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# Marine Biology

## Effects of ecosystem protection on scallop populations within a community-led temperate marine reserve --Manuscript Draft--

<b>Manuscript Number:</b>	MABI-D-14-00592R3
<b>Full Title:</b>	Effects of ecosystem protection on scallop populations within a community-led temperate marine reserve
<b>Article Type:</b>	Original paper
<b>Keywords:</b>	Scallops; Pecten maximus; Aequipecten opercularis; Marine Protected Areas (MPAs); No-Take Zone (NTZ); Lamlash Bay; Firth of Clyde; ecosystem-based fishery management; nursery habitats
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<b>Abstract:</b>	<p>This study investigated the effects of a newly established, fully protected marine reserve on benthic habitats and two commercially valuable species of scallop in Lamlash Bay, Isle of Arran, United Kingdom. Annual dive surveys from 2010 to 2013 showed the abundance of juvenile scallops to be significantly greater within the marine reserve than outside. Generalised linear models revealed this trend to be significantly related to the greater presence of macroalgae and hydroids growing within the boundaries of the reserve. These results suggest that structurally complex habitats growing within the reserve have substantially increased spat settlement and / or survival. The density of adult king scallops declined 3-fold with increasing distance from the boundaries of the reserve, indicating possible evidence of spillover or reduced fishing effort directly outside and around the marine reserve. However, there was no difference in the mean density of adult scallops between the reserve and outside. Finally, the mean age, size, and reproductive and exploitable biomass of king scallops were all significantly greater within the reserve. In contrast to king scallops, the population dynamics of queen scallops (<i>Aequipecten opercularis</i>) fluctuated randomly over the survey period and showed little difference between the reserve and outside. Overall, this study is consistent with the hypothesis that marine reserves can encourage the recovery of seafloor habitats, which in turn, can benefit populations of commercially exploited species, emphasising the importance of marine reserves in the ecosystem-based management of fisheries.</p>

**Effects of ecosystem protection on scallop populations within a community-led  
temperate marine reserve**

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**Corrections made**

- 1) Lat long border placed around map
- 2) Units of measurement no longer use / or per
- 3) References corrected to comply with journal style

# 1     **Effects of ecosystem protection on scallop populations within a** 2     **community-led temperate marine reserve**

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13

14    **Key words:** *Scallops*, *Pecten maximus*, *Aequipecten opercularis*, Marine Protected Areas (MPAs), No-  
15    Take Zone (NTZ), Lamlash Bay, Firth of Clyde, ecosystem-based fishery management, nursery habitats

16

## 17    **Abstract**

18    This study investigated the effects of a newly established, fully protected marine reserve on  
19    benthic habitats and two commercially valuable species of scallop in Lamlash Bay, Isle of Arran,  
20    United Kingdom. Annual dive surveys from 2010 to 2013 showed the abundance of juvenile  
21    scallops to be significantly greater within the marine reserve than outside. Generalised linear  
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28    difference in the mean density of adult scallops between the reserve and outside. Finally, the  
29    mean age, size, and reproductive and exploitable biomass of king scallops were all significantly  
30    greater within the reserve. In contrast to king scallops, the population dynamics of queen  
31    scallops (*Aequipecten opercularis*) fluctuated randomly over the survey period and showed  
32    little difference between the reserve and outside. Overall, this study is consistent with the  
33    hypothesis that marine reserves can encourage the recovery of seafloor habitats, which in  
34    turn, can benefit populations of commercially exploited species, emphasising the importance  
35    of marine reserves in the ecosystem-based management of fisheries.

## 36 **Introduction**

37 Never before has the general public been so well informed about the current state of the  
38 world's oceans. A recent surge in environmentally focused films, documentaries and  
39 campaigns has led to much greater awareness of the methods used to harvest marine  
40 resources, and of their impacts on the marine environment (Jacquet and Pauly 2007). In 2013,  
41 the United Kingdom (UK) based celebrity chef and environmentalist Hugh Fearnley-  
42 Whittingstall launched a television series campaigning for better protection of European  
43 waters in which the first episode videoed the damage to the seabed caused by a scallop  
44 dredger ([www.fishfight.net](http://www.fishfight.net)). Responses from the public and media were strong (Brown 2013;  
45 Greenpeace 2013; Renton 2013) with one major retailer pledging to stop selling dredge-caught  
46 scallops (Harvey 2013), sparking rebukes from both the fishing industry and their  
47 representatives (Gray 2013; SeaFish 2013). Despite the media attention, fisheries for shellfish  
48 are rapidly increasing in importance in many parts of the world, as are their environmental  
49 impacts (Pauly et al. 1998, 2002; Steneck et al. 2002; Essington et al. 2006; Estes et al. 2011;  
50 Howarth et al. 2013).

51 In the UK, landings of the king scallop (*Pecten maximus*) are growing faster than any other  
52 commercially targeted shellfish species. Generating over £68 million per year, king scallops  
53 represent the UK's second most valuable fishery resource, over 95% of which are caught by  
54 scallop dredgers (Keltz and Bailey 2010; Radford 2013). Scallop stocks located around Scotland  
55 account for over half of the UK king scallop fishery (Dobby et al. 2012) but concerns have  
56 recently been made over increasing mortality, and declining recruitment and spawning stock  
57 biomass in several major Scottish stocks (Hall-Spencer and Moore 2000; Howell et al. 2006;  
58 Hinz et al. 2011; Barreto and Bailey 2013). These problems are not unique. Scallop fisheries all  
59 over the world are well known for exhibiting dramatic fluctuations in recruitment, landings and  
60 abundance (Paulet et al. 1988; Orensanz et al. 1991; Beukers-Stewart et al. 2003; Beukers-  
61 Stewart and Beukers-Stewart 2009). Such fluctuations are difficult to incorporate into fisheries  
62 management strategies and can result in their sudden and unexpected collapse (Frank and  
63 Brickman 2001; Beukers-Stewart and Beukers-Stewart 2009). Furthermore, scallop recruitment  
64 and mortality are predicted to become increasingly more erratic in the future due to ocean  
65 acidification (Gazeau et al. 2007; Kurihara 2008; Watson et al. 2009), a process which is  
66 reducing the amount of carbonate available to scallops to form their protective shells (Sabine  
67 et al. 2004; Doney et al. 2009). Due to anthropogenic carbon dioxide emissions, ocean acidity  
68 is currently increasing at a rate unprecedented for tens of millions of years (Doney et al. 2009).  
69 This means scallop fisheries all over the world are at risk if the species they target cannot

