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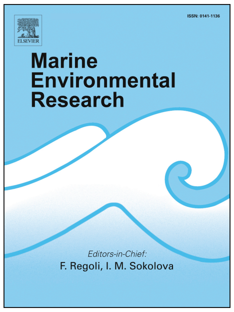

Sessile and mobile components of a benthic ecosystem display mixed trends within a temperate marine reserve

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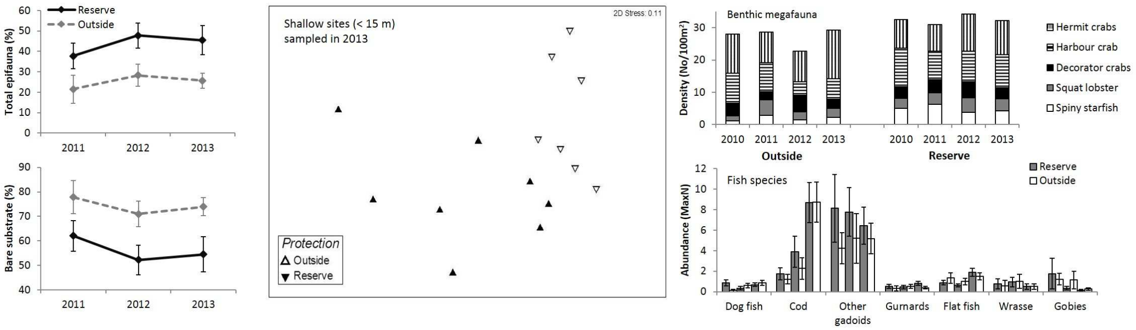
Reserve
Outside
Total epifauna (%)
60
50
40
30
20
10
0
2011
2012
2013
Bare substrate (%)
90
80
70
60
50
40
2011
2012
2013
Shallow sites (< 15 m)
sampled in 2013
2D Stress: 0.11
Protection
Outside
Reserve
Benthic megafauna
Density (No/100m²)
30
20
10
0
2010
2011
2012
2013
Outside
2010
2011
2012
2013
Reserve
Hermit crabs
Harbour crab
Decorator crabs
Squat lobster
Spiny starfish
Fish species
Abundance (MaxN)
12
10
8
6
4
2
0
Reserve
Outside
Dog fish
Cod
Other gadoids
Gurnards
Flat fish
Wrasse
Gobies

Sessile and mobile components of a benthic ecosystem display mixed trends within a temperate marine reserve

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ABSTRACT

Despite recent efforts to increase the global coverage of marine protected areas (MPAs), studies investigating the effectiveness of marine protected areas within temperate waters remain scarce. Furthermore, out of the few studies published on MPAs in temperate waters, the majority focus on specific ecological or fishery components rather than investigating the ecosystem as a whole. This study therefore investigated the dynamics of both benthic communities and fish populations within a recently established, fully protected marine reserve in Lamlash Bay, Isle of Arran, United Kingdom, over a four year period. A combination of photo and diver surveys revealed live maerl (*Phymatolithon calcareum*), macroalgae, sponges, hydroids, feather stars and eyelash worms (*Myxicola infundibulum*) to be significantly more abundant within the marine reserve than on surrounding fishing grounds. Likewise, the overall composition of epifaunal communities in and outside the reserve was significantly different. Both results are consistent with the hypothesis that protecting areas from fishing can encourage seafloor habitats to recover. In addition, the greater abundance of complex habitats within the reserve appeared to providing nursery habitat for juvenile cod (*Gadus morhua*) and scallops (*Pecten maximus* and *Aequipecten opercularis*). In contrast, there was little difference in the abundance of mobile benthic fauna, such as crabs and starfish, between the reserve and outside. Similarly, the use of baited underwater video cameras revealed no difference in the abundance and size of fish between the reserve and outside. Limited recovery of these ecosystem components may be due to the relatively small size (2.67 km^2) and young age of the reserve (< 5 years), both of which might have limited the extent of any benefits afforded to mobile fauna and fish communities. Overall, this study provides evidence that fully protected marine reserves can encourage seafloor habitats to recover, which in turn, can create a number of benefits that flow back to other species, including those of commercial importance.

Key words: Ecosystem recovery; benthos; megafauna; epifauna; nursery habitat; marine protected areas; ecosystem based fishery management; temperate seas

1. Introduction

Following a large number of recently established policies and initiatives, the global coverage of marine protected areas (MPAs) is set to increase dramatically over the next decade (Metcalfe et al., 2013). Globally agreed marine protection targets, such as the Convention on Biological Diversity's (CBD) '*Aichi Target*' are encouraging many governments to establish or expand existing MPA networks within their jurisdictions (CBD, 2011; Harrop, 2011; Wood et al., 2008; Wood, 2011). This interest is reflected in the European Union (EU) as the Marine Strategy Framework Directive (MSFD), Birds and Habitats Directives, OSPAR (The Convention for the Protection of the Marine Environment of the North-East Atlantic), HELCOM (Helsinki Commission) and Barcelona regional seas conventions, have all initiated the process of establishing a coherent network of MPAs within European waters (Fenberg et al., 2012; Metcalfe et al., 2013). On a national level, the continued implementation of Marine Conservation Zones (MCZs; England, Wales and Northern Ireland) and Scottish MPAs (Scotland) is leading to the creation of a network of MPAs around the United Kingdom (UK; JNCC, 2013; Jones, 2012). All these measures intend to achieve a variety of management goals; principally to conserve biodiversity and promote the sustainability of fisheries (Metcalfe et al., 2013; Pomeroy et al., 2005).

The growing use of MPAs as a management tool has co-occurred with a push towards "ecosystem-based fishery management"; with many scientists arguing that we need to shift away from traditional single-species management, to more holistic approaches where management priorities begin with the ecosystem rather than the target species (Pikitch et al., 2004; Zhou et al., 2010). To help guide these changes in management, it is important to better understand how MPAs promote the process of recovery within marine ecosystems (Götz et al., 2013; Van Rein et al., 2009), particularly in temperate environments, which have been less studied than tropical areas (Fenberg et al., 2012). Furthermore, out of the few studies published on temperate MPAs, the majority have investigated changes in specific ecological or fishery components rather than investigating the ecosystem as a whole; with many focussing on either changes to seafloor habitats and benthic species (e.g. Beukers-Stewart et al., 2005; Sheehan et al., 2013) or just species of commercial importance (e.g. Hoskin et al., 2011; Moland et al., 2012, 2013). However, growing evidence suggests there are strong links between the two (e.g. Beck et al., 2001; Gibb et al., 2007; Howarth et al., 2011; Kamenos et al., 2004a, b; Laurel et al., 2009) meaning it may be more informative to study several components of the ecosystem rather than one alone.

Of all fishing methods, the use of mobile fishing gears, such as dredges and trawls, is considered to be the most destructive to marine ecosystems (Collie et al., 2000; Kaiser et al., 2006). This is because they can cause substantial physical disruption of seafloor habitats by ploughing sediments and damaging epifaunal organisms such as hydroids, bryozoans and maerl beds (Dayton et al., 1995; Eleftheriou and Robertson, 1992; Jennings and Kaiser, 1998; Jennings et al., 2001; Kaiser et al., 2000). However, these organisms are functionally important to marine ecosystems as they provide an element of 3-dimensional structure to the seafloor. In doing so, they supply important refuges for small / juvenile fish from predators and unfavourable environmental conditions (Cacabelos et al., 2010; Monteiro et al., 2002; Ryer et al., 2004), represent important feeding sites for fish and invertebrates (Bradshaw et al., 2003; Warren et al., 2010) and provide essential habitat for the settlement of scallop spat and a range of other organisms, including the settlement of further epifauna (Bradshaw et al., 2001; Howarth et al., 2011; Howarth et al., 2015). Such locations are therefore often referred to as “nursery habitats” as they tend to be highly productive, support high levels of juvenile density, growth and survival, and contribute disproportionally to the production of adult recruits (Beck et al., 2001; Gibb et al., 2007; Laurel et al., 2009). Commonly cited nursery habitats include maerl (*Phymatolithon calcareum*) beds (Hall-Spencer et al., 2006; Kamenos et al., 2004a,b;), seagrass beds (Warren et al., 2010) and areas of dense macrophytes / macroalgae (Cacabelos et al., 2010; Christie et al., 2007; Howarth et al., 2011; Howarth et al., 2015), all of which have been shown to harbour high densities of commercially exploited species such as spider crabs, *Maja squinado,* juvenile cod, *Gadus morhua*, edible crab, *Cancer pagurus*, and edible sea urchins, *Echinus esculentus*. Many epifaunal species also support unique micro-communities, for example, caprellid amphipods on hydroids, the range of invertebrates associated with kelp forests, or the diversity of organisms associated with pomatocerid tube worm heads (Airoldi et al., 2008; Kaiser et al., 1999). Consequently, the damage sustained by nursery habitats from fishing gears can dramatically reduce an area’s capacity to support biodiversity and negatively impact the recruitment of commercially important species (Bradshaw et al., 2001, 2003; Collie et al., 1997; Kaiser, 2005).

In addition to damaging seafloor habitats, mobile fishing gears often capture a wide variety of non-target organisms, which can include species targeted by other fisheries (Bradshaw et al., 2001; Craven et al., 2013). Survival rates of by-catch are often very low, with the majority being discarded damaged, dying or dead (Beukers-Stewart et al., 2001; Jenkins et al., 2001; Diamond and Beukers-Stewart, 2011;). In addition to the by-catch landed on deck, large quantities of organisms are killed or damaged by passing gears but remain on the seafloor uncaptured (Jenkins et al., 2001). Both of these impacts can cause a decline in the abundance of target and non-target organisms (Currie and Parry, 1996; Bradshaw et al., 2001; Lambert et al., 2011). Paradoxically, some species are attracted to areas that have been fished and consequently increase in abundance. In disturbing the sediment, damaging / killing organisms and generating by-catch / discards, the local density of scavengers and predators can increase by up to 200 times in fished areas (Kaiser and Hiddink 2007; Veale et al., 2000), thereby elevating predation pressure on the surrounding community (Jenkins et al., 2004; Ramsay and Kaiser, 1998; Veale et al., 2000). Due to the dispersion of odour plumes, resettlement of sediment and predation of damaged organisms, the high densities of scavengers gathering at fishing grounds is likely to be a relatively short-lived event. Then again, Bradshaw et al., (2002) found that the abundance of mobile, robust, and scavenging invertebrate species in the Irish Sea had increased over a 60 year period of increasing fishing pressure, while slow-moving or sessile, fragile taxa had decreased. Likewise, a study in the Isle of Man found the density of scavenging dog fish to have substantially increased over a 14 year period, whereas the density of slow-growing yet commercially important monkfish decreased (Craven et al., 2013).

