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

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10 ABSTRACT

Despite recent efforts to increase the global coverage of marine protected areas (MPAs), 11 12 studies investigating the effectiveness of marine protected areas within temperate waters 13 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 14 ecosystem as a whole. This study therefore investigated the dynamics of both benthic 15 communities and fish populations within a recently established, fully protected marine reserve 16 17 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, 18 19 hydroids, feather stars and eyelash worms (Myxicola infundibulum) to be significantly more 20 abundant within the marine reserve than on surrounding fishing grounds. Likewise, the overall 21 composition of epifaunal communities in and outside the reserve was significantly different. 22 Both results are consistent with the hypothesis that protecting areas from fishing can 23 encourage seafloor habitats to recover. In addition, the greater abundance of complex habitats 24 within the reserve appeared to providing nursery habitat for juvenile cod (Gadus morhua) and 25 scallops (Pecten maximus and Aequipecten opercularis). In contrast, there was little difference 26 in the abundance of mobile benthic fauna, such as crabs and starfish, between the reserve and 27 outside. Similarly, the use of baited underwater video cameras revealed no difference in the 28 abundance and size of fish between the reserve and outside. Limited recovery of these 29 ecosystem components may be due to the relatively small size (2.67 km²) and young age of the 30 reserve (< 5 years), both of which might have limited the extent of any benefits afforded to 31 mobile fauna and fish communities. Overall, this study provides evidence that fully protected 32 marine reserves can encourage seafloor habitats to recover, which in turn, can create a 33 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

36

37 **1. Introduction**

38 Following a large number of recently established policies and initiatives, the global coverage of 39 marine protected areas (MPAs) is set to increase dramatically over the next decade (Metcalfe 40 et al., 2013). Globally agreed marine protection targets, such as the Convention on Biological 41 Diversity's (CBD) 'Aichi Target' are encouraging many governments to establish or expand 42 existing MPA networks within their jurisdictions (CBD, 2011; Harrop, 2011; Wood et al., 2008; 43 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 44 45 Protection of the Marine Environment of the North-East Atlantic), HELCOM (Helsinki 46 Commission) and Barcelona regional seas conventions, have all initiated the process of 47 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 48 Conservation Zones (MCZs; England, Wales and Northern Ireland) and Scottish MPAs 49 (Scotland) is leading to the creation of a network of MPAs around the United Kingdom (UK; 50 51 JNCC, 2013; Jones, 2012). All these measures intend to achieve a variety of management goals; 52 principally to conserve biodiversity and promote the sustainability of fisheries (Metcalfe et al., 53 2013; Pomeroy et al., 2005).

54 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 55 56 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., 57 58 2004; Zhou et al., 2010). To help guide these changes in management, it is important to better 59 understand how MPAs promote the process of recovery within marine ecosystems (Götz et al., 60 2013; Van Rein et al., 2009), particularly in temperate environments, which have been less 61 studied than tropical areas (Fenberg et al., 2012). Furthermore, out of the few studies 62 published on temperate MPAs, the majority have investigated changes in specific ecological or 63 fishery components rather than investigating the ecosystem as a whole; with many focussing 64 on either changes to seafloor habitats and benthic species (e.g. Beukers-Stewart et al., 2005; 65 Sheehan et al., 2013) or just species of commercial importance (e.g. Hoskin et al., 2011; 66 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.

70 Of all fishing methods, the use of mobile fishing gears, such as dredges and trawls, is 71 considered to be the most destructive to marine ecosystems (Collie et al., 2000; Kaiser et al., 72 2006). This is because they can cause substantial physical disruption of seafloor habitats by 73 ploughing sediments and damaging epifaunal organisms such as hydroids, bryozoans and 74 maerl beds (Dayton et al., 1995; Eleftheriou and Robertson, 1992; Jennings and Kaiser, 1998; 75 Jennings et al., 2001; Kaiser et al., 2000). However, these organisms are functionally important 76 to marine ecosystems as they provide an element of 3-dimensional structure to the seafloor. 77 In doing so, they supply important refuges for small / juvenile fish from predators and 78 unfavourable environmental conditions (Cacabelos et al., 2010; Monteiro et al., 2002; Ryer et 79 al., 2004), represent important feeding sites for fish and invertebrates (Bradshaw et al., 2003; 80 Warren et al., 2010) and provide essential habitat for the settlement of scallop spat and a 81 range of other organisms, including the settlement of further epifauna (Bradshaw et al., 2001; 82 Howarth et al., 2011; Howarth et al., 2015). Such locations are therefore often referred to as 83 "nursery habitats" as they tend to be highly productive, support high levels of juvenile density, 84 growth and survival, and contribute disproportionally to the production of adult recruits (Beck 85 et al., 2001; Gibb et al., 2007; Laurel et al., 2009). Commonly cited nursery habitats include 86 maerl (Phymatolithon calcareum) beds (Hall-Spencer et al., 2006; Kamenos et al., 2004a,b;), 87 seagrass beds (Warren et al., 2010) and areas of dense macrophytes / macroalgae (Cacabelos 88 et al., 2010; Christie et al., 2007; Howarth et al., 2011; Howarth et al., 2015), all of which have 89 been shown to harbour high densities of commercially exploited species such as spider crabs, 90 Maja squinado, juvenile cod, Gadus morhua, edible crab, Cancer pagurus, and edible sea 91 urchins, Echinus esculentus. Many epifaunal species also support unique micro-communities, 92 for example, caprellid amphipods on hydroids, the range of invertebrates associated with kelp 93 forests, or the diversity of organisms associated with pomatocerid tube worm heads (Airoldi et 94 al., 2008; Kaiser et al., 1999). Consequently, the damage sustained by nursery habitats from 95 fishing gears can dramatically reduce an area's capacity to support biodiversity and negatively 96 impact the recruitment of commercially important species (Bradshaw et al., 2001, 2003; Collie 97 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.,