70 adapt. Stronger efforts must therefore be made to safeguard the long-term sustainability of  
71 commercially important scallop stocks whilst reducing the environmental impact of their  
72 fisheries.

73 Although many different management measures exist for maintaining and supporting fish  
74 stocks, it has been argued that the establishment of Marine Protected Areas (MPAs) closed to  
75 some or all types of fishing can allow seafloor habitats to recover (Bradshaw et al. 2001;  
76 Howarth et al. 2011), increase the abundance and size of target species (Halpern and Warner  
77 2002; Halpern 2003; Lester et al. 2009), enhance local reproductive output (Roberts et al.  
78 2001; Gaines et al. 2003; Grantham et al. 2003) and improve the survival and growth of  
79 juveniles (Myers et al. 2000; Beukers-Stewart et al. 2005). All of these effects may then result  
80 in the greater production of eggs, larvae, juveniles and adults which can disperse ('spillover') to  
81 grounds outside MPAs and contribute to fishery landings (McClanahan and Mangi 2000;  
82 Harrison et al. 2012). Then again, establishing MPAs can displace fishing effort to surrounding  
83 areas (Bohnsack 2000; Kaiser 2005), which can cause wider environmental damage (Dinmore et  
84 al. 2003) and reduce profits through the loss of fishing grounds (Rassweiler et al. 2012). Hence,  
85 MPAs only truly yield benefits to fisheries when these negative effects are adequately offset by  
86 increased recruitment and landings.

87 For populations to benefit from the protection afforded by MPAs, it is necessary that a number  
88 of individuals spend a substantial part of their lives within their boundaries (Roberts et al.  
89 2005). Thanks to their sedentary nature and relatively fast growth, scallops have been shown  
90 to be particularly responsive to closed area protection. In 1994, three areas totalling 17,000  
91 km<sup>2</sup> were closed to fishing gears on Georges Bank in the Gulf of Maine, United States of  
92 America (USA). Ten years later, observations revealed that the reduction in fishing mortality  
93 was responsible for a 20-fold increase in scallop biomass within the closures, and increased  
94 catches in neighbouring fishing grounds (Murawski et al. 2000; Hart and Rago 2006; Hart et al.  
95 2013). The scallop fishery on Georges Bank is now the most valuable of any fishery in the USA  
96 (Lowther 2013). On a smaller scale, 17 years of protection of within a 2 km<sup>2</sup> area off the Isle of  
97 Man resulted in scallop densities 30 times greater than those observed prior to protection  
98 (Beukers-Stewart et al. 2005; Beukers-Stewart and Brand 2007). The reduction in fishing  
99 mortality also allowed individuals within the closed area to become older and reach larger  
100 sizes, with exploitable and reproductive biomass of scallops becoming 20 and 33 times higher  
101 respectively, than on adjacent fishing grounds. In addition, there is growing evidence that  
102 export of larval scallops, generated from high rates of breeding within the closed area, have

103 boosted surrounding populations and therefore the fishery (Beukers-Stewart et al. 2005, 2004;  
104 Beukers-Stewart and Brand 2007; Neill and Kaiser 2008).

105 In addition to increasing the abundance of target organisms, the exclusion of fishing from an  
106 area also eliminates the physical impacts created by mobile fishing gears such as dredges and  
107 trawls (Kaiser et al. 2000, 2007). Such gears can cause substantial physical disruption of  
108 seafloor habitats by ploughing sediments and fragmenting the biogenic structure of epifaunal  
109 assemblages such as hydroids, tunicates and maerl beds (Eleftheriou and Robertson 1992;  
110 Dayton et al. 1995; Jennings and Kaiser 1998; Kaiser et al. 2000; Jennings et al. 2001; Cook et  
111 al. 2013). However, these organisms provide essential habitat for the settlement of scallops  
112 and a large range of other invertebrates and fish species (Bradshaw et al. 2001; Kamenos et al.  
113 2004a). Consequently, such locations are often referred to as “nursery areas” as they tend to  
114 be highly productive, support high levels of juvenile density, growth and survival, and  
115 contribute disproportionately to the production of adult recruits (Beck et al. 2001; Gibb et al.  
116 2007; Laurel et al. 2009). The damage inflicted by fishing gears upon nursery habitats has  
117 therefore been shown to negatively impact scallop recruitment (Collie et al. 1997; Bradshaw et  
118 al. 2002), whilst the protection of nursery habitats has been shown to enhance scallop  
119 settlement levels (Howarth et al. 2011).