Since closing areas to fishing is the surest way of protecting marine ecosystems from the physical impacts of fishing gears (Beukers-Stewart et al., 2005; Roberts et al., 2005), MPAs should provide the best management tool available for encouraging their recovery. However, the implementation of MPAs is still at a relatively early stage in most parts of the world, including the UK (Fenberg et al., 2012; Metcalfe et al., 2013), and their effectiveness as a fishery management tool remains highly debated (Boersma and Parrish, 1999; Jones, 2007; Kaiser, 2004, 2005; Sciberras et al., 2013). This is partly because establishing MPAs can displace fishing effort to surrounding areas (Bohnsack, 2000; Kaiser, 2005), which can cause wider environmental damage (Dinmore et al., 2003) and reduce profits (at least in the short-term) through the loss of fishing grounds (Rassweiler et al., 2012). Hence, MPAs only truly yield fishery benefits when these negative effects are adequately offset by increased recruitment and landings.

In September 2008, Scotland’s first fully protected marine reserve was established in Lamlash Bay, Isle of Arran, UK, prohibiting all fishing within the reserve under the Inshore Fishing

(Scotland) Act of 1984 (Axelsson et al., 2009). The Firth of Clyde, in which the Isle of Arran sits, is known to be one of the most degraded marine environments in the UK, primarily due to over a century of intensive fisheries exploitation (Howarth et al., 2013; Thurstan and Roberts, 2010). The marine reserve was therefore passed by Scottish parliament under the rationale that the reduction in fishing pressure should help regenerate the local marine environment and enhance commercial shellfish and fish populations. Hence, our study sought to investigate changes in seabed habitats and species within the reserve and whether these changes have had further effects on species of commercial importance. This was achieved by testing the following hypotheses: (1) that the community composition of benthic assemblages within and outside the reserve would increasingly diverge over time; (2) the abundance of benthic organisms and fish would be greater within the reserve; (3) fish would be larger within the reserve; (4) structurally complex habitats would be more abundant within the reserve; and (5) fish assemblages would be positively related to the abundance of complex habitat. This was achieved by conducting a series of quantitative diver visual, photo and video surveys within and outside the reserve over a four-year period.

2. Methods

2.1.1. Study Area

We conducted our study in and around Lamlash Bay on the south-eastern shore of the Isle of Arran, off the west coast of Scotland in The Firth of Clyde (Fig. 1). Lamlash Bay Marine Reserve covers 2.67 km^2 (Thurstan and Roberts, 2010), with water depths ranging between 0 and 29 m below chart datum, but reaching as deep as 43 and 50 m outside to the east and the west of the reserve, respectively (Admiralty Chart, 1864; Baxter et al., 2008). Previous surveys (Axelsson et al., 2009; Duncan, 2003) indicated a seabed of mixed sediments (i.e. mud, sand and gravel with various proportions of shell) but that the central and southern regions of the bay tend to be characterised by softer sediment, mainly muddy sand. In addition, the area has long been identified as containing important maerl beds, although recent evidence points to deterioration in their health (Howarth et al., 2011, 2015). Lamlash Bay marine reserve was originally proposed by a local group of SCUBA divers that operated in the area. They proposed Lamlash Bay as an ideal location for a marine reserve as it would be easy to delineate on a map, and would be easy for fishermen to tell if they were within its boundaries. It was also chosen to protect areas of maerl.

Unofficial observations made by the Community of Arran Seabed Trust (www.arrancoast.com) indicate that fishing effort had been consistently low in unprotected parts of Lamlash Bay during recent years, averaging at 2-4 trawling / scallop vessels operating within the area per year since 2008. However, several static fishermen (i.e. employing creels / lobster pots) targeting lobster and crab routinely operate in the area, in addition to a small team of commercial scallop divers. Although these latter fishing methods appear to cause little direct damage to the seafloor, they can potentially alter ecosystems by removing large numbers of targeted species (Coleman et al., 2013; Eno et al., 2001).

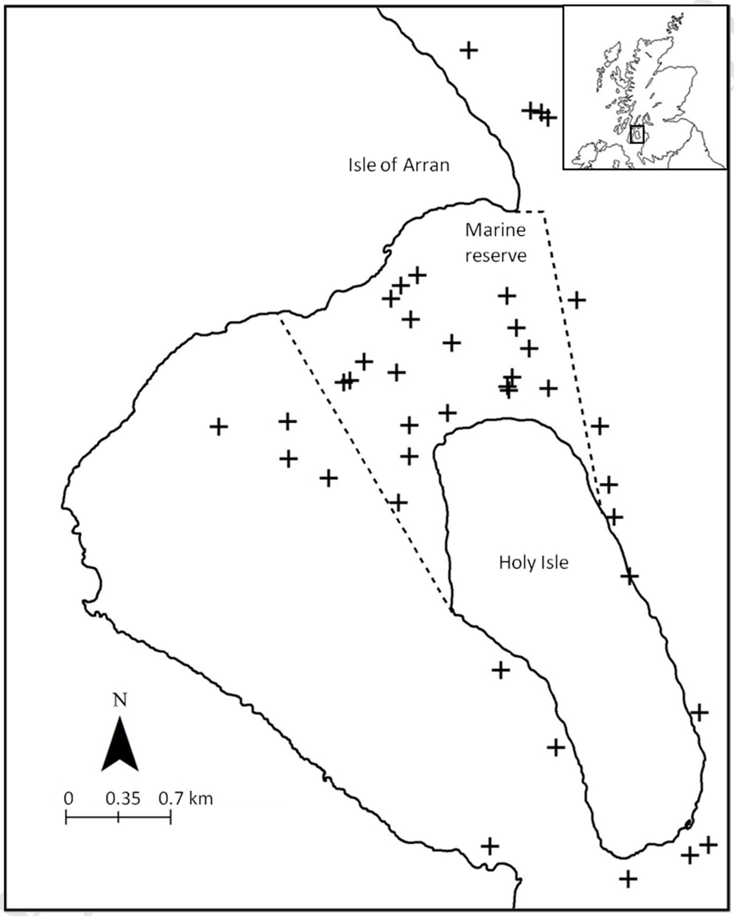

Fig. 1. Site locations of dive transects for all years. Also displayed are the boundaries of the Lamlash Bay fully protected marine reserve. The inset shows the location of the Isle of Arran off the west coast of Scotland, United Kingdom.

2.2. Data collection

2.2.1. Diver and Photo Transects

We began monitoring Lamlash Bay in the summer of 2010 (see Howarth et al., 2011). Initially 40 sites were surveyed, half within the reserve and half outside (Fig. 1). These surveys were then repeated and expanded in the summers (July-August) of 2011, 2012 and 2013 by adding more survey methods but reducing the number of study sites. Therefore, we surveyed 28 sites in 2011, 31 sites in 2012, and 32 sites in 2013. Again, sites were divided so that half fell within the boundaries of the marine reserve. Sites were chosen so that each one within the reserve could be paired with at least one other suitable control outside, based on similar depth and predominant substrate type (Table A.1-A.4). Due to lack of data and prior knowledge of the area, the initial experimental design was relatively imbalanced. For example, 12 deep muddy sand sites were surveyed outside the reserve in 2010 compared to just 6 inside. However, this improved with every year, and by 2012, our experimental design was completely balanced. Sites were limited to areas of the seabed shallow enough to remain within diver no decompression limits after a 25 minute survey (i.e. <30m depth). Surveys were also conducted parallel to depth contours to ensure the depth of a single survey did not change by more than 3 m.

Transects were surveyed along a 50 m leaded line laid out straight across the seabed. Weighted anchors at each end held the line in place, in addition to two floating buoys which reached the surface. A team of two divers then made their way from one end to the other, recording the abundance of all megafauna (e.g. fish and crustaceans) encountered within 1.5 m either side of the transect, the width of which was marked by a 3 m long pole which the divers pushed ahead of themselves This gave a total survey area of 150 m^2 for each dive transect. After a surface interval of approximately two hours, divers returned to the transect line and placed a 1 m^2 quadrat parallel to the transect, but at a distance of 2 m from the leaded line, thereby ensuring the area about to be photographed had not been disturbed by the line or the previous survey. The quadrat was divided into four 0.25 m^2 sub-quadrats which were photographed from directly overhead. This process was repeated every 5 m along the transect, giving a total of 40 images for each transect. Sub-quadrats were later combined for statistical analysis, giving a total of 10 quadrats for each transect.

2.2.2. Still Image Analysis

Photoquadrats were analysed using the software Coral Point Count with Excel Extensions (CPCe) v 4.1 (Kohler and Gill, 2006). The quadrat border was positioned and sized manually before overlaying 50 stratified points (10 rows x 5 columns containing 1 point each) which were randomly generated for every image. Any organism lying under a point was then identified to species level where possible. If there was no organism, the substrate type was identified instead (i.e. mud, pebble, cobble, boulder or detritus). Initial attempts used just 25 points and 40 images but because the seafloor within Lamlash Bay contained a relatively low proportion of benthic fauna, the likelihood of a randomly distributed point falling upon anything other than bare substrate was very low. Hence, the number of points was doubled and the number of images for each site halved.

2.2.3. Baited Remote Underwater Video (BRUV)

At the same time as the diver surveys, a BRUV was deployed at each site between the hours of 09.00-14.00 for the surveys conducted in 2011, 2012 and 2013. For these, a video camera was fitted to one end of a commercial lobster pot frame and a porous bait box was fitted to the other (Fig. 2). Two video lights provided lighting. Rope was spliced to all four corners of the frame and joined at the centre along with three cork floats to prevent the ropes from sinking into view of the camera. As initial surveys in 2010 indicated that fish abundance was relatively low, 200g of coarsely cut mackerel was placed inside the bait box prior to deployment in order to attract fish from a wider area. Once recording began, a 40m long rope and surface marker buoy were attached to the frame and the BRUV was carefully lowered to the seafloor. The system's negative buoyancy ensured the BRUV landed upright and remained in a stable position. After approximately one hour, the BRUV was hauled back to the boat, the bait replaced, and the BRUV was ready for redeployment at another site.