100 2001; Craven et al., 2013). Survival rates of by-catch are often very low, with the majority 101 being discarded damaged, dying or dead (Beukers-Stewart et al., 2001; Jenkins et al., 2001; 102 Diamond and Beukers-Stewart, 2011;). In addition to the by-catch landed on deck, large 103 quantities of organisms are killed or damaged by passing gears but remain on the seafloor 104 uncaptured (Jenkins et al., 2001). Both of these impacts can cause a decline in the abundance 105 of target and non-target organisms (Currie and Parry, 1996; Bradshaw et al., 2001; Lambert et 106 al., 2011). Paradoxically, some species are attracted to areas that have been fished and 107 consequently increase in abundance. In disturbing the sediment, damaging / killing organisms 108 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 109 110 elevating predation pressure on the surrounding community (Jenkins et al., 2004; Ramsay and 111 Kaiser, 1998; Veale et al., 2000). Due to the dispersion of odour plumes, resettlement of 112 sediment and predation of damaged organisms, the high densities of scavengers gathering at 113 fishing grounds is likely to be a relatively short-lived event. Then again, Bradshaw et al., (2002) 114 found that the abundance of mobile, robust, and scavenging invertebrate species in the Irish 115 Sea had increased over a 60 year period of increasing fishing pressure, while slow-moving or 116 sessile, fragile taxa had decreased. Likewise, a study in the Isle of Man found the density of 117 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). 118

Since closing areas to fishing is the surest way of protecting marine ecosystems from the 119 120 physical impacts of fishing gears (Beukers-Stewart et al., 2005; Roberts et al., 2005), MPAs 121 should provide the best management tool available for encouraging their recovery. However, 122 the implementation of MPAs is still at a relatively early stage in most parts of the world, 123 including the UK (Fenberg et al., 2012; Metcalfe et al., 2013), and their effectiveness as a 124 fishery management tool remains highly debated (Boersma and Parrish, 1999; Jones, 2007; 125 Kaiser, 2004, 2005; Sciberras et al., 2013). This is partly because establishing MPAs can displace 126 fishing effort to surrounding areas (Bohnsack, 2000; Kaiser, 2005), which can cause wider 127 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 128 129 fishery benefits when these negative effects are adequately offset by increased recruitment 130 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

133 (Scotland) Act of 1984 (Axelsson et al., 2009). The Firth of Clyde, in which the Isle of Arran sits, 134 is known to be one of the most degraded marine environments in the UK, primarily due to 135 over a century of intensive fisheries exploitation (Howarth et al., 2013; Thurstan and Roberts, 136 2010). The marine reserve was therefore passed by Scottish parliament under the rationale 137 that the reduction in fishing pressure should help regenerate the local marine environment 138 and enhance commercial shellfish and fish populations. Hence, our study sought to investigate 139 changes in seabed habitats and species within the reserve and whether these changes have 140 had further effects on species of commercial importance. This was achieved by testing the 141 following hypotheses: (1) that the community composition of benthic assemblages within and 142 outside the reserve would increasingly diverge over time; (2) the abundance of benthic 143 organisms and fish would be greater within the reserve; (3) fish would be larger within the 144 reserve; (4) structurally complex habitats would be more abundant within the reserve; and (5) 145 fish assemblages would be positively related to the abundance of complex habitat. This was 146 achieved by conducting a series of quantitative diver visual, photo and video surveys within 147 and outside the reserve over a four-year period.

148 **2. Methods**

149 2.1.1. Study Area

We conducted our study in and around Lamlash Bay on the south-eastern shore of the Isle of 150 151 Arran, off the west coast of Scotland in The Firth of Clyde (Fig. 1). Lamlash Bay Marine Reserve 152 covers 2.67 km² (Thurstan and Roberts, 2010), with water depths ranging between 0 and 29 m 153 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 154 155 (Axelsson et al., 2009; Duncan, 2003) indicated a seabed of mixed sediments (i.e. mud, sand 156 and gravel with various proportions of shell) but that the central and southern regions of the 157 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 158 159 deterioration in their health (Howarth et al., 2011, 2015). Lamlash Bay marine reserve was 160 originally proposed by a local group of SCUBA divers that operated in the area. They proposed 161 Lamlash Bay as an ideal location for a marine reserve as it would be easy to delineate on a 162 map, and would be easy for fishermen to tell if they were within its boundaries. It was also 163 chosen to protect areas of maerl.

Unofficial observations made by the Community of Arran Seabed Trust (<u>www.arrancoast.com</u>)
 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).



172

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.

176 2.2. Data collection

177 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

181 more survey methods but reducing the number of study sites. Therefore, we surveyed 28 sites

182 in 2011, 31 sites in 2012, and 32 sites in 2013. Again, sites were divided so that half fell within 183 the boundaries of the marine reserve. Sites were chosen so that each one within the reserve 184 could be paired with at least one other suitable control outside, based on similar depth and 185 predominant substrate type (Table A.1-A.4). Due to lack of data and prior knowledge of the 186 area, the initial experimental design was relatively imbalanced. For example, 12 deep muddy 187 sand sites were surveyed outside the reserve in 2010 compared to just 6 inside. However, this 188 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 189 190 decompression limits after a 25 minute survey (i.e. <30m depth). Surveys were also conducted 191 parallel to depth contours to ensure the depth of a single survey did not change by more than 192 3 m.

193 Transects were surveyed along a 50 m leaded line laid out straight across the seabed. 194 Weighted anchors at each end held the line in place, in addition to two floating buoys which 195 reached the surface. A team of two divers then made their way from one end to the other, 196 recording the abundance of all megafauna (e.g. fish and crustaceans) encountered within 1.5 197 m either side of the transect, the width of which was marked by a 3 m long pole which the 198 divers pushed ahead of themselves This gave a total survey area of 150 m² for each dive 199 transect. After a surface interval of approximately two hours, divers returned to the transect 200 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 201 or the previous survey. The quadrat was divided into four 0.25 m² sub-quadrats which were 202 203 photographed from directly overhead. This process was repeated every 5 m along the transect, 204 giving a total of 40 images for each transect. Sub-quadrats were later combined for statistical 205 analysis, giving a total of 10 quadrats for each transect.