120 The implementation of MPAs may therefore provide a “win-win” solution to safeguarding the  
121 long-term sustainability of commercially important scallop stocks. Not only can MPAs provide  
122 fisheries benefits, they also help sustain healthy marine ecosystems by addressing the physical  
123 impacts of fishing gears (Bradshaw et al. 2002; Kaiser et al. 2000, 2007) which can then  
124 generate numerous benefits that flow back to the species targeted by fisheries (Jennings and  
125 Kaiser, 1998; Howarth et al. 2011). It is these ideas that underlie the current push towards  
126 ‘ecosystem-based fishery management’, where management priorities begin with the  
127 ecosystem, moving away from traditional single-species approaches (Pikitch et al. 2004; Zhou  
128 et al. 2010). However, the implementation of MPAs in Europe is still at a very early stage  
129 (Fenberg et al. 2012; Metcalfe et al. 2013) and their use as an ecosystem-based fishery  
130 management tool remains a highly contentious issue (Boersma and Parrish 1999; Kaiser 2004,  
131 2005; Jones 2007; Sciberras et al. 2013).

132 MPAs can be implemented via top-down processes which are government led and enforced, or  
133 by bottom-up mechanisms, whereby local communities and stakeholders propose the  
134 establishment of an MPA and help with its management, enforcement and monitoring  
135 (Kelleher 1999; Jones 2012). There is growing evidence that community and stakeholder

136 involvement in setting up and running MPAs builds greater support and reduces management  
137 costs due to lower infringements rates (Pollnac et al. 2012). Although community-led MPAs are  
138 relatively common in tropical waters (Johannes 2002), they are very rare in temperate areas  
139 and almost non-existent in the UK (Fenberg et al 2012). As an exception, a fully protected  
140 marine reserve was established in Lamlash Bay, Isle of Arran, UK, in September 2008  
141 prohibiting all fishing within the reserve under the Inshore Fishing (Scotland) Act of 1984  
142 (Axelsson et al. 2009). The Firth of Clyde, in which the Isle of Arran sits, is known to be one of  
143 the most degraded marine environments in the UK, primarily due to over a century of  
144 intensive fisheries exploitation (Thurstan and Roberts 2010; Howarth et al. 2013). The reserve  
145 was therefore passed by the Scottish parliament under the rationale that the reduction in  
146 fishing pressure should help regenerate the local marine environment and enhance  
147 commercial shellfish and fish populations in and around Lamlash Bay, particularly with regards  
148 to scallops. Lamlash Bay Marine Reserve came in effect after a decade of campaigning by local  
149 residents for better protection of their seas (Community of Arran Seabed Trust or “COAST”;  
150 [www.arrancoast.com](http://www.arrancoast.com)) and is the first and only fully protected marine reserve in Scotland, and  
151 the only statutory reserve in the UK that was originally proposed by a local community which  
152 bans all extractive activities (Prior 2011). Lamlash Bay is also unique in that the majority of  
153 MPAs in the UK were proposed either for conservation (e.g. Lundy Marine Nature reserve and  
154 Lyme Bay Marine Reserve) or fishery purposes (e.g. closed areas off the Isle of Man), not for  
155 both.

156 Our study therefore sought to test the hypotheses that: (1) there is a positive relationship  
157 between scallop settlement and the abundance of nursery habitat; (2) the marine reserve  
158 contains a greater abundance of these nursery habitats; and (3) that the density, age, size,  
159 biomass and growth rates of scallops are higher within the marine reserve than areas located  
160 outside its boundaries. This was achieved by conducting a series of quantitative diver surveys  
161 over a four-year study period.

## 162 **Materials and methods**

### 163 Study area and scallop fishery

164 Lamlash Bay Marine Reserve encompasses an area of 2.67 km<sup>2</sup> (Fig. 1), with water depths  
165 ranging between 0 and 29 m below chart datum, but reaching as deep as 43 and 50 m outside  
166 to the east and the west of the reserve, respectively (Admiralty Chart 1864; Baxter et al. 2008).  
167 Previous surveys (Duncan 2003; Axelsson et al. 2009) indicated a seabed of mixed sediments



168 (i.e. mud, sand and gravel with various proportions of shell) but that the central and southern  
169 regions of the bay tend to be characterised by softer sediment, mainly muddy sand. In  
170 addition, the area has long been identified as containing important maerl beds, although  
171 recent evidence points to deterioration in their health (Howarth et al. 2011).

172 The king scallop (*Pecten maximus*) fishery is the second most valuable in Scotland and has  
173 consistently ranked in the top five most valuable UK fisheries for the past 10 years (Dobby et  
174 al. 2012). In contrast, landings of the comparatively smaller queen scallop (*Aequipecten*  
175 *opercularis*) have fluctuated greatly, meaning they tend to be fished opportunistically by  
176 fishers and are worth considerably less (Beukers-Stewart and Beukers-Stewart 2009).  
177 European Union (EU) legislation specifies a minimum landing size of 100 mm length for king  
178 scallops (Council Regulation (EC) No. 850/98). There are no size limits for queen scallops  
179 (although it is generally uneconomic to process them when smaller than 50 mm in width), and  
180 there are no limits on landings for either species. Under the Prohibition of Fishing for Scallops  
181 (Scotland) Order 2003, scallop fishing vessels are permitted to tow up to a maximum of 8  
182 individual dredges per side in Scottish inshore waters (out to six nautical miles). The Order also  
183 prohibits the use of “French” dredges (a design incorporating water deflecting plates and rigid  
184 fixed teeth). The Firth of Clyde scallop fleet is also subject to a weekend ban (Dobby et al.  
185 2012). Unofficial observations made by the Community of Arran Seabed Trust  
186 ([www.arrancoast.com](http://www.arrancoast.com)) indicate fishing effort by trawlers and dredgers has been consistently  
187 low outside the boundaries of Lamlash Bay Marine Reserve in recent years, averaging at 2-4  
188 fishing boats operating within the area per year since 2008. A small team of commercial  
189 scallop divers also operate locally within the area.