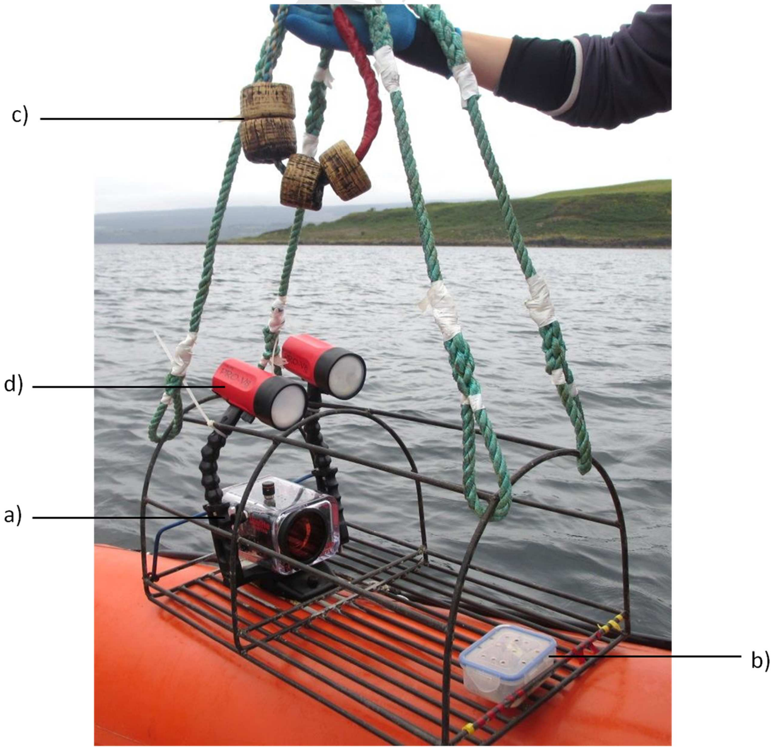

Fig. 2. The Baited Underwater Video Camera (BRUV) set-up comprised of a video camera (a) mounted to a lobster pot frame in view of a porous box containing mackerel bait (b). Ropes

were used to lower the system to the seafloor and cork floats (c) prevented these from descending in front of the camera. Two video lights provided lighting (d).

2.2.4. Video Analysis

To standardise video footage, analysis began from two minutes after the BRUV landed on the seabed and terminated 60 minutes later. For each video the following variables were recorded for all fish: (*i*) identity and total number of species; (*ii*) total number of families; (*iii*) time of first appearance for each species; (*iv*) maximum number of individuals for each species observed within the same frame (MaxN). Due to the inability of an observer to recognise repeated entrances of the same individual, MaxN was used as an indicator of abundance (Cappo et al., 2004); (*v*) time of MaxN; and (*vi*) the body length (for fish) or carapace width (for crustaceans) of all individuals at MaxN that faced side-on to the camera and were aligned between the two front posts of the BRUV frame. This was estimated by using 10 mm reference markers which were painted on the front frame of the BRUV.

2.3. Data Analysis

2.3.1. Benthic Epifauna

Data on the percentage cover of epibenthic organisms were extracted from CPCe. These taxa included anemones (e.g. *Ceriaanthus lloydi*), soft corals (e.g. *Alcyonium digitatum*), hydroids (e.g. *Nemertesia ramosa*), sponges (e.g. *Cliona celata*), tunicates (e.g. *Corella paralellogramma*) and macroalgae (e.g. *Laminaria hyperborea*). The DIVERSE function within the software package PRIMER v6 (Clarke and Gorley, 2006) was then used to generate univariate measures of biodiversity such as total number of species, total number of individuals, Pielou's evenness and Shannon's biodiversity. Differences in these univariate measures of biodiversity tested between depths using a Pearson's product-moment correlation analysis. Similarly, one-way ANOVAs were used to test if these measures of biodiversity were different among substrates. To explore the effects of protection, the percentage of the various epifaunal taxa, along with the percentage cover of total epifauna and bare substrate, and the univariate measures of biodiversity, were all tested for significance with a two-way Analysis of Variance (ANOVA) using treatment and year as fixed factors in the software package SPSS v22. To correct for multiple testing, the False Discovery Rate (FDR) endpoint adjustment was applied to reduce the likelihood of Type I errors (Yoav and Hochburg, 1995). Following this, any significant trends were explored further by creating line plots fitted with error bars of ±1 Standard Error (SE).

A resemblance matrix using the Bray-Curtis similarity measure (Bray and Curtis, 1957) was created in PRIMER and a Permutational Multivariate Analysis of Variance (PERMANOVA+) was conducted to test for differences in epifaunal community composition. The analytical design had four factors: Year (fixed: 2011, 2012, 2013), Treatment (fixed: reserve, outside), Depth (fixed: shallow <15 m and deep >15 m), and Substrate (fixed: soft, maerl and hard). Soft substrates referred to muddy and sandy, whilst hard substrates referred to sites containing cobbles and boulders. Each term in the analyses used 9999 permutations. Any significant multi-level interactions were further explored using PERMANOVA+ pairwise tests. PERMANOVA was considered to be an appropriate test as it is robust to datasets with many zeros (due to being based on the Bray-Curtis similarity measure), and allows the testing of interactions in complex multifactorial designs. It has significant advantages over conventional MANOVA in that it makes no assumptions about underlying data distributions and is robust to unbalanced survey designs, as is the case with this study (Anderson and Ter Braak, 2003). Visualisation of the similarity matrices was achieved using non-metric Multi-Dimensional Scaling (nMDS). Additionally, a Similarity Profile (SIMPROF) routine was used to highlight if any alternative *a posteri* groups existed within the data. Finally, a Similarity of Percentages (SIMPER) was performed to determine the contribution of individual species to the average dissimilarity between treatments.

2.3.2. Benthic Megafauna

Similar to before, the total number of species, individuals, Pielou's evenness and Shannon's biodiversity of benthic megafauna observed during the diver transects were tested between depths and substrates using one-way ANOVAs and Pearson's correlations. To explore the effects of protection, these univariate measures of biodiversity were also tested between treatments and years using two-way ANOVAs with FDR. In addition, the density of the 10 most abundant species was investigated for differences between years and treatments by creating stacked bar charts and using two-way ANOVAs. PERMANOVA+ was then used to test for differences in overall community composition using the same analytical design as before.

2.3.3. Fish Assemblages

The abundance of dog fish (*Scyliorhinus canicula*), gurnards (Family: Triglidae), flat fish (Family: Pleuronectidae), wrasse (Family: Labridae), gobies (Family: Gobiidae), cod and other gadoids (i.e. saithe - *Pollachius virens*, pollack - *Pollachius pollachius*, whiting - *Merlangius merlangus*, haddock - *Melanogrammus aeglefinus*, and poor cod - *Trisopterus minutus*) observed during the BRUV surveys were tested for differences between treatments using two-way ANOVAs (factors as above). Additionally, the total number of species, individuals, Pielou's evenness and Shannon's biodiversity were also tested in the same way. The mean size of fish were then combined across all years (due to small sample size) and tested for differences between treatments using One-way ANOVAs. In rare cases (4 out of the 82 BRUV surveys), large pelagic shoals of mackerel and sand eels consisting of many hundreds of individuals were recorded. These were excluded from statistical analysis to reduce variability.

To determine whether environmental and benthic data affected the distribution and abundance of cod and other gadoids, negative binomial Generalised Linear Models (GLM) were created. Predictor variables used in the GLMs were protection, depth, the abundance of benthic megafauna, and the percentage cover of bare substrate, bryozoans, soft coral, hydroids, macroalgae, sponges, tunicates, and dead and live maerl. Before construction of a GLM, scatter plot and intercorrelation matrices (based upon Spearman's rank correlation) were created to explore basic relationships and determine whether any variables were strongly intercorrelated (i.e. $-0.7 \geq r \leq 0.7$) as such variables would not be allowed together within a GLM (Crawley, 2005). The percentage cover of macroalgae was found to be negatively intercorrelated with depth and the percentage cover of bare substrate. Therefore a total of four GLMs were constructed, two testing cod abundance (one including macroalgae and the other including bare substrate and depth) and two testing the abundance of other gadoids (same design as before). Backward-forward stepwise reductions were then conducted to create minimal adequate models. Diagnostic and Cleveland dotplots were then used to explore how well the models fitted the data and to identify any extreme outliers. The proportion of variance (i.e. deviance) explained by the models was calculated by the following equation:

$$\text{Deviance (\%)} = 1 - (\text{Residual Deviance} / \text{Null Deviance})$$

Lastly, analyses of deviance utilising Pearson's Chi-square test (χ^2) were then conducted to determine if the reduced models accounted for significantly less deviance than the full models.

3. Results

3.1. Composition of Benthic Epifauna

A total of 77 different epibenthic species were recorded from the photoquadrat surveys. The total percentage cover by epifaunal taxa (r^2 = -0.5), as well as the total number of species (r^2 = -

0.3) were both significantly negatively correlated with depth (Pearson's Correlation; N = 87; $P < 0.05$). In contrast, Pielou's evenness (r^2 = 0.5) and Shannon's Diversity (r^2 = 0.3) Index were both positively correlated with depth (Pearson's Correlation; N = 87; $P < 0.05$). Substrate type was also found to be having a significant influence on these univariate measures of biodiversity, as the total percentage cover by epifaunal taxa and the total number of species were both found to be significantly greater in sites composed predominantly of maerl, compared to soft and hard sediments (One-way ANOVA; $F_{(1,\ 87)}$ = 5.1-6.8, $P < 0.05$).

In terms of protection, the mean number of species (Fig. 3) was significantly greater within the reserve than surrounding areas (Table 1), as was the percentage cover of live maerl, sponges, hydroids, macroalgae and all epifaunal species combined. The percentage cover of these different taxa were found to be between 2 - 4 times greater within the reserve than in neighbouring fishing grounds. In many cases, their abundance within the reserve appeared to increase over the survey period but there was no significant interaction between year and protection across all taxa. In contrast to epibenthic abundance, the percentage cover of bare substrate was significantly lower within the reserve than outside. Two-way ANOVAs showed that protection, year and the interaction between the two were not significantly influencing Pielou's evenness, Shannon's diversity index and the percentage cover of soft coral, anemones, worms, bryozoans and tunicates (Table A.5).