206 2.2.2. Still Image Analysis

207 Photoquadrats were analysed using the software Coral Point Count with Excel Extensions 208 (CPCe) v 4.1 (Kohler and Gill, 2006). The quadrat border was positioned and sized manually 209 before overlaying 50 stratified points (10 rows x 5 columns containing 1 point each) which 210 were randomly generated for every image. Any organism lying under a point was then 211 identified to species level where possible. If there was no organism, the substrate type was 212 identified instead (i.e. mud, pebble, cobble, boulder or detritus). Initial attempts used just 25 213 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 214

- anything other than bare substrate was very low. Hence, the number of points was doubledand the number of images for each site halved.
- 217 2.2.3. Baited Remote Underwater Video (BRUV)

218 At the same time as the diver surveys, a BRUV was deployed at each site between the hours of 219 09.00-14.00 for the surveys conducted in 2011, 2012 and 2013. For these, a video camera was 220 fitted to one end of a commercial lobster pot frame and a porous bait box was fitted to the 221 other (Fig. 2). Two video lights provided lighting. Rope was spliced to all four corners of the 222 frame and joined at the centre along with three cork floats to prevent the ropes from sinking 223 into view of the camera. As initial surveys in 2010 indicated that fish abundance was relatively 224 low, 200g of coarsely cut mackerel was placed inside the bait box prior to deployment in order 225 to attract fish from a wider area. Once recording began, a 40m long rope and surface marker 226 buoy were attached to the frame and the BRUV was carefully lowered to the seafloor. The 227 system's negative buoyancy ensured the BRUV landed upright and remained in a stable 228 position. After approximately one hour, the BRUV was hauled back to the boat, the bait 229 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).

235

236

237 2.2.4. Video Analysis

238 To standardise video footage, analysis began from two minutes after the BRUV landed on the 239 seabed and terminated 60 minutes later. For each video the following variables were recorded 240 for all fish: (i) identity and total number of species; (ii) total number of families; (iii) time of first 241 appearance for each species; (iv) maximum number of individuals for each species observed 242 within the same frame (MaxN). Due to the inability of an observer to recognise repeated 243 entrances of the same individual, MaxN was used as an indicator of abundance (Cappo et al., 244 2004); (v) time of MaxN; and (vi) the body length (for fish) or carapace width (for crustaceans) 245 of all individuals at MaxN that faced side-on to the camera and were aligned between the two 246 front posts of the BRUV frame. This was estimated by using 10 mm reference markers which 247 were painted on the front frame of the BRUV.

248 2.3. Data Analysis

249 2.3.1. Benthic Epifauna

250 Data on the percentage cover of epibenthic organisms were extracted from CPCe. These taxa 251 included anemones (e.g. Ceriaanthus lloydi), soft corals (e.g. Alcyonium digitatum), hydroids 252 (e.g. Nemertesia ramosa), sponges (e.g. Cliona celata), tunicates (e.g. Corella 253 paralellogramma) and macroalgae (e.g. Laminaria hyperborea). The DIVERSE function within 254 the software package PRIMER v6 (Clarke and Gorley, 2006) was then used to generate 255 univariate measures of biodiversity such as total number of species, total number of 256 individuals, Pielou's evenness and Shannon's biodiversity. Differences in these univariate measures of biodiversity tested between depths using a Pearson's product-moment 257 correlation analysis. Similarly, one-way ANOVAs were used to test if these measures of 258 259 biodiversity were different among substrates. To explore the effects of protection, the 260 percentage of the various epifaunal taxa, along with the percentage cover of total epifauna 261 and bare substrate, and the univariate measures of biodiversity, were all tested for significance 262 with a two-way Analysis of Variance (ANOVA) using treatment and year as fixed factors in the 263 software package SPSS v22. To correct for multiple testing, the False Discovery Rate (FDR) 264 endpoint adjustment was applied to reduce the likelihood of Type I errors (Yoav and Hochburg,

265 1995). Following this, any significant trends were explored further by creating line plots fitted266 with error bars of ±1 Standard Error (SE).

267 A resemblance matrix using the Bray-Curtis similarity measure (Bray and Curtis, 1957) was 268 created in PRIMER and a Permutational Multivariate Analysis of Variance (PERMANOVA+) was 269 conducted to test for differences in epifaunal community composition. The analytical design 270 had four factors: Year (fixed: 2011, 2012, 2013), Treatment (fixed: reserve, outside), Depth 271 (fixed: shallow <15 m and deep >15 m), and Substrate (fixed: soft, maerl and hard). Soft 272 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 273 274 multi-level interactions were further explored using PERMANOVA+ pairwise tests. 275 PERMANOVA was considered to be an appropriate test as it is robust to datasets with many 276 zeros (due to being based on the Bray-Curtis similarity measure), and allows the testing of 277 interactions in complex multifactorial designs. It has significant advantages over conventional 278 MANOVA in that it makes no assumptions about underlying data distributions and is robust to 279 unbalanced survey designs, as is the case with this study (Anderson and Ter Braak, 2003). 280 Visualisation of the similarity matrices was achieved using non-metric Multi-Dimensional 281 Scaling (nMDS). Additionally, a Similarity Profile (SIMPROF) routine was used to highlight if any 282 alternative a posteri groups existed within the data. Finally, a Similarity of Percentages 283 (SIMPER) was performed to determine the contribution of individual species to the average 284 dissimilarity between treatments.

285 2.3.2. Benthic Megafauna

286 Similar to before, the total number of species, individuals, Pielou's evenness and Shannon's 287 biodiversity of benthic megafauna observed during the diver transects were tested between 288 depths and substrates using one-way ANOVAs and Pearson's correlations. To explore the 289 effects of protection, these univariate measures of biodiversity were also tested between 290 treatments and years using two-way ANOVAs with FDR. In addition, the density of the 10 most 291 abundant species was investigated for differences between years and treatments by creating 292 stacked bar charts and using two-way ANOVAs. PERMANOVA+ was then used to test for 293 differences in overall community composition using the same analytical design as before.

