggesting there may also be an effect of habitat type or geographical location influencing the distribution of these species.

Sharks are indicators of ecosystem health and are in decline globally (Yagnesh et al., 2020), but it is unclear whether MPAs have the ability to support shark species, most of which are long-lived with wide ranges. Vulnerable or near threatened shark and ray species were not observed in high enough numbers to assess which could either be related to an inappropriateness of BRUVs to detect these species, or generally low populations of these species in Jersey's shallow water marine environments. As BRUVs have been used in other locations to assess sharks and rays (White et al., 2013) it seems unlikely that the methodology is a factor in this and is most likely related to low population size, as

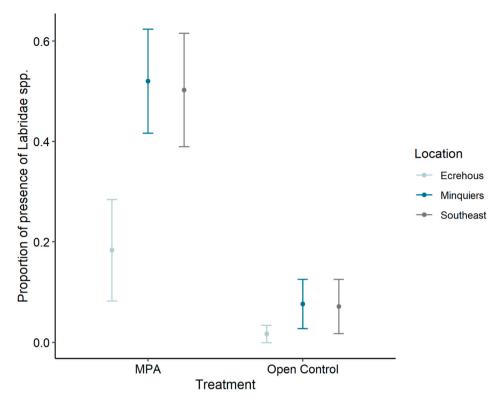


Fig. 8. The proportion of presence of Labridae spp. at each Location (light green: Ecrehous, dark green: Minquiers, grey: Southeast) and Treatment (MPA and Open Control). Points and error bars show modelled mean estimates and standard error. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

General Linear Mixed Effects Model outputs for baited video presence of adult and juvenile *Spondyliosoma cantharus* as a function of Treatment with Year and Site as random effects. Figures in bold denote a significant result.

Terms	Estimate	Std. Error	Z value	Р			
Adult Spondyliosoma cantharus							
Intercept	2.640	0.788	3.350	< 0.0001***			
MPA - Open	-0.801	1.050	-0.766	0.44			
Juvenile Spond	Juvenile Spondyliosoma cantharus						
Intercept	-0.232	0.279	-0.830	0.41			
MPA - Open	-1.350	0.478	-2.830	< 0.0001***			

suggested by the IUCN as they are in decline or at risk of being in decline (Nieto et al., 2015). MPAs alone are not sufficient to protect wide ranging species such as sharks and rays which will move beyond the boundaries of protection to forage, mate or migrate (Gaines et al., 2010; White et al., 2013). However, MPAs may provide improved foraging grounds for these species but species-specific management such as zero bycatch allowances or improvements in fishing techniques to decrease the capture of these species, or in the case of ray that are still legally targeted, decreased quotas, are needed to prevent further declines. In 2017, a zero-catch limit for *G. galeus* was implemented in Jersey, so this BRUV survey sets a baseline for this species against which future changes can be compared to. This ban on fishing combined with the MPAs may support the recovery of this species which is in global decline (Walker et al., 2020). It may be that the replication required to detect these species is much greater than for more abundant species.

Jersey's fishery is dependent on five key shellfish species (Lobster *Homarus gammarus*, brown crab *Cancer pagurus*, spider crab *Maja bra-chydactyla*, whelk *Buccinum undatum* and king scallop *Pecten maximus*), and all bar spider crab are not readily detected by BRUVs due to their life histories and behaviours. King scallop are sedentary filter feeders and so will not be observed on BRUVs. Whelk are attracted to the bait but are

generally too slow to reach the unit during the deployment period. Lobster and brown crab are the more valuable of the three crustaceans but both are primarily active at night (Lawton and Lavalli, 1995; Skajaa et al., 1998). Therefore, BRUVs deployed in the day will not provide accurate assessments of these species as was also observed by Howarth et al. (2015) despite lobsters being common in the study area (Stewart et al., 2020). Spider crab is the one commercial species that is readily attracted to the BRUVs and spider crab was found to be in lower abundance within the Southeast and Ecrehous MPAs compared to Open Controls. While spider crab are protected from mechanical damage from bottom-towed fishing gear inside the MPAs, they are not protected from potting. Potting levels are difficult to measure in Jersey as all potting vessels are less than 12 m in length, meaning they are not required to have VMS and their spatial fishing activity unknown. It may be that potting levels have increased within the MPAs following the exclusion of bottom-towed fishing, as has been observed elsewhere (Mangi et al., 2011), and is preventing any changes in the spider crab populations being observed. Landings data from within Jersey's waters shows that both catch and effort of spider crab is increasing but this cannot be attributed to the MPAs.