PERMANOVA+ analysis revealed the composition of the epibenthic community to significantly differ between treatments, depth and year (Table 2). The interaction protection x depth was also found to be significant and subsequent pairwise testing showed that differences between the reserve and outside only existed for sites located at shallow depths. Exploring these differences further, nMDS of shallow sites in 2011 revealed substantial variation in community composition between the reserve and outside (Fig. 4a). Consequently, SIMPROF could not distinguish samples from within and outside the reserve ($P > 0.05$) and clustered them all together. However, nMDS of shallow sites sampled in 2013 revealed that epibenthic communities located within the reserve had become comparatively more distinguishable from communities located outside (Fig. 4b). Therefore, in contrast to 2011, SIMPROF detected statistical differences between treatments ($P < 0.05$) and clearly separated sites located within the reserve from sites located outside.

Table 1. Two-way ANOVA comparing the total number of species and percentage cover by different epifaunal assemblages between the marine reserve and outside across the years 2011-2013. Adjusted critical values obtained from FDR are shown in bold. Significant results are denoted by (*).

Source	Test	SS	*df*	MS	*F*	*P*	**FDR α**
No of species	Year	370.3	2	185.1	5.86	*0.004	**0.06**
	Protection	403.8	1	403.8	12.78	*0.001	
	Year * Protection	60.2	2	30.1	0.95	0.39	
	Residual	2558.3	81	31.5			
Total epifauna	Year	7476.9	1	7476.9	14.40	0.381	**0.055**
	Protection	1012.7	2	506.3	0.97	*0.002	
	Year * Protection	53.4	2	26.7	0.05	0.95	
	Residual	42559.6	82	519			
Bare substrate	Year	7037.5	1	7037.5	13.81	0.384	**0.5**
	Protection	986.6	2	493.3	0.96	*0.004	
	Year * Protection	52.1	2	26.1	0.051	0.95	
	Residual	41775.5	82	509.4			
Hydroids	Year	40.3	1	40.3	3.71	0.053	**0.045**
	Protection	66.3	2	33.1	3.05	*0.041	
	Year * Protection	17.8	2	8.9	0.82	0.444	
	Residual	891.8	82	10.8			
Live maerl	Year	11.1	1	11.1	5.77	0.859	**0.04**
	Protection	0.5	2	0.2	0.15	*0.019	
	Year * Protection	0.9	2	0.4	0.24	0.783	
	Residual	158.6	82	1.9			
Macro algae	Year	3720.3	1	3720.3	7.9	0.852	**0.035**
	Protection	1507	2	75.3	0.16	*0.006	
	Year * Protection	114.5	2	57.2	0.12	0.886	
	Residual	38604.8	82	470.7			
Sponge	Year	0.3	1	0.3	8.7	0.148	**0.03**
	Protection	0.1	2	0.07	1.95	*0.004	
	Year * Protection	0.07	2	0.03	0.95	0.388	
	Residual	3.2	82	0.03			

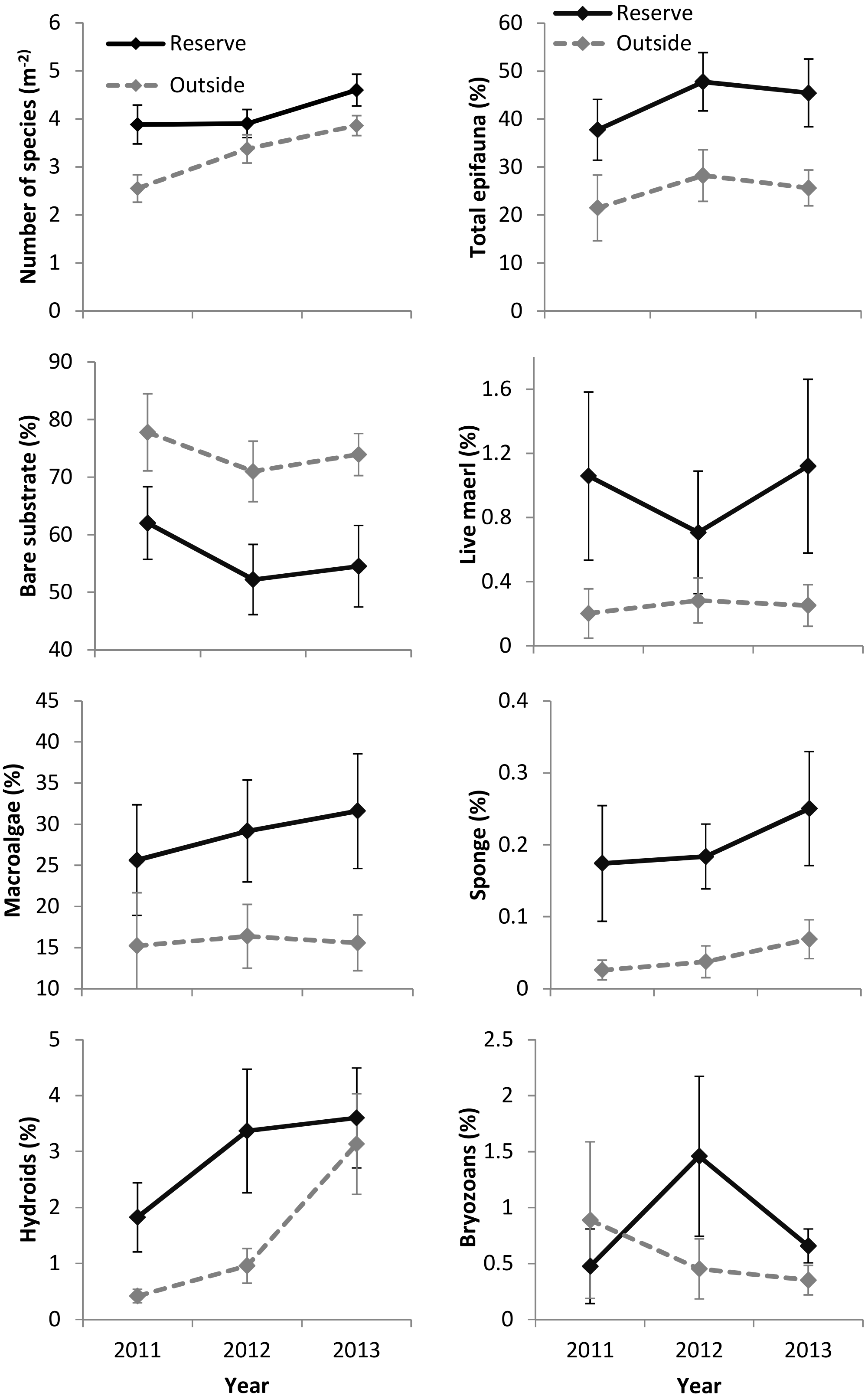

Fig. 3. The mean number of species recorded per m^2 and percentage cover of the seafloor by different epifaunal assemblages recorded by photoquadrat surveys across three years. Error bars represent ±1 SE.

Table 2. Results from the PERMANOVA+ analysis of epibenthic community composition. a) Main test and b) pairwise testing for the interaction Protection x Depth. Pr = level of protection, De = depth, Ye = year, Su = substrate, Out = sites outside the reserve, Res = sites within the reserve.

a)

Source	*df*	SS	MS	*F*	*P*
Pr	1	7549.2	7549.2	3.28	*0.001
De	1	26222	26222	11.4	*0.001
Ye	2	11581	5790.3	2.51	*0.002
Su	2	14321	4680.1	0.48	0.576
PrxDe	1	7826.7	7826.7	3.4	*0.002
PrxYe	2	5011.8	2505.9	1.08	0.356
PrxSu	2	4625.1	2762.6	0.99	0.45
DexYe	2	4505.1	2252.6	0.97	0.46
DexSu	2	4115.1	2992.2	0.98	0.47
YexDe	3	5175	1725.1	0.97	0.492
YexSu	6	1031	1719.4	0.96	0.562

b)

	Shallow		**Deep**	
Groups	t	*P*	t	*P*
Out, Res	2.4	*0.001	1.09	0.285

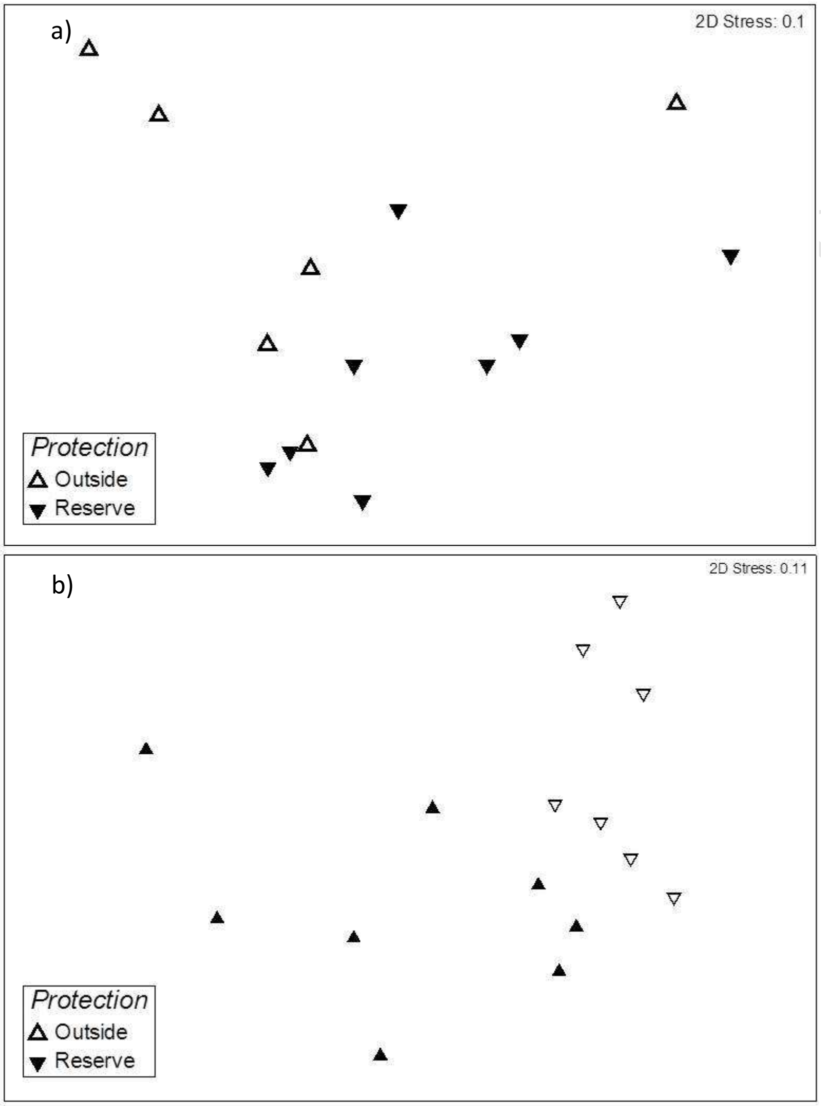

Fig. 4. nMDS plots illustrating similarities in epibenthic assemblages between shallow sites (< 15 m depth) within and outside the marine reserve sampled in 2011 (a) and 2013 (b).