294 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

297 (i.e. saithe - Pollachius virens, pollack - Pollachius pollachius, whiting - Merlangius merlangus, 298 haddock - Melanogrammus aeglefinus, and poor cod - Trisopterus minutus) observed during 299 the BRUV surveys were tested for differences between treatments using two-way ANOVAs 300 (factors as above). Additionally, the total number of species, individuals, Pielou's evenness and 301 Shannon's biodiversity were also tested in the same way. The mean size of fish were then 302 combined across all years (due to small sample size) and tested for differences between 303 treatments using One-way ANOVAs. In rare cases (4 out of the 82 BRUV surveys), large pelagic 304 shoals of mackerel and sand eels consisting of many hundreds of individuals were recorded. 305 These were excluded from statistical analysis to reduce variability.

306 To determine whether environmental and benthic data affected the distribution and 307 abundance of cod and other gadoids, negative binomial Generalised Linear Models (GLM) 308 were created. Predictor variables used in the GLMs were protection, depth, the abundance of 309 benthic megafauna, and the percentage cover of bare substrate, bryozoans, soft coral, 310 hydroids, macroalgae, sponges, tunicates, and dead and live maerl. Before construction of a 311 GLM, scatter plot and intercorrelation matrices (based upon Spearman's rank correlation) 312 were created to explore basic relationships and determine whether any variables were 313 strongly intercorrelated (i.e. $-0.7 \ge r \le 0.7$) as such variables would not be allowed together 314 within a GLM (Crawley, 2005). The percentage cover of macroalgae was found to be negatively 315 intercorrelated with depth and the percentage cover of bare substrate. Therefore a total of 316 four GLMs were constructed, two testing cod abundance (one including macroalgae and the 317 other including bare substrate and depth) and two testing the abundance of other gadoids 318 (same design as before). Backward-forward stepwise reductions were then conducted to 319 create minimal adequate models. Diagnostic and Cleveland dotplots were then used to explore 320 how well the models fitted the data and to identify any extreme outliers. The proportion of 321 variance (i.e. deviance) explained by the models was calculated by the following equation:

322

Deviance (%) = 1 – (Residual Deviance / 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.

326 **3. Results**

327 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).

337 In terms of protection, the mean number of species (Fig. 3) was significantly greater within the 338 reserve than surrounding areas (Table 1), as was the percentage cover of live maerl, sponges, 339 hydroids, macroalgae and all epifaunal species combined. The percentage cover of these 340 different taxa were found to be between 2 - 4 times greater within the reserve than in 341 neighbouring fishing grounds. In many cases, their abundance within the reserve appeared to 342 increase over the survey period but there was no significant interaction between year and 343 protection across all taxa. In contrast to epibenthic abundance, the percentage cover of bare 344 substrate was significantly lower within the reserve than outside. Two-way ANOVAs showed 345 that protection, year and the interaction between the two were not significantly influencing 346 Pielou's evenness, Shannon's diversity index and the percentage cover of soft coral, 347 anemones, worms, bryozoans and tunicates (Table A.5).

348 PERMANOVA+ analysis revealed the composition of the epibenthic community to significantly 349 differ between treatments, depth and year (Table 2). The interaction protection x depth was 350 also found to be significant and subsequent pairwise testing showed that differences between 351 the reserve and outside only existed for sites located at shallow depths. Exploring these 352 differences further, nMDS of shallow sites in 2011 revealed substantial variation in community 353 composition between the reserve and outside (Fig. 4a). Consequently, SIMPROF could not 354 distinguish samples from within and outside the reserve (P > 0.05) and clustered them all 355 together. However, nMDS of shallow sites sampled in 2013 revealed that epibenthic 356 communities located within the reserve had become comparatively more distinguishable from 357 communities located outside (Fig. 4b). Therefore, in contrast to 2011, SIMPROF detected 358 statistical differences between treatments (P < 0.05) and clearly separated sites located within 359 the reserve from sites located outside.

360

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	Р	FDR α
	Year	370.3	2	185.1	5.86	*0.004	
No of	Protection	403.8	1	403.8	12.78	*0.001	0.00
species	Year * Protection	60.2	2	30.1	0.95	0.39	0.06
	Residual	2558.3	81	31.5			
	Year	7476.9	1	7476.9	14.40	0.381	
Total	Protection	1012.7	2	506.3	0.97	*0.002	0.055
epifauna	Year * Protection	53.4	2	26.7	0.05	0.95	0.055
	Residual	42559.6	82	519			
	Year	7037.5	1	7037.5	13.81	0.384	
Bare	Protection	986.6	2	493.3	0.96	*0.004	0.5
substrate	Year * Protection	52.1	2	26.1	0.051	0.95	
	Residual	41775.5	82	509.4			
	Year	40.3	1	40.3	3.71	0.053	
Undroide	Protection	66.3	2	33.1	3.05	*0.041	0.045
Hydroids	Year * Protection	17.8	2	8.9	0.82	0.444	0.045
	Residual	891.8	82	10.8			
	Year	11.1	1	11.1	5.77	0.859	
Live	Protection	0.5	2	0.2	0.15	*0.019	0.04
maerl	Year * Protection	0.9	2	0.4	0.24	0.783	0.04
	Residual	158.6	82	1.9			
	Year	3720.3	1	3720.3	7.9	0.852	
Macro	Protection	1507	2	75.3	0.16	*0.006	0.025
algae	Year * Protection	114.5	2	57.2	0.12	0.886	0.055
	Residual	38604.8	82	470.7			
	Year	0.3	1	0.3	8.7	0.148	
(nongo	Protection	0.1	2	0.07	1.95	*0.004	0.02
shouge	Year * Protection	0.07	2	0.03	0.95	0.388	0.05
	Residual	3.2	82	0.03			



379 380 Fig. 3. The mean number of species recorded per m² and percentage cover of the seafloor by different epifaunal assemblages recorded by photoquadrat surveys across three years. Error 381 382 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	Р
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)					
	Sh	allow	De	eep	
Groups	t	Р	t	Р	
Out, Res	2.4	*0.001	1.09	0.285	



395

Fig. 4. nMDS plots illustrating similarities in epibenthic assemblages between shallow sites (< 396 15 m depth) within and outside the marine reserve sampled in 2011 (a) and 2013 (b). 397