#### 190 Dive surveys

191 We began monitoring Lamlash Bay in 2010 (see Howarth et al. 2011). Initially, 40 sites were  
192 surveyed, half of which were located within the reserve and the other half outside. These  
193 surveys were then repeated and expanded in 2011, 2012 and 2013 by using a greater variety  
194 of survey techniques but reducing the number of study sites. Therefore we surveyed 28 sites in  
195 2011, 31 sites in 2012, and 32 sites in 2013. Again, these sites were divided so that half fell  
196 within the boundaries of the marine reserve (Fig. 1). Sites were chosen so that each one within  
197 the reserve could be paired with at least one other suitable control outside, based on similar  
198 depth and predominant substrate type (S1-4). It must be noted that this matching of sites was  
199 based on visual inspection of the substrate. Ideally, data on several physical characteristics of  
200 these sites (e.g. particle size analysis, current speed, percentage cover of benthic habitats)

201 would have been collected prior to protection to ensure these sites were statistically similar.  
202 However, no such data existed prior to protection and the collection of such physical data was  
203 beyond the scope of this study. Then again we did collect data on the percentage cover of  
204 benthic habitats but this only began two after the reserve had been established; at which point  
205 differences in seafloor habitats would be expected between sites protected and unprotected  
206 from fishing gears.

207 Due to lack of data and prior knowledge of the area, the initial experimental design was a little  
208 unbalanced. For example, 12 deep muddy sand sites were surveyed outside the reserve in  
209 2010 compared to just 6 inside. This improved with each survey, and by 2012 our experimental  
210 design was fully balanced. Sites were limited to areas of the seabed that were shallow enough  
211 to remain within diver no decompression limits (i.e. <30m depth). Surveys were also  
212 conducted parallel to depth contours to ensure the depth of a single survey did not change by  
213 more than 3m.

214 Transects were surveyed along a 50m leaded line that was laid out straight across the seabed.  
215 GPS coordinates used for surveys in 2010 and 2011 provided the start and end location of each  
216 transect. Attached to both ends of the leaded line were weighted anchors to hold the line in  
217 place, in addition to two floating buoys which reached the surface. A team of two divers then  
218 made their way from one end of the transect to the other, recording the abundance of all  
219 adult unattached scallops and other megafauna (e.g. fish, echinoderms and crustaceans)  
220 encountered within 1.5m either side of the transect. The width of the transect was marked by  
221 a 3m long pipe that the divers pushed ahead of themselves, creating a total area surveyed of  
222 150m<sup>2</sup> for each transect. To generate semi-quantitative estimates of the abundance of juvenile  
223 scallops (taken to be any scallop still attached to the substrata via byssal threads), a SACFOR  
224 abundance scale (superabundant, abundant, common, frequent, occasional, rare) was used  
225 (see Connor et al. 2004). Unfortunately, distinguishing between juvenile king and queen  
226 scallops whilst underwater was difficult and so these had to be grouped as one category. In  
227 addition, every adult scallop encountered along the transect was collected and brought back  
228 to the surface. These were then scrubbed with a wire brush (to help reveal their annual growth  
229 rings) and aged (Chauvaud et al. 2012), measured for shell length (Jennings et al. 2001) and  
230 returned to the sea.

231 A SACFOR abundance scale was also used by the divers to estimate the abundance of different  
232 benthic taxa. These were live maerl (e.g. *Phymatolithon calcareum* and *Lithothamnion glaciale*),  
233 dead maerl, macroalgae (e.g. *Laminaria* and *Ceramium* spp) sponges (e.g. *Pachymatisma*

234 *johnstonia*), anemones (e.g. *Cerianthus lloydi*), tunicates (e.g. *Clavelina lepadiformis* and  
235 *Diazona violacea*), hydroids (e.g. *Obelia geniculata*), bryozoans (e.g. *Alcyonidium diaphanum*  
236 and *Flustra foliacea*) and soft corals (e.g. *Alcyonium digitatum*). The SACFOR method was  
237 chosen to provide quick underwater estimates of benthic cover.

#### 238 Laboratory analysis

239 Scallop dissections were conducted in the years 2010, 2011 and 2013. For these years, 60 king  
240 scallops and 60 queen scallops were retained for dissection, with half of these individuals  
241 collected from within the reserve (under a permit from Marine Scotland), and the other half  
242 from outside. As the number of scallops taken from the reserve was limited, these scallops  
243 were chosen to cover the full range of different shell lengths observed within the Lamlash Bay  
244 area. Scallops were maintained in seawater to be dissected within 24 hours of their collection.  
245 All tissues were then dissected from the samples and blotted dry. From these tissues, the wet  
246 weight of the total tissue biomass, exploitable biomass (gonad weight and adductor muscle  
247 weight combined) and reproductive biomass (gonad weight only) were obtained. The  
248 importance of recording reproductive and exploitable biomass was considered two fold.  
249 Firstly, the mass of the gonad organ is an indicator of potential reproductive output (Shephard  
250 et al. 2010). Secondly, the adductor muscle is important both economically, as it partly decides  
251 the sale value of a scallop, and biologically as it forms the main mechanism of protection from  
252 predators such as the common starfish, *Asterias rubens* (Kaiser et al. 2007) and is used for  
253 swimming and escaping predation (Labrecque and Guderley 2011).