SIMPER analysis also found strong differences between the reserve and outside (Table 3). Sites were characterised by a similar range of species, however, sites within the reserve were characterised more strongly by bushy red seaweeds (*Heterosiphonia plumose*), kelps (*Lamanaria saccharina* and *Lamanaria hyperborea*), thin branching brown seaweeds, and upright hydroids (*Nemertesia antennia*), whereas sites outside the reserve were characterised more strongly by red algal turf and burrowing anemones (*Cerianthus lloydi*). Overall, 91.6% of variation within the epibenthic community situated in the reserve was characterised by 10 species, whilst 91.8% of the community outside the reserve was characterised by just 7.

Table 3. Results from the SIMPER analysis of epibenthic communities sampled in shallow sites within and outside the marine reserve in 2013. This analysis was conducted after a PERMANOVA+ indicated an interaction between protection and depth (see Table 2).

Treatment	Taxon	Average abundance	% contribution	Cumulative %	Overall similarity
Outside	Red algal turf	5.36	30.13	30.13	34.38
	Heterosiphonia japonica	3.85	20.85	50.98	
	Cerianthus lloydi	4.43	15.45	66.44	
	Filamentous brown seaweeds	2.49	12.31	78.74	
	Laminaria saccharina	1.87	8.47	87.22	
	Laminaria hyperborea	1.04	2.68	89.89	
	Dark encrusting reds	2.07	1.92	91.81	
Reserve	*Heterosiphonia japonica*	20.1	40.43	40.43	42.26
	Filamentous brown seaweeds	7.24	16.11	56.54	
	Laminaria saccharina	6.64	8.7	65.24	
	Nemertesia antennia	7.17	5.78	71.02	
	Heterosiphonia plumosa	4.98	4.87	75.88	
	Laminaria hyperborea	3.42	3.94	79.82	
	Dark encrusting reds	1.61	3.72	83.54	
	Red algal turf	3.54	3.04	86.58	
	Thin branched browns	2.99	2.85	89.43	
	Cerianthus lloydi	3.94	2.22	91.64	

3.2. Composition of Benthic Megafauna

A total of 50 different benthic megafaunal species were recorded from the dive transects. There was no relationship between depth and the total number of species, number of individuals, Pielou's evenness and Shannon's Diversity Index (Pearson's Correlation; r^2 = -0.1-0.1; N = 87; $P > 0.05$). Likewise, there was no difference in the total number of species, diversity or evenness between substrate types (One-way ANOVA; $F_{(1, 131)}$ =1.5-3.5, $P > 0.05$). However, hard substrates did contain significantly more individuals (One-way ANOVA; $F_{(1, 87)}$ = 6.3, $P < 0.05$).

Overall, the 10 most abundant species in descending order were hermit crabs (*Pagurus* spp), feather stars (Crinoidea), harbour crabs (*Liocarcinus depurator*), king scallops (*Pecten maximus*), common starfish (*Asterias rubens*), parchment worms (*Chaetopterus* spp), queen scallops (*Aequipecten opercularis*), cushion stars (*Porania pulivillus*) and decorator crabs (*Macropodia* spp). As the population dynamics of king and queen scallops have already been explored in depth by parallel studies (see Howarth et al., 2011, 2015), the dynamics of the 11th and 12th most abundant species were explored in their place (respectively, these were the spiny starfish, *Marthasterias glacialis,* and the eyelash worm, *Myxicola infundibulum*). Separating these taxa into mobile and sessile groups revealed little difference in the abundance of mobile megafauna between the reserve and outside, and over time (Fig. 5a). In contrast, both feather stars and eyelash worms were significantly more abundant within the reserve than outside (Table 4), and although their abundance appeared to increase over the survey period (Fig. 5b), no significant interaction was found between year and protection. However, the total number of megafauna species did significantly increase during the study period and was significantly greater within the reserve than outside (Table 4). Two-way ANOVAs also revealed that year significantly influenced the abundance of harbour crabs, spiny starfish and the total number of species (Table 4) but that year, protection and the interaction between the two were not significantly influencing the total number of individuals, evenness and biodiversity (Table A.6).

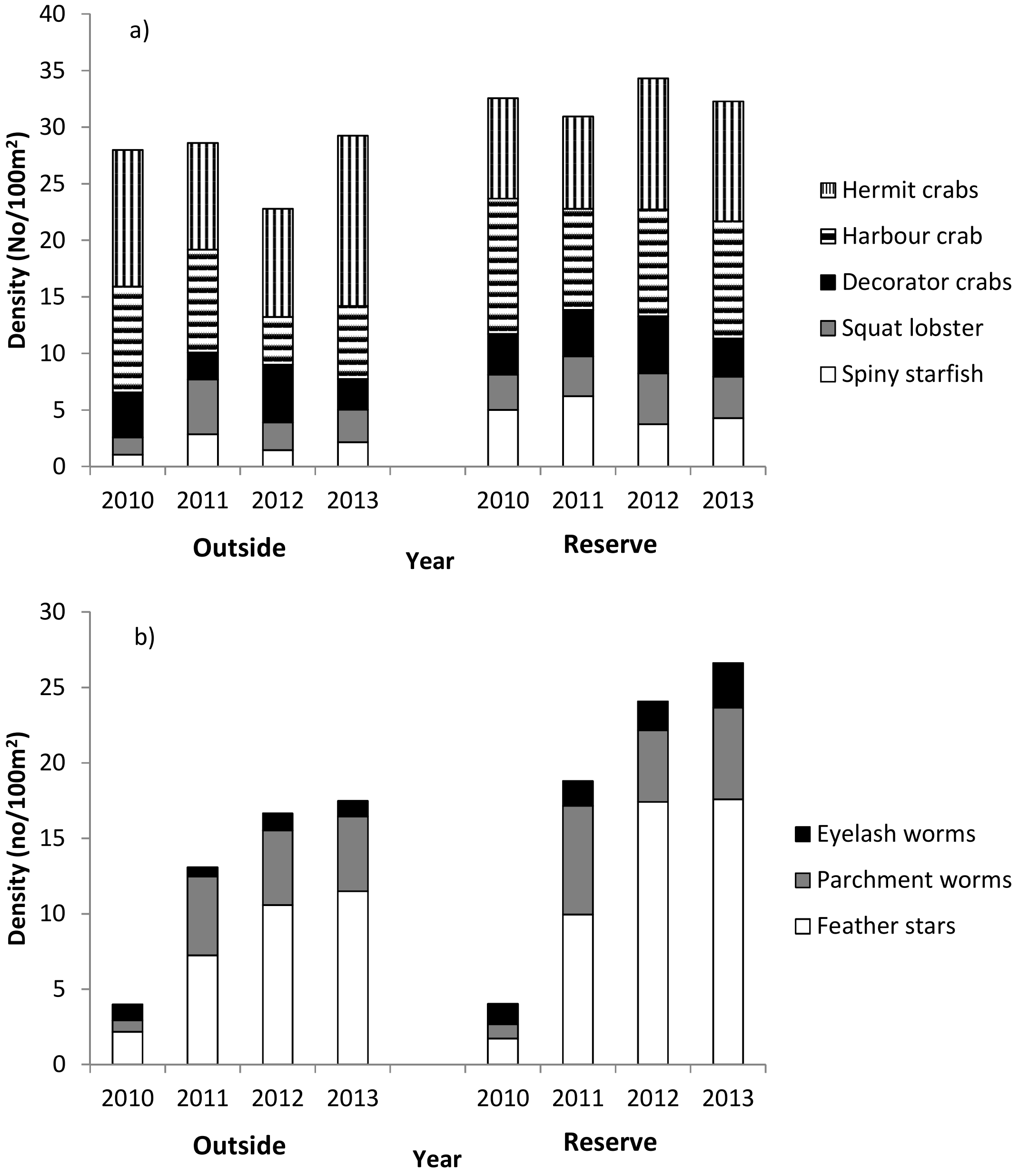

Fig. 5. The density (mean no./100m2) of the 10 most abundant benthic megafaunal species across the years 2010-2013 split between mobile (a) and sessile (b) species.

Table 4. Two-way ANOVA comparing the density of different benthic fauna between the marine reserve and outside across the years 2010-2013. Adjusted critical values obtained from FDR are shown in bold Significant results are denoted by (*).