398 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 399 400 characterised more strongly by bushy red seaweeds (Heterosiphonia plumose), kelps 401 (Lamanaria saccharina and Lamanaria hyperborea), thin branching brown seaweeds, and 402 upright hydroids (Nemertesia antennia), whereas sites outside the reserve were characterised 403 more strongly by red algal turf and burrowing anemones (Cerianthus lloydi). Overall, 91.6% of 404 variation within the epibenthic community situated in the reserve was characterised by 10 405 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
	Red algal turf	5.36	30.13	30.13	
	Heterosiphonia japonica	3.85	20.85	50.98	
	Cerianthus lloydi	4.43	15.45	66.44	
Outside	Filamentous brown seaweeds	2.49	12.31	78.74	34.38
	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	
	Heterosiphonia japonica	20.1	40.43	40.43	
	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	42.26
Reserve	Laminaria hyperborea	3.42	3.94	79.82	42.26
	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	

409

410 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). 425 426 Separating these taxa into mobile and sessile groups revealed little difference in the 427 abundance of mobile megafauna between the reserve and outside, and over time (Fig. 5a). In 428 contrast, both feather stars and eyelash worms were significantly more abundant within the 429 reserve than outside (Table 4), and although their abundance appeared to increase over the 430 survey period (Fig. 5b), no significant interaction was found between year and protection. 431 However, the total number of megafauna species did significantly increase during the study 432 period and was significantly greater within the reserve than outside (Table 4). Two-way 433 ANOVAs also revealed that year significantly influenced the abundance of harbour crabs, spiny 434 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 435 436 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.



443

445 **Table 4.** Two-way ANOVA comparing the density of different benthic fauna between the 446 marine reserve and outside across the years 2010-2013. Adjusted critical values obtained from

447 FDR are shown in bold Significant results are denoted by (*).

Source	Test	SS	df	MS	F	Р	FDR α
	Year	711.5	1	711.5	0.6	0.103	
	Protection	7498.4	3	2499.5	2.1	*0.041	
Feather stars	Year * Protection	525.6	3	175.2	0.15	0.931	0.06
	Residual	146213.4	123	1188.7			7
	Year	73.4	1	73.4	5.35	0.494	
Eyelash	Protection	33.0	3	11	0.8	*0.022	0.055
worms	Year * Protection	27.1	3	9	0.66	0.579	0.055
	Residual	1686.7	123	13.7			
	Year	5.1	1	5.1	0.14	*0.002	
Parchment	Protection	1677.4	3	559.1	15.14	0.711	0.05
worms	Year * Protection	71.7	3	23.9	0.65	0.586	
	Residual	4542.5	123	36.9	Y		
	Year	610.2	1	610.19	8.51	*0.004	
Harbour	Protection	593.8	3	197.95	2.76	0.551	0.045
crabs	Year * Protection	261.3	3	87.09	1.21	0.308	
	Residual	8823.7	123	71.74			
	Year	24.0	1	24.01	1.31	0.255	
Decorator	Protection	254.3	3	84.7567	4.609194	0.104	0.04
crabs	Year * Protection	50.3	3	16.78	0.91	0.437	0.04
	Residual	2261.8	123	18.39			
	Year	625.6	1	625.63	18.41	*0.001	
Spiny starfish	Protection	137.4	3	45.79	1.35	0.262	0.035
Spiny stariish	Year * Protection	46.0	3	15.35	0.45	0.717	0.035
	Residual	4180.9	123	33.99			
	Year	0.0	1	0.00	0.01	0.939	
Diversity	Protection	1.1	3	0.38	3.38	0.12	0.03
Diversity	Year * Protection	0.1	3	0.02	0.20	0.894	0.05
	Residual	13.8	123	0.11			
	Year	55.1	1	55.1	5.7	*0.018	
No of chooses	Protection	436.9	3	145.6	15.06	0.101	0.025
NO OF SPECIES	Year * Protection	11.2	3	3.7	0.39	0.764	0.025
	Residual	1189.2	123	9.7			

448

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

454 using nMDS and SIMPROF did not clearly distinguish between sites located within and outside 455 the reserve (P > 0.05). Although, SIMPER did suggest that maerl, soft and hard substrates 456 within the reserve were more strongly characterised by eyelash worms and feather stars.

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

a)						
Source	df	SS	MS	F	Р	
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)						
	r	naerl	sc	oft	har	d
Groups	t	Р	Y _t	Р	t	Р
Out, Res	1.3	*0.08	1.5	*0.009	1.4	*0.044

461

462 3.3. Composition of Fish Assemblages

463 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 464 within the reserve and 644 from outside. Despite more individuals being recorded within the 465 reserve, neither year (Two-way ANOVA; $F_{(1, 82)} = 1.6$, P > 0.05) nor protection (Two-way ANOVA; 466 467 $F_{(1, 82)} = 2.7$, P > 0.05) significantly influenced fish abundance (MaxN). Overall, the most 468 common species were all gadoids of which cod were the most abundant (408 observations), 469 followed by whiting (303 observations) and haddock (163 observations). Over 98% of these 470 gadoids were in their juvenile form. In rare cases (4 out of the 82 BRUV surveys), large pelagic 471 shoals of mackerel and sand eels consisting of many hundreds of individuals were recorded.

472 One-way ANOVAs revealed that the size of individuals was not significantly different between 473 the reserve and outside for cod (One-way ANOVA; $F_{(1, 146)} = 2$, P > 0.05), other gadoids (One-474 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 475 gurnards, wrasse and gobies as the sample size was too low. Comparing the abundance of 476 477 different taxa over time also revealed little difference between the reserve and outside (Fig. 6). 478 Cod abundance did exponentially and significantly increase over the study period, but did not 479 significantly differ between the reserve and outside, nor was there an interaction between 480 those two factors (Table 6). In contrast, the abundance of other gadoids appeared to increase 481 outside the reserve over time and decrease inside. However, neither year, nor protection, nor 482 the interaction between the two, were significant.



483

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.

487 **Table 6**. Two-way ANOVA comparing the abundance of cod and other gadoids between the 488 reserve and outside over the years 2011-2013. Significant terms are denoted by (*).