This study provides the first baseline for mobile species assemblage compositions across geographically separate MPAs in Jersey's waters, where the mobile species associated with mixed sedimentary habitat in between reef habitats have responded positively to the exclusion of bottom towed fishing. Following protection, the differences observed in benthic species assemblages are in line with results from similar studies worldwide and further adds to the evidence base that multi-use MPAs can improve ecological condition, provided bottom towed fishing is excluded from all areas within the MPA boundary. Given that roughly 70% sedimentary habitats within MPAs in English waters are unprotected from bottom towed fishing gear (MPA Reality Check, 2022) there is scope to greatly improve the ability of MPAs to support the recovery of biodiversity. This initial observation of recovery can be expected to improve and species assemblage composition to continue to change over

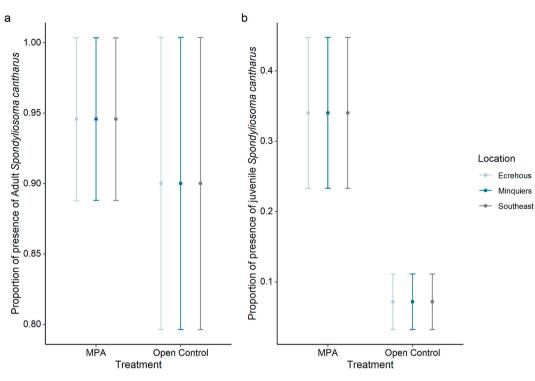


Fig. 9. The proportion of presence of a) adult and b) juvenile *Spondyliosoma cantharus* at each Location (light green: Ecrehous, dark green: Minquiers, grey: Southeast) and Treatment (MPA and Open Control). Points and error bars show modelled mean estimates and standard error. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

General Linear Mixed Effects Model outputs for baited video presence of adult and juvenile *Spondyliosoma cantharus* as a function of Treatment with Year and Site as random effects. Figures in bold denote a significant result.

Terms	Estimate	Std. Error	Z value	Р			
Adult Spondylic	Adult Spondyliosoma cantharus						
Intercept	2.640	0.788	3.350	< 0.0001***			
MPA - Open	-0.801	1.050	-0.766	0.44			
Juvenile Spond	Juvenile Spondyliosoma cantharus						
Intercept	-0.232	0.279	-0.830	0.41			
MPA - Open	-1.350	0.478	-2.830	< 0.0001***			

decadal time spans. The longest monitoring of a whole-site MPA in temperate waters detected change in biological communities 12 years after implementation (Davies et al., 2021). Further field studies are needed to monitor changes as it may take several years, if not decades, for biological communities to stabilise within the MPAs. It is therefore recommended that monitoring is continued to further understand changes in species assemblages and distributions in response to protection measures and to provide reference areas to compare fished areas against, to inform best practice. Further, the impact of other fishing pressures may confound the ability of an MPA to improve commercial species stocks, and the implementation of NTZs is recommended to better understand more natural population structures and abundances of exploited species.

CRediT authorship contribution statement

Samantha R. Blampied: Conceptualization, Data curation, Formal analysis, Investigation, Funding acquisition, Methodology, Project administration, Resources, Visualization, Writing – original draft, Writing – review & editing. Sian E. Rees: Conceptualization, Project administration, Supervision, Writing – review & editing. Martin J. Attrill: Conceptualization, Methodology, Supervision, Writing – review & editing. **Francis C.T. Binney:** Conceptualization, Project administration, Resources, Supervision, Writing – review & editing. **Emma V. Sheehan:** Conceptualization, Methodology, Project administration, Supervision, Validation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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S.R. Blampied et al.

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