Source	Test	SS	*df*	MS	*F*	*P*	**FDR α**
Feather stars	Year	711.5	1	711.5	0.6	0.103	**0.06**
	Protection	7498.4	3	2499.5	2.1	*0.041	
	Year * Protection	525.6	3	175.2	0.15	0.931	
	Residual	146213.4	123	1188.7			
Eyelash worms	Year	73.4	1	73.4	5.35	0.494	**0.055**
	Protection	33.0	3	11	0.8	*0.022	
	Year * Protection	27.1	3	9	0.66	0.579	
	Residual	1686.7	123	13.7			
Parchment worms	Year	5.1	1	5.1	0.14	*0.002	**0.05**
	Protection	1677.4	3	559.1	15.14	0.711	
	Year * Protection	71.7	3	23.9	0.65	0.586	
	Residual	4542.5	123	36.9			
Harbour crabs	Year	610.2	1	610.19	8.51	*0.004	**0.045**
	Protection	593.8	3	197.95	2.76	0.551	
	Year * Protection	261.3	3	87.09	1.21	0.308	
	Residual	8823.7	123	71.74			
Decorator crabs	Year	24.0	1	24.01	1.31	0.255	**0.04**
	Protection	254.3	3	84.7567	4.609194	0.104	
	Year * Protection	50.3	3	16.78	0.91	0.437	
	Residual	2261.8	123	18.39			
Spiny starfish	Year	625.6	1	625.63	18.41	*0.001	**0.035**
	Protection	137.4	3	45.79	1.35	0.262	
	Year * Protection	46.0	3	15.35	0.45	0.717	
	Residual	4180.9	123	33.99			
Diversity	Year	0.0	1	0.00	0.01	0.939	**0.03**
	Protection	1.1	3	0.38	3.38	0.12	
	Year * Protection	0.1	3	0.02	0.20	0.894	
	Residual	13.8	123	0.11			
No of species	Year	55.1	1	55.1	5.7	*0.018	**0.025**
	Protection	436.9	3	145.6	15.06	0.101	
	Year * Protection	11.2	3	3.7	0.39	0.764	
	Residual	1189.2	123	9.7			

PERMANOVA+ analysis revealed the composition of the benthic megafauna community to significantly differ between depths, year and substrates but not between levels of protection (Table 5). The interaction between protection and substrate was also found to be significant, and subsequent pairwise testing revealed that differences between the reserve and outside existed for maerl, soft and hard substrates. However, further exploration of these differences using nMDS and SIMPROF did not clearly distinguish between sites located within and outside the reserve ($P > 0.05$). Although, SIMPER did suggest that maerl, soft and hard substrates within the reserve were more strongly characterised by eyelash worms and feather stars.

Table 5. Results from the PERMANOVA+ analysis of benthic megafaunal community composition. a) Main test and b) pairwise testing for the interaction Protection x Substrate. Pr = level of protection, De = depth, Ye = year, Su = substrate, Out = sites outside the reserve, Res = sites within the reserve.

a)

Source	*df*	SS	MS	*F*	*P*
Pr	1	1908.2	1908.2	1.07	0.382
Ye	3	13076	4358.8	2.45	*0.001
De	1	6393.1	6393.1	3.60	*0.001
Su	2	10692	5346.1	3.01	*0.001
PrxYe	3	5284.8	1761.6	0.99	0.488
PrxDe	1	1661.3	1661.3	0.94	0.503
PrxSu	2	5476.3	2738.2	1.54	*0.039
YexDe	3	5175.3	1725.1	0.97	0.492
YexSu	6	10316	1719.4	0.97	0.562
DexSu	2	5466.8	2733.4	1.54	0.054

b)

	maerl		**soft**		**hard**	
Groups	t	*P*	t	*P*	t	*P*
Out, Res	1.3	*0.08	1.5	*0.009	1.4	*0.044

3.3. Composition of Fish Assemblages

A total of 1447 individual fish were recorded from the BRUV surveys, these were from 30 different species belonging to 14 different families. Of these individuals, 803 were recorded within the reserve and 644 from outside. Despite more individuals being recorded within the reserve, neither year (Two-way ANOVA; $F_{(1, 82)} = 1.6$, $P > 0.05$) nor protection (Two-way ANOVA; $F_{(1, 82)} = 2.7$, $P > 0.05$) significantly influenced fish abundance (MaxN). Overall, the most common species were all gadoids of which cod were the most abundant (408 observations), followed by whiting (303 observations) and haddock (163 observations). Over 98% of these gadoids were in their juvenile form. In rare cases (4 out of the 82 BRUV surveys), large pelagic shoals of mackerel and sand eels consisting of many hundreds of individuals were recorded.

One-way ANOVAs revealed that the size of individuals was not significantly different between the reserve and outside for cod (One-way ANOVA; $F_{(1, 146)} = 2$, $P > 0.05$), other gadoids (One-way ANOVA; $F_{(1, 146)} = 0.6$, $P > 0.05$), flat fish (One-way ANOVA; $F_{(1, 146)} = 0.2$, $P > 0.05$), and dog fish (One-way ANOVA; $F_{(1,\ 146)} = 0.6$, $P > 0.05$). This analysis could not be carried out for gurnards, wrasse and gobies as the sample size was too low. Comparing the abundance of different taxa over time also revealed little difference between the reserve and outside (Fig. 6). Cod abundance did exponentially and significantly increase over the study period, but did not significantly differ between the reserve and outside, nor was there an interaction between those two factors (Table 6). In contrast, the abundance of other gadoids appeared to increase outside the reserve over time and decrease inside. However, neither year, nor protection, nor the interaction between the two, were significant.

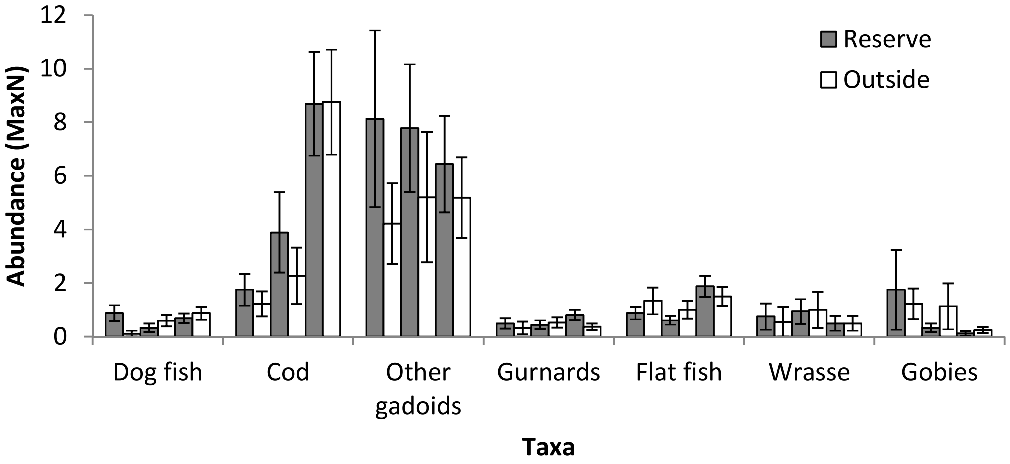

Fig. 6. The abundance of a range of fish taxa within and outside the marine reserve across the years 2011-2013. For each taxa, the year increases from 2011, to 2012 and 2013 going from the left to the right.

Table 6. Two-way ANOVA comparing the abundance of cod and other gadoids between the reserve and outside over the years 2011-2013. Significant terms are denoted by (*).

Source	Test	SS	*df*	MS	*F*	*P*
Other gadoids	Year	7.4	2	3.7	0.06	0.946
	Protection	123.6	1	123.6	1.85	0.177
	Year * Protection	20.3	2	10.2	0.15	0.859
	Residual	5068.3	76	66.7		
Cod	Year	772.5	2	386.2	10.59	*0.001
	Protection	9.0	1	9.0	0.25	0.621
	Year * Protection	11.7	2	5.9	0.16	0.852
	Residual	2772.2	76	36.5		

As gadoids are of commercial importance and were the most abundant fish species recorded throughout the BRUV surveys, GLMs were constructed to determine what environmental and benthic factors were important in determining their abundance and distribution. After employing backward-forward stepwise reduction, models indicated that cod abundance was significantly positively associated with year and with the presence of macroalgae and maerl, but was negatively associated with the presence of anemones and echinoderms (Table 7). In contrast, the abundance of other gadoid species was found to be positively associated with the percentage cover of bare substrate, year, treatment and crustacean abundance, but negatively associated with the presence of sponges. A GLM including macroalgae, but excluding depth and the percentage cover of bare substrate, could not be constructed for other gadoid species as the model would not converge, likely because it had insufficient predictive power. In all cases, the reduced models did not explain significantly less variance than the full models (Pearson's Chi-squared; df = 81, $\chi^2 = 0.78$, $P > 0.05$).

Table 7. The reduced models created from negative binomial GLMs to test whether environmental and benthic data reflected the distribution and abundance of cod and other gadoid species. Also shown are the response variables tested, and the combination of predictor variables used to construct the GLMs. Significant terms are denoted by (*).

Response variable	Predictor variables	Deviance explained	Variable	SE	*Z*	*P*
Cod	Included macroalgae, excluded bare substrate and depth	60.43%	Year	0.24	5.63	*0.001
			Anemones	0.12	-2.29	*0.022
			Echinoderm	0.5	-2.3	*0.019
			Macroalgae	0.28	1.87	*0.041
			Maerl	0.1	2.72	*0.006
Cod	Included bare substrate and depth, excluded macroalgae	71.40%	Year	0.25	5.09	*0.001
			Bare substrate	0.01	-0.48	0.632
			Protection	0.21	0.435	0.664
			Crustacean	1.13	1.09	0.273
			Sponge	0.84	-1.6	0.11
Other gadoids	Included bare substrate and depth, excluded macroalgae	68.53%	Year	0.16	4.51	*0.001
			Bare substrate	0.01	3.7	*0.001
			Protection	0.14	2.91	*0.003
			Crustacean	0.73	3.04	*0.002
			Sponge	0.55	-3.16	*0.001

4. Discussion

Our study highlights a number of differences in ecological communities between the fully protected marine reserve in Lamlash Bay and neighbouring fishing grounds. However, before we discuss our results, it must be stressed that there is no data available prior to the establishment of the reserve. Ideally, a before-after control-impact (BACI) approach would have been employed, capable of demonstrating that differences between the reserve and outside were due to the protection afforded by the marine reserve (Hilborn et al., 2004; Sale et al., 2005). As this was not possible, we instead compared sites within the reserve to reference sites located outside its boundaries over a study period of three to four years, in order to test for increased rates of recovery within the reserve over time. As almost all the trends explored in this study showed no interaction between year and protection, we have evidence that differences between the reserve and outside exist, but in most cases we cannot definitively conclude that protection was responsible for creating them. Importantly, however, protection within the reserve is highly likely to be helping to maintain any pre-existing differences between the two areas.

Overall, we found a large number of differences between the marine reserve and outside. Four years after its establishment, live maerl (348% greater), macroalgae (100% greater), sponges (268% greater), hydroids (15-267% greater), eyelash worms (184% greater), feather stars (52% greater), parchment worms (36% greater) and total epifauna (77% greater) were all found to be significantly more abundant within the reserve than on neighbouring fishing grounds. Although the abundance of macroalgae, sponges, hydroids and eyelash worms appeared to steadily increase within the reserve over the duration of the study, no significant interaction between year and protection was found. Likewise, nMDS plots and SIMPER analysis suggested an increasing divergence between the epifaunal community within and outside the reserve, but again no significant interaction was found.