#### 254 **Data analysis**

##### 255 Multivariate analyses of juvenile scallop distribution

256 All data were tested for normality using histograms, boxplots, QQ plots and the Shapiro–Wilk  
257 test. These basic exploratory measures were conducted within the statistical package R  
258 ([www.r-project.org](http://www.r-project.org)). The Shapiro–Wilk test was chosen as it is widely accepted to be the most  
259 suitable for small and medium-size samples ( $N$  up to 2000; Royston 1982, Conover 1999). For  
260 statistical analysis, the SACFOR scale used to estimate juvenile scallop abundance and benthic  
261 cover was converted into numerical categories ranging from 0 to 6, where a value of 0 would  
262 indicate the absence of a taxon and 6 would represent the superabundance of a taxon as  
263 denoted by the SACFOR scale. The counts of adult scallops collected by both divers were  
264 pooled and adjusted for each transect to generate densities of organisms  $\times 100 \text{ m}^{-2}$ .

265 The abundance of juvenile scallops was compared between the two treatments (i.e. 'reserve'  
266 and 'fishing grounds') and across the years using a two-way ANOVA, with protection and year  
267 as the two fixed factors. Levene's test for equality of variances showed that there was  
268 homogeneity of variance between the two treatments ( $P > 0.05$ ). To determine whether  
269 environmental and ecological data recorded during diver surveys reflected the distribution and  
270 abundance of juvenile scallops, a Generalised Linear Model (GLM) was created. Predictor  
271 variables used in the GLM were treatment, depth, density of predators, and the SACFOR  
272 abundance estimates of maerl, macroalgae, sponges, hydroids, anemones, bryozoans,  
273 tunicates and soft corals. Predators of scallops were taken to be all species of starfish,  
274 although this is likely to be just a partial characterisation of the total predator assemblage for  
275 scallops (see Beukers-Stewart et al. 2005). Although our monitoring program collected higher  
276 resolution data on the percentage cover of different benthic taxa through the use of  
277 photographic surveys, these surveys did not begin until 2011 and therefore could not be used  
278 in this full analysis. Before construction of a GLM, scatter plot and intercorrelation matrices  
279 (based upon Spearman's rank correlation) were used to explore basic relationships and  
280 determine whether any variables were strongly intercorrelated (i.e.  $-0.7 \leq r \leq 0.7$ ) as such  
281 variables would not be allowed together within a GLM (Crawley 2005). As a Kolmogorov-  
282 Smirnov (K-S) test found juvenile abundance to not significantly differ from a Poisson  
283 distribution ( $P > 0.05$ ), a GLM based upon a Poisson family error was created in R. Backward-  
284 forward stepwise reduction was then used to create a minimal adequate model. Diagnostic  
285 and Cleveland dotplots were subsequently used to explore how well the models fitted the data  
286 and to identify any extreme outliers. An Analysis of Deviance utilising Pearson's Chi-square test  
287 ( $\chi^2$ ) was then conducted to determine if the reduced model accounted for significantly less  
288 variance than the full model.

#### 289 Density of king and queen scallops

290 Densities of king and queen scallops were compared between the two treatments and across  
291 the years using a two-way ANOVA as before. However, the density data had to be square root  
292 transformed to comply with the assumption of normality. Density data from 2013 was also  
293 split between individuals of sub-legal and legal size classes. For king scallops, this was any  
294 individual greater than 100 mm in length (Keltz and Bailey 2010). For queen scallops, a size of  
295 50 mm was used as the cut-off point (see above). Differences in the density of these size  
296 classes between the two treatments were tested for significance using a Mann-Whitney-

297 Wilcoxon test as the data no longer complied with the assumption of normality when split  
298 between different size classes.

299 In an attempt to investigate any spillover of scallops and / or a potential “halo effect” of  
300 reduced fishing effort close to the boundaries of the reserve (see discussion), the distance of  
301 each sampling site from the boundaries of the marine reserve was calculated in the  
302 Geographical software ArcGIS 10.1. The mean density of king scallops was then calculated for  
303 all sites within the reserve, and sites 0.5 km, 1 km, 1.5 km and >2 km away from the marine  
304 reserve. These data were then plotted against distance utilising error bars of  $\pm 1$  Standard Error  
305 (SE) and tested for significance using the Pearson product-moment correlation coefficient.

#### 306 Population structure of king and queen scallops

307 Size and age distributions were compared between the two treatments using a K–S two  
308 sample test for each year. In addition, a one-way ANOVA was used to test the final difference  
309 in mean size and age between treatments for data collected during the last year of monitoring  
310 in 2013. Size composition data on king scallops (greater than minimum legal landing size) were  
311 then compared with government fisheries size data on king scallops caught and landed within  
312 the Firth of Clyde region in 2012 and 2013 (data provided by Shona Kinnear of Marine Scotland  
313 Science). This was done by performing two K–S tests, one to compare the size of scallops  
314 landed within the Clyde against the size of scallops sampled within the reserve, and the other  
315 to compare the size of scallops landed within the Clyde against the size of scallops sampled  
316 outside the reserve.

#### 317 Mortality and growth rates

318 The mean density per age class of king scallops combined across all years was compared  
319 between the two treatments using a line graph. A catch curve analysis was then performed by  
320 transforming the data (natural log) and fitting linear trendlines. However, due to poor fit of the  
321 catch curve, this was only carried out for scallops greater than 5 years old old. The gradient of  
322 this trend line then provided an indication of total mortality ( $Z$ ). In addition, the mean length at  
323 age for both scallop species was plotted using the statistical software Simply Growth (version  
324 1.7, <http://www.pisces-conservation.com/>) and fitted with two Von Bertalanffy growth curves  
325 to the separate treatments. The log-likelihood ratio test of co-incident curves (Kimura 1980)  
326 was then used to test whether the two sampled population curves would differ from a curve  
327 created by combining the two sampled populations.