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

489

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

493 employing backward-forward stepwise reduction, models indicated that cod abundance was 494 significantly positively associated with year and with the presence of macroalgae and maerl, 495 but was negatively associated with the presence of anemones and echinoderms (Table 7). In 496 contrast, the abundance of other gadoid species was found to be positively associated with the 497 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 498 499 and the percentage cover of bare substrate, could not be constructed for other gadoid species 500 as the model would not converge, likely because it had insufficient predictive power. In all 501 cases, the reduced models did not explain significantly less variance than the full models (Pearson's Chi-squared; df = 81, χ^2 = 0.78, *P* > 0.05). 502

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	Ζ	Р
	Included		Year	0.24	5.63	*0.001
	macroalgae,		Anemones	0.12	-2.29	*0.022
Cod	excluded	60 43%	Echinoderm	0.5	-2.3	*0.019
cou	bare	00.1370	Macroalgae	0.28	1.87	*0.041
	substrate		Maerl	0.1	2.72	*0.006
	and depth					
	Included		Year	0.25	5.09	*0.001
	bare		Bare substrate	0.01	-0.48	0.632
Cod	substrate	71 40%	Protection	0.21	0.435	0.664
004	and depth,	,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	Crustacean	1.13	1.09	0.273
	excluded		Sponge	0.84	-1.6	0.11
	macroalgae		1 0			
	Included		Year	0.16	4.51	*0.001
	bare		Bare substrate	0.01	3.7	*0.001
Other	substrate	68 53%	Protection	0.14	2.91	*0.003
gadoids	and depth,	08.5576	Crustacean	0.73	3.04	*0.002
	excluded		Spongo	0.55	2.16	*0.001
	macroalgae		Shouge	0.55	-5.10	0.001

507

508 4. Discussion

509 Our study highlights a number of differences in ecological communities between the fully 510 protected marine reserve in Lamlash Bay and neighbouring fishing grounds. However, before 511 we discuss our results, it must be stressed that there is no data available prior to the 512 establishment of the reserve. Ideally, a before-after control-impact (BACI) approach would 513 have been employed, capable of demonstrating that differences between the reserve and

514 outside were due to the protection afforded by the marine reserve (Hilborn et al., 2004; Sale 515 et al., 2005). As this was not possible, we instead compared sites within the reserve to 516 reference sites located outside its boundaries over a study period of three to four years, in 517 order to test for increased rates of recovery within the reserve over time. As almost all the 518 trends explored in this study showed no interaction between year and protection, we have 519 evidence that differences between the reserve and outside exist, but in most cases we cannot 520 definitively conclude that protection was responsible for creating them. Importantly, however, 521 protection within the reserve is highly likely to be helping to maintain any pre-existing 522 differences between the two areas.

523 Overall, we found a large number of differences between the marine reserve and outside. Four 524 years after its establishment, live maerl (348% greater), macroalgae (100% greater), sponges 525 (268% greater), hydroids (15-267% greater), eyelash worms (184% greater), feather stars (52% 526 greater), parchment worms (36% greater) and total epifauna (77% greater) were all found to 527 be significantly more abundant within the reserve than on neighbouring fishing grounds. 528 Although the abundance of macroalgae, sponges, hydroids and eyelash worms appeared to 529 steadily increase within the reserve over the duration of the study, no significant interaction 530 between year and protection was found. Likewise, nMDS plots and SIMPER analysis suggested 531 an increasing divergence between the epifaunal community within and outside the reserve, 532 but again no significant interaction was found.

533 The greater abundance of macroalgae within Lamlash Bay Marine Reserve was one of the first 534 observations made when monitoring began in 2010 (Howarth et al., 2011). Several well-known 535 studies have also reported differences in macroalgal abundance between reserves and 536 reference sites (Hawkins and Roberts 2004; Langlois and Ballantine, 2005; Shears and Babcock, 537 2003). In these cases, differences were due to populations of predators and herbivores 538 recovering within marine reserves, thereby altering the grazing rates on macroalgae. On the 539 other hand, our study did not detect any major changes in herbivore or predator abundance 540 other than for juvenile cod, which exponentially increased in both the reserve and outside over 541 the three year study period. However, as the diet of juvenile cod consists predominantly of 542 copepods and other planktonic crustaceans (Demain et al., 2011) there is unlikely to be any 543 connection between their abundance and the prevalence of macroalgae. Notably, an 544 associated study (Howarth et al., 2015) found that the greater abundance of macroalgae and 545 hydroids growing within Lamlash Bay Marine Reserve significantly increased the settlement 546 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).

552 It is interesting that live maerl was over 300% more abundant within the reserve, as evidence 553 suggests that recovery of maerl beds should take several decades, due to their extremely slow 554 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 555 556 signs of increasing over the study period, the greater levels of maerl within the reserve may 557 just be an artefact of maerl being more prevalent within the reserve than outside prior to its 558 establishment. In addition, the abundance of live maerl was very low throughout both study 559 areas, varying between 0 - 8%. These low levels of live maerl contrast greatly with earlier 560 studies of Lamlash Bay (Kamenos et al., 2004c), which detected over 90% live maerl in some 561 maerl beds, suggesting recent degradation in their health. Nonetheless, the reserve should act 562 as a safe haven for any patches of live maerl remaining within the reserve and may encourage 563 their recovery in the future. However, given the slow growth rates of maerl, such recovery may 564 be a lengthy process.

565 In addition to observing differences in specific species, there were also a number of differences 566 in the overall epifaunal community between the reserve and outside. Four years after the 567 reserve was established, PERMANOVA+ analysis revealed strong differences in community 568 composition between the two treatments for sites less than 15 m in depth. Shallow sites 569 within the reserve were more strongly characterised by a range of bushy and upright seaweeds 570 and hydroids, whereas sites outside the reserve were more strongly characterised by red algal 571 turf and fast-growing burrowing anemones. Sites outside the reserve are therefore likely to be 572 providing comparatively less structural complexity and may, in turn, be providing a smaller 573 range of physical niches. However, despite observing broad differences in epifaunal 574 communities, there was no difference in overall community evenness and diversity, or in the 575 abundance of soft coral, anemones, bryozoans and tunicates.