The greater abundance of macroalgae within Lamlash Bay Marine Reserve was one of the first observations made when monitoring began in 2010 (Howarth et al., 2011). Several well-known studies have also reported differences in macroalgal abundance between reserves and reference sites (Hawkins and Roberts 2004; Langlois and Ballantine, 2005; Shears and Babcock, 2003). In these cases, differences were due to populations of predators and herbivores recovering within marine reserves, thereby altering the grazing rates on macroalgae. On the other hand, our study did not detect any major changes in herbivore or predator abundance other than for juvenile cod, which exponentially increased in both the reserve and outside over the three year study period. However, as the diet of juvenile cod consists predominantly of copepods and other planktonic crustaceans (Demain et al., 2011) there is unlikely to be any connection between their abundance and the prevalence of macroalgae. Notably, an associated study (Howarth et al., 2015) found that the greater abundance of macroalgae and hydroids growing within Lamlash Bay Marine Reserve significantly increased the settlement levels of juvenile scallops by providing nursery habitat. These results are therefore consistent with the hypothesis that protection can encourage seafloor habitats to recover which can generate benefits that flow back to commercially important species. In the long term, these effects should increase the numbers of juvenile scallops entering the adult stock as a greater proportion of juveniles survive to reach maturity (Beukers-Stewart et al., 2003; Vause et al., 2007).

It is interesting that live maerl was over 300% more abundant within the reserve, as evidence suggests that recovery of maerl beds should take several decades, due to their extremely slow growth (Foster, 2001; Giraud and Cabioch, 1976; Grall and Hall-Spencer, 2003; Hall-Spencer and Moore, 2000; Kamenos et al., 2003;). As the abundance of live maerl showed no clear signs of increasing over the study period, the greater levels of maerl within the reserve may just be an artefact of maerl being more prevalent within the reserve than outside prior to its establishment. In addition, the abundance of live maerl was very low throughout both study areas, varying between 0 - 8%. These low levels of live maerl contrast greatly with earlier studies of Lamlash Bay (Kamenos et al., 2004c), which detected over 90% live maerl in some maerl beds, suggesting recent degradation in their health. Nonetheless, the reserve should act as a safe haven for any patches of live maerl remaining within the reserve and may encourage their recovery in the future. However, given the slow growth rates of maerl, such recovery may be a lengthy process.

In addition to observing differences in specific species, there were also a number of differences in the overall epifaunal community between the reserve and outside. Four years after the reserve was established, PERMANOVA+ analysis revealed strong differences in community composition between the two treatments for sites less than 15 m in depth. Shallow sites within the reserve were more strongly characterised by a range of bushy and upright seaweeds and hydroids, whereas sites outside the reserve were more strongly characterised by red algal turf and fast-growing burrowing anemones. Sites outside the reserve are therefore likely to be providing comparatively less structural complexity and may, in turn, be providing a smaller range of physical niches. However, despite observing broad differences in epifaunal communities, there was no difference in overall community evenness and diversity, or in the abundance of soft coral, anemones, bryozoans and tunicates.

Considering that physical properties and sediment characteristics are regularly cited to be a major factor in influencing the structure of benthic communities (Gray, 1981; Seider and Newell, 1999; van Dalfsen et al. 2000), it was surprising that there was no difference in the community composition of epibenthic communities between different substrate types.

However, this lack of variation could be a consequence of grouping sites into substrate categories that were too broad (i.e. maerl, soft and hard substrates). This approach was used as sites were grouped together based on visual inspection of the substrate, rather than Particle Size Analysis (e.g. Bath and Flippen, 1995). The latter would have been able to separate sites to a much higher resolution with a higher degree of confidence, but was unfortunately beyond the scope of this study. Then again, the physical properties of sites was found to be significantly influencing the epifaunal communities in other ways. Sites composed predominantly of maerl substrates contained both a higher number of species and percentage cover of epifaunal taxa compared to other substrates. This was not considered unusual as maerl beds are renowned for their high diversity of flora and fauna (Steller et al., 2003; Kamenos et al., 2004a). Also of interest was that the total number of species and percentage cover by all epifaunal taxa combined were both negatively correlated with depth. This was likely a result of shallow sites being dominated by a wide range of kelp and seaweed species, the abundance of which naturally declined with increasing depth.

In contrast with the epifaunal community, comparisons between the reserve and outside in the abundance of mobile benthic fauna revealed little difference. This was unexpected considering the number of studies that have reported changes in the abundance of scavengers and predators, such as dog fish and star fish, in response to protection (Brown, 2013; Marino et al., 2007) and differing levels of fishing disturbance (Craven et al., 2013; Bradshaw et al., 2001; Jenkins et al., 2004; Kaiser and Hiddink, 2007; Veale et al., 2000). However, comparisons of the abundance of sessile fauna did reveal several differences between the reserve and outside. Both feather stars and eyelash worms were found to strongly characterise communities sampled within the marine reserve. This was because they were 52% and 184% more abundant within the reserve than outside respectively, although again, no significant interaction between protection and year was found. These organisms can be important to benthic diversity and commercially valuable species as they provide structural complexity to the seabed, and they can modify local hydrodynamics and influence the vertical and horizontal flux of nutrients (Auster et al., 1995; Thrush et al., 2001; Thrush and Dayton 2002).

Compared to other taxa, relatively few trends were detected in fish populations. The most common fish species were all gadoids, a group containing commercially important species such as cod, haddock and whiting. Over 98% of these individuals were in their juvenile form, suggesting that Lamlash Bay is providing nursery habitats to several commercially important species. This was confirmed by constructing several models, which found cod abundance to be positively associated with the presence of macroalgae, live maerl and year of study. In some respects this came as no surprise, as coastal areas containing high levels of kelp, seaweeds and maerl are often reported to support large numbers of juvenile cod (Borg et al., 1997; Caddy, 2013; Gibb et al., 2007; Kamenos et al., 2004c; Laurel et al., 2009). Although cod abundance appeared greater within the reserve than outside, this difference was not statistically significant. Likewise, there were no significant differences in mean fish size between in and outside of the reserve. Nonetheless, in protecting macroalgal and maerl beds, the marine reserve should, to some degree, help boost the early survival of juvenile cod as they make the important transition from pelagic to benthic habitats (Demain et al., 2011). Cod abundance was also found to increase exponentially over the survey period both within and outside the reserve, and is thought to be the result of exceptionally cold winter temperatures in recent years (Sophie Elliott, University of Glasgow, pers. comm). In contrast to cod, models found the abundance of haddock and whiting to be positively associated with the percentage cover of bare substrate, crustacean abundance, and level of protection (an artefact of more gadoids being detected within the reserve). This was supported by diver observations which regularly reported high levels of whiting and haddock on deep soft / muddy sediments. Stocks of adult finfish (especially cod and other gadoids) are currently at historically low levels in the Clyde (Heath and Speirs 2011; McIntyre et al., 2012; Thurstan and Roberts 2010). Hence, an important area for future research is to establish the origin of these gadoid recruits and whether they are contributing to the recovery of stocks. Unfortunately, there are strong indications that high levels of by-catch from the Clyde *Nephrops* trawl fishery may limit the chances of these fish reaching maturity (Bergman et al., 2002).

One of the most commonly cited results of establishing MPAs and marine reserves has been an increase in fish abundance, biomass and size (Hawkins and Roberts, 2004; Lester et al., 2009; Micheli et al., 2004; Moland et al., 2013; Mumby et al., 1995;). However, this study found no statistical difference in fish abundance between the reserve and outside. This was likely due to the young age of the reserve (5 years) and its small size (2.67km^2), both of which are known to reduce the effects of marine reserves on mobile fish species (Edgar et al., 2014; Halpern, 2003; Molloy et al., 2009), and the generally low abundance of fish (particularly adults) in the area (see earlier references). Additionally, when analysing the BRUV footage it was not possible to recognise repeated entrances of the same individual, meaning estimators of abundance had to be used; in this case, the maximum number of fish sighted within a single frame (MaxN). As it is unlikely that all individuals of a species are recorded within the same frame, BRUVs can only detect a proportion of the fish that are attracted to the bait, which can make their estimates relatively conservative (Cappo et al., 2004; Willis and Babcock, 2000). This means that any differences detected between sites within and outside MPAs are also likely to be conservative. More worryingly, recent research has shown in some areas there is little correlation between the abundance estimates generated by MaxN and those created from underwater visual census (Dunlop, 2013). Our study also revealed no difference in fish size between the reserve and outside. Again this may be due to the age and size of the reserve, or the method we used to estimate fish size. The use of recently developed technologies, such as stereo video cameras would have generated much more accurate and precise estimates of fish size than those obtained in this study, which would reduce variation and increase the chance of detecting differences in fish size, if they exist (Cappo et al., 2004; Harvey et al., 2001; Langlois et al., 2010).

In summary, epifaunal assemblages, such as feather stars, eyelash worms, maerl, sponges, hydroids and macroalgae were all found to be significantly more abundant within the reserve than outside. As well as increasing the structural complexity of the seabed, the greater abundance of these habitats has substantially increased the recruitment of commercially important scallops (Howarth et al., 2015), suggesting that protecting areas from fishing can generate ecological benefits that flow back to species commercially targeted by fisheries. In contrast, there was no difference in the abundance of mobile benthic fauna and fish populations between the reserve and outside. This may be due to the short duration of protection received to date, the small size of the reserve, and / or the methods used to estimate the abundance and size of fish. Nonetheless, it was revealed that the marine reserve contained significantly more nursery habitat for juvenile cod, which may help boost their early survival as they make the important transition from pelagic to benthic habitats.

The relative scarcity of studies on temperate MPAs (particularly highly protected ones) has been used as an argument against their implementation (reviewed in Caveen et al. 2013; Roberts et al. 2005). This study joins a growing band which indicates MPAs can indeed provide both conservation and fisheries benefits in temperate waters, but suggests recovery rates may be complicated and vary according to reserve size, duration of protection and species biology. These characteristics should be used to manage expectations and guide management objectives. Our results are therefore highly relevant to informing the design and implementation of MPAs in temperate areas, particularly as is currently taking place in European, and indeed UK waters.

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Appendices

Table A1. The depth below chart datum (BCD), substrate types, treatment and assigned category for each site surveyed in 2010. Sites highlighted in grey were located within the marine reserve.