328 Biomass data

329 For the years where scallop dissections were conducted, exploitable and reproductive biomass  
330 for both species were tested for differences between the two treatments and across all years  
331 using two-way ANOVA. To investigate for any differences in the weight of gonads and adductor  
332 muscle per unit shell length between the reserve and outside, the weight of the adductor  
333 muscle and the reproductive biomass of king scallops greater than 100 mm length were  
334 plotted against shell length and fitted with linear trendlines. ANCOVAs were then performed  
335 which took into account differences in body size (i.e. with shell length as the covariate). For  
336 this, a Levene's Test of Equality of Error Variances showed homogeneity of variance between  
337 the two samples ( $P > 0.05$ ) and comparing the beta values revealed that samples had equal co-  
338 variance.

### 339 **Results**

340 Juvenile scallop abundance and the relationship with benthic habitats

341 The abundance of juvenile scallops was significantly greater within the marine reserve than  
342 outside for all years except 2013, when only two sites out of the 32 surveyed contained any  
343 juvenile scallops, both of which were located outside the reserve (Table 1). Year, protection  
344 and the interaction between the two were all found to be significantly influencing the  
345 abundance of juvenile scallops. Overall, the abundance of juvenile scallops has fluctuated from  
346 low to high every two years (Fig. 2), with 2010 and 2012 being years of high abundance, and  
347 2011 and 2013 being years of low abundance. It should be noted that graphical  
348 representations of these differences are very conservative as they treat differences between  
349 abundance categories as proportional, whereas measures of abundance on the SACFOR scale  
350 actually differ on an exponential scale.

351 In 2010, we found the higher levels of juvenile scallop abundance to be associated with greater  
352 levels of macroalgae and other nursery habitats growing within the marine reserve's  
353 boundaries (see Howarth et al. 2011). To further explore these relationships, SACFOR  
354 estimates of benthic cover and juvenile scallop abundance were combined for the years 2010  
355 and 2012 (i.e. years of high juvenile scallop abundance). After employing backward-forward  
356 stepwise reduction, a GLM indicated protection and the presence of macroalgae, sponges and  
357 hydroids to be significantly influencing the distribution of juvenile scallops (Table 2). This  
358 reduced model accounted for 66% of the variance in juvenile scallop abundance and did not  
359 explain significantly less variance than the full model (Pearson's Chi-squared;  $df = 67$ ,  $\chi^2 = 0.78$ ,

360  $P > 0.05$ ). The relationship between juvenile scallop abundance and the presence of  
361 macroalgae was found to be positive (Fig. 3a) as was their relationship with hydroids (Fig. 3b).  
362 A parallel study (Howarth et al. in review) revealed the percentage cover of these benthic  
363 habitats to be significantly greater within the reserve than outside, and that their abundance  
364 steadily increased over the study period. In contrast, the relationship between juvenile  
365 scallops and sponges was negative.

#### 366 Comparisons of scallop density

367 When monitoring began in 2010, the mean density of king scallops was initially lower within  
368 the boundaries of the marine reserve; estimated at  $6.2 \text{ individuals} \times 100 \text{ m}^{-2}$  ( $\pm 2.1 \text{ SE}$ ) within  
369 the reserve compared to a value of  $7.6$  ( $\pm 2.3 \text{ SE}$ ) outside the reserve. However, surveys  
370 conducted over the following three years revealed that the density of king scallops had  
371 steadily increased within the reserve but decreased outside (Fig. 4). Despite these apparent  
372 differences, a two-way ANOVA identified neither year nor level of protection (i.e. in or outside  
373 the reserve) as having a significant influence on king scallop density (Table 3).

374 Compared to king scallops, queen scallop abundance fluctuated greatly over the study period  
375 (S5). In 2010, queen scallop densities did not differ between the reserve and outside;  
376 estimated at densities of  $6.1$  ( $\pm 1.8 \text{ SE}$ ) and  $6.0$  ( $\pm 2.1 \text{ SE}$ )  $\times 100 \text{ m}^{-2}$  in and outside the reserve  
377 respectively. Since then, the density of queen scallops has been in decline, fluctuating from  
378 being greater within the reserve some years, to being lower within the reserve for others. For  
379 example, the density of queen scallops was 206% greater within the reserve in 2011, but fell to  
380 just 29% greater in 2012, before falling to 30% lower within the reserve than outside in 2013.  
381 In 2013, the density of queen scallops hit a low of  $3 \times 100 \text{ m}^{-2}$  ( $\pm 0.8 \text{ SE}$ ) inside the reserve and  
382  $2.3$  ( $\pm 0.9 \text{ SE}$ ) outside. As a consequence of these strong yearly fluctuations, multivariate  
383 analysis found only the year to significantly affect queen scallop density (Table 3).

384 Splitting scallop density data between sub-legal and legal size classes appeared to generate  
385 differences between the reserve and outside (Fig. 5). King scallops over 100 mm in length (i.e.  
386 individuals of legal landing size) were on average 79.3% more abundant within the reserve  
387 than outside in 2013. However, this trend was not significant (Mann-Whitney:  $U = 84$ ,  $N = 32$ ,  $P$   
388  $> 0.05$ ). Similarly, queen scallops over 50 mm were 39% more abundant within the reserve  
389 than outside but was also non-significant (Mann-Whitney:  $U = 71$ ,  $N = 32$ ,  $P > 0.05$ ). In contrast,  
390 the mean density of king scallops less than 100 mm was 80% lower within the reserve than  
391 outside (Mann-Whitney:  $U = 84$ ,  $N = 32$ ,  $P > 0.05$ ) and queen scallops less than 50 mm were

392 96% less abundant within the reserve (Mann-Whitney:  $U = 118$ ,  $N = 32$ ,  $P > 0.05$ ). Again, none  
393 of these differences were significant.