576 Considering that physical properties and sediment characteristics are regularly cited to be a 577 major factor in influencing the structure of benthic communities (Gray, 1981; Seider and 578 Newell, 1999; van Dalfsen et al. 2000), it was surprising that there was no difference in the 579 community composition of epibenthic communities between different substrate types.

580 However, this lack of variation could be a consequence of grouping sites into substrate 581 categories that were too broad (i.e. maerl, soft and hard substrates). This approach was used 582 as sites were grouped together based on visual inspection of the substrate, rather than Particle 583 Size Analysis (e.g. Bath and Flippen, 1995). The latter would have been able to separate sites to 584 a much higher resolution with a higher degree of confidence, but was unfortunately beyond 585 the scope of this study. Then again, the physical properties of sites was found to be 586 significantly influencing the epifaunal communities in other ways. Sites composed predominantly of maerl substrates contained both a higher number of species and percentage 587 588 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; 589 590 Kamenos et al., 2004a). Also of interest was that the total number of species and percentage 591 cover by all epifaunal taxa combined were both negatively correlated with depth. This was 592 likely a result of shallow sites being dominated by a wide range of kelp and seaweed species, 593 the abundance of which naturally declined with increasing depth.

594 In contrast with the epifaunal community, comparisons between the reserve and outside in 595 the abundance of mobile benthic fauna revealed little difference. This was unexpected 596 considering the number of studies that have reported changes in the abundance of scavengers 597 and predators, such as dog fish and star fish, in response to protection (Brown, 2013; Marino 598 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 599 600 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 601 602 communities sampled within the marine reserve. This was because they were 52% and 184% 603 more abundant within the reserve than outside respectively, although again, no significant 604 interaction between protection and year was found. These organisms can be important to 605 benthic diversity and commercially valuable species as they provide structural complexity to 606 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). 607

608 Compared to other taxa, relatively few trends were detected in fish populations. The most 609 common fish species were all gadoids, a group containing commercially important species such 610 as cod, haddock and whiting. Over 98% of these individuals were in their juvenile form, 611 suggesting that Lamlash Bay is providing nursery habitats to several commercially important 612 species. This was confirmed by constructing several models, which found cod abundance to be

613 positively associated with the presence of macroalgae, live maerl and year of study. In some 614 respects this came as no surprise, as coastal areas containing high levels of kelp, seaweeds and 615 maerl are often reported to support large numbers of juvenile cod (Borg et al., 1997; Caddy, 616 2013; Gibb et al., 2007; Kamenos et al., 2004c; Laurel et al., 2009). Although cod abundance 617 appeared greater within the reserve than outside, this difference was not statistically 618 significant. Likewise, there were no significant differences in mean fish size between in and 619 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 620 621 important transition from pelagic to benthic habitats (Demain et al., 2011). Cod abundance 622 was also found to increase exponentially over the survey period both within and outside the 623 reserve, and is thought to be the result of exceptionally cold winter temperatures in recent 624 years (Sophie Elliott, University of Glasgow, pers. comm). In contrast to cod, models found the 625 abundance of haddock and whiting to be positively associated with the percentage cover of 626 bare substrate, crustacean abundance, and level of protection (an artefact of more gadoids 627 being detected within the reserve). This was supported by diver observations which regularly 628 reported high levels of whiting and haddock on deep soft / muddy sediments. Stocks of adult 629 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 630 631 important area for future research is to establish the origin of these gadoid recruits and 632 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 633 634 chances of these fish reaching maturity (Bergman et al., 2002).

635 One of the most commonly cited results of establishing MPAs and marine reserves has been an 636 increase in fish abundance, biomass and size (Hawkins and Roberts, 2004; Lester et al., 2009; 637 Micheli et al., 2004; Moland et al., 2013; Mumby et al., 1995;). However, this study found no 638 statistical difference in fish abundance between the reserve and outside. This was likely due to 639 the young age of the reserve (5 years) and its small size (2.67km^2) , both of which are known to 640 reduce the effects of marine reserves on mobile fish species (Edgar et al., 2014; Halpern, 2003; 641 Molloy et al., 2009), and the generally low abundance of fish (particularly adults) in the area 642 (see earlier references). Additionally, when analysing the BRUV footage it was not possible to 643 recognise repeated entrances of the same individual, meaning estimators of abundance had to 644 be used; in this case, the maximum number of fish sighted within a single frame (MaxN). As it 645 is unlikely that all individuals of a species are recorded within the same frame, BRUVs can only 646 detect a proportion of the fish that are attracted to the bait, which can make their estimates

647 relatively conservative (Cappo et al., 2004; Willis and Babcock, 2000). This means that any 648 differences detected between sites within and outside MPAs are also likely to be conservative. 649 More worryingly, recent research has shown in some areas there is little correlation between 650 the abundance estimates generated by MaxN and those created from underwater visual 651 census (Dunlop, 2013). Our study also revealed no difference in fish size between the reserve 652 and outside. Again this may be due to the age and size of the reserve, or the method we used 653 to estimate fish size. The use of recently developed technologies, such as stereo video cameras 654 would have generated much more accurate and precise estimates of fish size than those 655 obtained in this study, which would reduce variation and increase the chance of detecting 656 differences in fish size, if they exist (Cappo et al., 2004; Harvey et al., 2001; Langlois et al., 657 2010).

658 In summary, epifaunal assemblages, such as feather stars, eyelash worms, maerl, sponges, 659 hydroids and macroalgae were all found to be significantly more abundant within the reserve 660 than outside. As well as increasing the structural complexity of the seabed, the greater 661 abundance of these habitats has substantially increased the recruitment of commercially 662 important scallops (Howarth et al., 2015), suggesting that protecting areas from fishing can 663 generate ecological benefits that flow back to species commercially targeted by fisheries. In 664 contrast, there was no difference in the abundance of mobile benthic fauna and fish 665 populations between the reserve and outside. This may be due to the short duration of 666 protection received to date, the small size of the reserve, and / or the methods used to 667 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 668 669 survival as they make the important transition from pelagic to benthic habitats.