Assigned Category	Treatment	Depth BCD (m)	Substrate types
Deep boulders	Out	23.1	Boulders, sand
	Out	24.5	Boulders, muddy sand
	Reserve	16.8	Boulders, sand
	Reserve	17	Boulders, muddy sand, dead maerl
	Reserve	19.1	Boulders, muddy sand
	Reserve	27	Boulders, muddy sand
	Reserve	28	Boulders, muddy sand, cobbles
Deep muddy sand	Out	16.75	Muddy sand
	Out	17.2	Muddy sand
	Out	18	Muddy sand
	Out	18	Muddy sand, dead maerl
	Out	19	Muddy sand
	Out	21	Muddy sand, pebbles, cobbles
	Out	21.9	Muddy sand
	Out	21.9	Muddy sand
	Out	22.4	Muddy sand
	Out	22.7	Muddy sand
	Out	22.7	Muddy sand
	Out	23.7	Muddy sand, pebbles, cobbles
	Reserve	18.7	Muddy sand, dead maerl
	Reserve	18.9	Muddy sand
	Reserve	19	Muddy sand, dead maerl
	Reserve	21.1	Muddy sand
	Reserve	23	Muddy sand, pebbles, cobbles
	Reserve	23.1	Muddy sand
Maerl	Out	15.1	Dead maerl, muddy sand
	Out	14.3	Dead maerl, muddy sand, pebbles
	Reserve	9.1	Dead maerl
	Reserve	10	Dead maerl
	Reserve	10.7	Dead maerl, muddy sand
	Reserve	12.5	Dead maerl, muddy sand
	Reserve	13.8	Dead maerl, sand, pebbles, boulders
Mud	Out	19	Mud
	Out	20.8	Mud
	Reserve	13.3	Mud
	Reserve	18.7	Mud
Shallow muddy sand	Out	11.8	Muddy sand
	Out	13.5	Muddy sand
	Reserve	15.5	Muddy sand, pebbles, cobbles
	Reserve	15.5	Muddy sand

Table A.2. The depth below chart datum (BCD), substrate types, treatment and assigned category for each site surveyed in 2011. Sites highlighted in grey were located within the marine reserve.

Assigned Category	Treatment	Depth BCD (m)	Substrate types
Deep boulders	Out	18.5	Boulders, sandy mud, pebbles
	Reserve	17	Boulders, muddy sand, cobbles
Deep muddy sand	Out	19.3	Muddy sand
	Out	16.48	Muddy sand
	Out	17	Muddy sand, dead maerl
	Out	22.8	Muddy sand, cobbles
	Out	21.5	Muddy sand, pebbles
	Reserve	19	Muddy sand
	Reserve	17.4	Muddy sand
	Reserve	20.8	Muddy sand, cobbles
Maerl	Out	8	Dead maerl
	Out	10.7	Dead maerl
	Reserve	6.8	Dead maerl, sand
	Reserve	11.2	Dead maerl, muddy sand
	Reserve	8.45	Dead maerl, muddy sand
Mud	Out	24	Mud
	Reserve	15.6	Fine muddy sand
Shallow boulders	Out	14.35	Boulders, muddy sand, cobbles
	Out	15.4	Boulders, muddy sand, dead maerl
	Reserve	13.8	Boulders, muddy sand, pebbles
	Reserve	15.2	Boulders, dead maerl
	Reserve	10.8	Boulders, sand, dead maerl, cobbles
Shallow muddy sand	Out	11.6	Muddy sand, pebbles
	Out	15.2	Muddy sand, pebbles
	Out	15	Muddy sand, pebbles
	Reserve	11.25	Muddy sand, cobbles
	Reserve	15.2	Muddy sand, dead maerl
	Reserve	15.1	Muddy sand

Table A.3. The depth below chart datum (BCD), substrate types, treatment and assigned category for each site surveyed in 2012. Sites highlighted in grey were located within the marine reserve.

Assigned Category	Treatment	Depth BCD (m)	Substrate types
Deep boulders	Out	20	Boulders, sand
	Out	18.5	Boulders, sand, dead maerl
	Out	18.5	Boulders, sand
	Reserve	27.5	Boulders, muddy sand, dead maerl
	Reserve	20.2	Boulders, muddy sand, pebbles
	Reserve	17.35	Boulders, sandy mud
Deep muddy sand	Out	16.1	Muddy sand
	Out	23.4	Muddy sand, pebbles, cobbles
	Out	21.3	Muddy sand
	Out	24.5	Muddy sand
	Reserve	18.6	Muddy sand
	Reserve	18	Muddy sand, pebbles
	Reserve	19	Muddy sand
	Reserve	22.5	Muddy sand, pebbles, cobbles
	Reserve	21.4	Muddy sand
Maerl	Out	13.8	Dead mearl, muddy sand, boulders
	Out	12.7	Dead maerl, sand
	Out	11.5	Dead maerl
	Reserve	9.2	Dead maerl, sand
	Reserve	14.1	Dead maerl
	Reserve	10	Dead maerl, sand, pebbles
Shallow boulders	Out	14.4	Boulders, muddy sand
	Out	14.9	Boulders, muddy sand
	Reserve	11.8	Boulders, muddy sand, dead maerl
	Reserve	14.9	Boulders, muddy sand, dead maerl
Shallow muddy sand	Out	13.6	Muddy sand, pebbles
	Out	14.2	Muddy sand
	Out	12	Muddy sand, cobbles, lebbles
	Reserve	13.3	Muddy sand, pebbles
	Reserve	14	Muddy sand, dead maerl
	Reserve	15.2	Muddy sand

Table A.4. The depth below chart datum (BCD), substrate types, treatment and assigned category for each site surveyed in 2013. Sites highlighted in grey were located within the marine reserve.

Assigned Category	Treatment	Depth BCD (m)	Substrate types
Deep Boulders	Out	22.15	Boulders, muddy sand, pebbles
	Out	20.25	Boulders, muddy sand, pebbles
	Reserve	22.65	Boulders, cobbles, muddy sand
	Reserve	27.6	Boulders, muddy sand, pebbles
Deep muddy sand	Out	16.55	Muddy sand, cobbles
	Out	18.65	Muddy sand, cobbles, dead maerl
	Out	23.35	Muddy sand
	Out	15.45	Muddy sand, pebbles
	Out	15.7	Muddy sand
	Out	20	Muddy sand
	Reserve	18.7	Muddy sand
	Reserve	18.7	Muddy sand
	Reserve	19.05	Muddy sand
	Reserve	16.2	Muddy sand
	Reserve	18.15	Muddy sand, cobbles
	Reserve	24.05	Muddy sand
Maerl	Out	10.2	Dead maerl
	Out	8.95	Dead maerl
	Reserve	8.7	Dead maerl
	Reserve	10.4	Dead maerl
Shallow muddy sand	Out	13.75	Muddy sand, dead maerl
	Out	9.8	Muddy sand, pebbles
	Out	8.9	Muddy sand
	Out	13.8	Muddy sand
	Reserve	12.75	Muddy sand, cobbles
	Reserve	12.5	Muddy sand
	Reserve	13.25	Muddy sand
	Reserve	13.85	Muddy sand
Shallow Boulders	Out	12.85	Boulders, sand
	Out	10.35	Boulders, sand
	Reserve	11.45	Boulders, sand
	Reserve	15.05	Boulders, muddy sand

Table A.5. Two-way ANOVA comparing percentage cover by different epifaunal assemblages, as well as Pielou's Evenness and Shannon's Diversity Index, between the marine reserve and outside across the years 2011-2013.

Source	Test	SS	*df*	MS	*F*	*P*
Soft coral	Year	0.003	1	0.003	0.403	0.527
	Protection	0.016	2	0.031	4.344	0.16
	Year * Protection	0.002	2	0.001	0.112	0.894
	Residual	0.58	82	0.007		
Worms	Year	0.576	1	22.212	2.904	0.271
	Protection	0.91	2	1.584	17.509	0.214
	Year * Protection	0.886	2	4.599	0.34	0.861
	Residual	201.48	82	0.25		
Anemones	Year	22.212	1	22.212	0.517	0.474
	Protection	84.89	2	42.445	0.988	0.377
	Year * Protection	0.991	2	0.496	0.012	0.989
	Residual	354.091	82	42.977		
Bryozoans	Year	1.961	1	1.961	0.786	0.378
	Protection	3.168	2	1.584	0.635	0.533
	Year * Protection	6.986	2	3.493	1.4	0.252
	Residual	204.563	82	2.495		
Tunicates	Year	0.001	1	0.476	1.904	0.171
	Protection	9.198	2	4.599	18.409	0.12
	Year * Protection	0.12	2	0.01	0.04	0.961
	Residual	20.487	82	0.25		
Eveness	Year	10.45	1	0.574	2.013	0.845
	Protection	12.1	2	4.644	16.112	0.775
	Year * Protection	0.554	2	0.04	0.008	0.901
	Residual	19.66	82	0.55		
Diversity	Year	8.62	1	0.866	1.804	0.15
	Protection	3.64	2	5.669	21.21	0.12
	Year * Protection	10.98	2	0.04	0.18	0.864
	Residual	25.41	82	0.21		

Table A.6. Two-way ANOVA comparing the univariate measures of benthic megafauna abundance between the marine reserve and outside across the years 2010-2013.

Source	Test	SS	*df*	MS	*F*	*P*
No of individuals	Year	551.521	1	551.521	0.18	0.670
	Protection	23555.904	3	7851.968	2.59	0.056
	Year * Protection	9062.647	3	3020.882	0.99	0.396
	Residual	372463.157	123	3028.156		
Evenness	Year	0.000	1	0.00	0.01	0.924
	Protection	0.001	3	0.00	0.04	0.991
	Year * Protection	0.002	3	0.00	0.06	0.981
	Residual	1.390	123	0.01		
Diversity	Year	0.001	1	0.00	0.01	0.939
	Protection	1.138	3	0.38	3.38	0.120
	Year * Protection	0.068	3	0.02	0.20	0.894
	Residual	13.793	123	0.11		

Highlights

- We explored the dynamics of benthic communities and fish populations within a fully protected marine reserve
- A combination of photo, video and diver surveys were employed
- After four years of protection, a number of sessile benthic organisms were more abundant within the reserve
- There was no difference in the abundance of mobile benthic fauna and fish
- This study provides evidence that fully protected marine reserves can encourage seafloor habitats to recover