394 Plotting the mean density of king scallops combined for all years against distance from the  
395 boundaries of the marine reserve revealed a strong spatial interaction (Fig. 6). Scallop density  
396 significantly declined with increasing distance from the marine reserve (Pearson Correlation;  $N$   
397 = 91,  $R = -2.4$ ,  $P < 0.05$ ). In fact, sites within or close to the marine reserve supported scallop  
398 densities three times greater than sites located over two kilometres away.

#### 399 Comparisons of population structure

400 For both scallop species, the mean size and age were significantly greater within the marine  
401 reserve than outside across all years (S6). In 2010, king scallops were on average 18 mm larger  
402 (ANOVA,  $F_{(1,109)} = 40.45$ ,  $P < 0.05$ ) and 1.1 years older (ANOVA,  $F_{(1,109)} = 42.99$ ,  $P < 0.05$ ) within  
403 the reserve than outside. In 2013, these differences were greater with king scallops being on  
404 average 28 mm larger (ANOVA,  $F_{(1,250)} = 66.51$ ,  $P < 0.05$ ) and 1.7 years older (ANOVA,  $F_{(1,250)} =$   
405  $47.88$ ,  $P < 0.05$ ) within the reserve than outside. Queen scallops were on average 13 mm larger  
406 (ANOVA,  $F_{(1,108)} = 11.96$ ,  $P < 0.05$ ) and 0.8 years older (ANOVA,  $F_{(1,108)} = 10.88$ ,  $P < 0.05$ ) within  
407 the reserve than outside in 2013.

408 Comparing the overall size and age distributions for both species of scallop between the two  
409 areas also revealed scallops within the marine reserve to be made up of significantly older and  
410 larger individuals (Table 4). In greater detail, the size (Fig. 7) and age (Fig. 8) of king scallops  
411 were continually higher within the reserve for all four years. In 2010, king scallops peaked at  
412 131-140 mm in length and 4 years in age within the reserve, and at 101-110 mm and 2 years in  
413 age outside. The subsequent year saw this peak size class within the reserve strengthen whilst  
414 the peak age class increased to 6 years. This was then followed by the peak size class within  
415 the reserve increasing to 141-150 mm in 2012 and finally becoming bi-modal in 2013. In  
416 contrast, outside the reserve scallop densities declined across all size and age classes after the  
417 first year of monitoring. Subsequent years saw scallop densities outside the reserve recover  
418 slightly but remain at levels far lower than those observed in 2010. The year 2013 saw a boost  
419 in recruitment of young / small scallops outside the reserve. However, this event was far less  
420 pronounced within the marine reserve.

421 In 2010, queen scallops differed from king scallops in that their size (Fig. 9) and age (Fig. 10)  
422 distributions were similar. However, as observed for king scallops, queen scallop abundance  
423 suddenly declined across all age and size classes outside the reserve. Queen scallops then



424 began to recover in 2012 and 2013 to sizes and ages slightly lower than those observed within  
425 the reserve.

426 Utilising government data on the size composition of king scallops caught and landed within  
427 the Firth of Clyde region revealed scallop populations in the Lamlash Bay area to be made of  
428 larger individuals compared to the Firth of Clyde region as a whole (Fig. 11). When only  
429 scallops of legal landing size were considered, individuals sampled within the marine reserve  
430 were the largest in size, followed by individuals sampled directly outside it. For example, in  
431 2012, king scallops were on average 21 mm larger ( $\pm 1.77$  SE) within the reserve compared to  
432 those landed from the wider Firth of Clyde, whilst scallops located directly outside the  
433 boundaries of Lamlash Bay Marine Reserve were 5 mm larger ( $\pm 2.66$  SE). These size  
434 distributions were found to be significantly different in both 2012 (K-S;  $N = 8966$ ,  $Z = 3.54$ ,  $P <$   
435  $0.05$ ) and 2013 (K-S;  $N = 9241$ ,  $Z = 3.74$ ,  $P < 0.05$ ).

#### 436 Comparisons of mortality rates

437 Combining the mean density-at-age data for all four years also revealed distinct differences in  
438 the population dynamics of king scallops between the two areas (Fig. 12a). Catch curve  
439 analysis (Fig. 12b) of these data for scallops aged between 5-10 years (natural log transformed)  
440 produced linear regressions that estimated the total mortality of scallops in the fished area ( $Z$   
441  $= 0.89$ ) to be higher than in the closed area ( $Z = 0.77$ ) (Fig. 12b).

#### 442 Comparisons of growth rates

443 Overlaying Von Bertalanffy growth curves for king scallops within and outside the reserve  
444 across all years suggested a faster instantaneous growth rate (or more accurately, rate of  
445 approach to theoretical maximum size) for scallops within the reserve ( $k = 0.46$ ,  $L_{\infty} = 151.01$ ,  $T_0$   
446  $= 0.13$ ) compared to outside ( $k = 0.38$ ,  $L_{\infty} = 153.18$ ,  $T_0 = 0.13$ ). The Kimura likelihood ratio test  
447 of co-incident curves revealed that these two growth models were significantly different from  
448 one another ( $RSS_{\omega} = 26784.47$ ,  $X_2 = 6.77$ ,  $df = 1$ ,  $P < 0.05$ ). In contrast, there was no difference in  
449 growth rates between in and outside the reserve for queen scallops ( $RSS_{\omega} = 10215.69$ ,  $X_2 = 5.30$ ,  
450  $df = 1$ ,  $P > 0.05$ ). Plotted growth curves are available in S 7.