670 The relative scarcity of studies on temperate MPAs (particularly highly protected ones) has 671 been used as an argument against their implementation (reviewed in Caveen et al. 2013; 672 Roberts et al. 2005). This study joins a growing band which indicates MPAs can indeed provide 673 both conservation and fisheries benefits in temperate waters, but suggests recovery rates may 674 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 675 676 objectives. Our results are therefore highly relevant to informing the design and 677 implementation of MPAs in temperate areas, particularly as is currently taking place in 678 European, and indeed UK waters.

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987 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
		Out	23.1	Boulders, sand
		Out	24.5	Boulders, muddy sand
		Reserve	16.8	Boulders, sand
	Deep boulders	Reserve	17	Boulders, muddy sand, dead maerl
		Reserve	19.1	Boulders, muddy sand
		Reserve	27	Boulders, muddy sand
		Reserve	28	Boulders, muddy sand, cobbles
		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
	Deep 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
	()	Out	15.1	Dead maerl, muddy sand
		Out	14.3	Dead maerl, muddy sand, pebbles
		Reserve	9.1	Dead maerl
	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
		Out	19	Mud
	Mud	Out	20.8	Mud
	Ividu	Reserve	13.3	Mud
		Reserve	18.7	Mud
X		Out	11.8	Muddy sand
	Shallow muddy cand	Out	13.5	Muddy sand
	Shahow muuuy Sahu	Reserve	15.5	Muddy sand, pebbles, cobbles
		Reserve	15.5	Muddy sand

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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
Deenhouldere	Out	18.5	Boulders, sandy mud, pebbles
Deep boulders	Reserve	17	Boulders, muddy sand, cobbles
	Out	19.3	Muddy sand
	Out	16.48	Muddy sand
	Out	17	Muddy sand, dead maerl
	Out	22.8	Muddy sand, cobbles
Deep muddy sand	Out	21.5	Muddy sand, pebbles
	Reserve	19	Muddy sand
	Reserve	17.4	Muddy sand
	Reserve	20.8	Muddy sand, cobbles
	Out	8	Dead maerl
	Out	10.7	Dead maerl
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
IVIUU	Reserve	15.6	Fine muddy sand
	Out	14.35	Boulders, muddy sand, cobbles
	Out	15.4	Boulders, muddy sand, dead maerl
Shallow boulders	Reserve	13.8	Boulders, muddy sand, pebbles
	Reserve	15.2	Boulders, dead maerl
	Reserve	10.8	Boulders, sand, dead maerl, cobbles
	Out	11.6	Muddy sand, pebbles
	Out	15.2	Muddy sand, pebbles
Challow muddy cand	Out	15	Muddy sand, pebbles
Shallow Huuuuy Sahu	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		
	Out	16.1	Muddy sand		
	Out	23.4	Muddy sand, pebbles, cobbles		
	Out	21.3	Muddy sand		
	Out	24.5	Muddy sand		
Deep 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		
	Out	13.8	Dead mearl, muddy sand, boulders		
	Out	12.7	Dead maerl, sand		
Maarl	Out	11.5	Dead maerl		
WIdell	Reserve	9.2	Dead maerl, sand		
	Reserve	14.1	Dead maerl		
	Reserve	10	Dead maerl, sand, pebbles		
	Out	14.4	Boulders, muddy sand		
Shallow boulders	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
	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
Doon muddy cand	Out	20	Muddy sand
Deep muduy sanu	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
	Out	10.2	Dead maerl
Maarl	Out	8.95	Dead maerl
IVIdel1	Reserve	8.7	Dead maerl
	Reserve	10.4	Dead maerl
	Out	13.75	Muddy sand, dead maerl
	Out	9.8	Muddy sand, pebbles
	Out	8.9	Muddy sand
Shallow muddy cand	Out	13.8	Muddy sand
Shahow muuuy sahu	Reserve	12.75	Muddy sand, cobbles
	Reserve	12.5	Muddy sand
	Reserve	13.25	Muddy sand
	Reserve	13.85	Muddy sand
	Out	12.85	Boulders, sand
Shallow Boulders	Out	10.35	Boulders, sand
Silanow Boulders	Reserve	11.45	Boulders, sand
	Reserve	15.05	Boulders, muddy sand

1032 Table A.5. Two-way ANOVA comparing percentage cover by different epifaunal assemblages,

1033 as well as Pielou's Evenness and Shannon's Diversity Index, between the marine reserve and

1034 outside across the years 2011-2013.

Source	Test	SS	df	MS	F	Р
	Year	0.003	1	0.003	0.403	0.527
	Protection	0.016	2	0.031	4.344	0.16
Solutional	Year * Protection	0.002	2	0.001	0.112	0.894
	Residual	0.58	82	0.007		
	Year	0.576	1	22.212	2.904	0.271
Marma	Protection	0.91	2	1.584	17.509	0.214
worms	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		
	Year	1.961	1	1.961	0.786	0.378
	Protection	3.168	2	1.584	0.635	0.533
Bryozoans	Year * Protection	6.986	2	3.493	1.4	0.252
	Residual	204.563	82	2.495		
	Year	0.001	1	0.476	1.904	0.171
- · ·	Protection	9.198	2	4.599	18.409	0.12
Tunicates	Year * Protection	0.12	2	0.01	0.04	0.961
	Residual	20.487	82	0.25		
	Year	10.45	1	0.574	2.013	0.845
-	Protection	12.1	2	4.644	16.112	0.775
Eveness	Year * Protection	0.554	2	0.04	0.008	0.901
	Residual	19.66	82	0.55		
	Year	8.62	1	0.866	1.804	0.15
	Protection	3.64	2	5.669	21.21	0.12
Diversity	Year * Protection	10.98	2	0.04	0.18	0.864
	Residual	25.41	82	0.21		

1042 Table A.6. Two-way ANOVA comparing the univariate measures of benthic megafauna
1043 abundance between the marine reserve and outside across the years 2010-2013.

Source	Test	SS	df	MS	F	Р
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