#### 451 Comparisons of exploitable and reproductive biomass

452 For the years in which scallop dissections were conducted, the exploitable (Fig. 13a) and  
453 reproductive (Fig. 13b) biomass of king scallops were substantially greater within the reserve

454 than outside. In 2010, the average exploitable and reproductive biomass of king scallops was  
455 18% and 39% greater within the reserve respectively. The following years saw the biomass of  
456 king scallops increase within the reserve but remain relatively static outside. By 2013, the  
457 exploitable and reproductive biomass of king scallops within the reserve had increased to  
458 become 2 and 2.5 times more than in the fished area. Two-way ANOVA found level of  
459 protection, but neither year nor the interaction between the two, to significantly affect king  
460 scallop biomass (Table 5).

461 Similar to the fluctuations in queen scallop density, the exploitable and reproductive biomass  
462 of queen scallops also fluctuated greatly over time. In 2010, there was little difference in both  
463 the exploitable and reproductive biomass of queen scallops between the reserve and outside.  
464 However, in 2011, the exploitable biomass of queen scallops tripled within the reserve before  
465 returning to approximately 2010 levels in 2013. Overall, the exploitable biomass of queen  
466 scallops was higher within the reserve across all years. In contrast, reproductive biomass was  
467 lower within the reserve across all years and also fluctuated substantially. Two-way ANOVA  
468 found level of protection, but not year nor the interaction between the two, to significantly  
469 influence the exploitable biomass of queen scallops (Table 5). In comparison, level of  
470 protection, year and the interaction between the two were all found to significantly influence  
471 the reproductive biomass of queen scallops.

472 Plotting the exploitable and reproductive biomass of king scallops greater than 100 mm in  
473 length combined for all years against shell length revealed little difference between the  
474 reserve and outside, suggesting that the weight of gonads and adductor muscle per unit shell  
475 length were not greater within the reserve than outside. Confirming this, ANCOVAs that took  
476 into account differences in body size did not find any significant difference in the exploitable  
477 biomass (ANCOVA;  $F_{(1, 180)} = 0.05$ ,  $P > 0.05$ ) and reproductive biomass (ANCOVA;  $F_{(1, 180)} = 0.34$ ,  $P$   
478  $> 0.05$ ) of king scallops between the reserve and outside.

## 479 **Discussion**

480 This paper highlights a number of differences in the abundance, age, size and biomass of two  
481 commercially important scallop species between a fully protected marine reserve and  
482 surrounding fishing grounds. However, it must be stressed that there is no data available prior  
483 to the establishment of the reserve. Ideally, a before-after control-impact (BACI) approach  
484 would have been employed, capable of identifying that any differences between the reserve  
485 and outside were due to the protection afforded by the marine reserve (Hilborn et al. 2004;

486 Sale et al. 2005). As this was not possible, we instead compared sites within the reserve to  
487 reference sites located outside its boundaries over a study period of four years. In some cases,  
488 the differences between the reserve and fishing grounds significantly increased over time,  
489 meaning that the protection afforded by the marine reserve is likely to be responsible. For  
490 instance, both the abundance of juvenile scallops and the reproductive biomass of queen  
491 scallops displayed a significant interaction between year and protection. For all other cases, we  
492 have evidence that differences between the reserve and outside exist but cannot confidently  
493 conclude that protection is responsible for creating them.

494 Juvenile scallops were between two to five times more abundant within the marine reserve  
495 than surrounding areas. Their greater abundance was related to a greater presence of nursery  
496 habitat growing within the boundaries of the marine reserve. That is, the distribution of  
497 juvenile scallops was strongly positively associated with the presence of macroalgae and  
498 hydroids, showing that scallop spat settle more successfully in structurally complex habitats  
499 (Paul 1981; Minchin 1992; Bradshaw et al. 2001; Kamenos et al. 2004a, b). Although data prior  
500 to the establishment of the reserve was not collected, a parallel study (Howarth et al. in  
501 review) found the abundance of these nursery habitats to be twice as great within the reserve  
502 than on neighbouring fishing grounds, and that the abundance of these habitats had steadily  
503 increased within the reserve over the four year study period. Theory and empirical evidence  
504 suggest that differences between MPAs and references sites should become more pronounced  
505 the longer the reserve is established (Roberts et al. 2005; Edgar et al. 2014). These results  
506 therefore add to previous studies (e.g. Kaiser et al. 2000; Bradshaw et al. 2002; Howarth et al.  
507 2011) which indicate that protecting areas from fishing can allow seafloor habitats to recover,  
508 and as a result, can generate benefits that flow back to commercially important species. In the  
509 long term, these effects are highly likely to increase the numbers of juvenile scallops entering  
510 the adult stock as a greater proportion of juveniles survive to reach maturity (Beukers-Stewart  
511 et al. 2003; Vause et al. 2007).

512 Over the four year study period, we found the abundance of juvenile scallops to fluctuate  
513 greatly, alternating between high and low levels every two years. Since king and queen  
514 scallops typically undergo at least one major spawning event around spring/summer (Brand  
515 2006; Orensanz et al. 2006), and as our dive surveys were conducted between June-  
516 September, it is unlikely that they were conducted too early in the year to detect the presence  
517 of juvenile scallops. Rather, it is more likely that the populations were exhibiting the strong  
518 natural fluctuations in recruitment typically observed in most scallop species (Paulet et al.

519 1988; Orensanz et al. 1991; Beukers-Stewart et al. 2003; Beukers-Stewart and Beukers-Stewart  
520 2009). Nonetheless, it is argued that by allowing populations and spawning stock biomass to  
521 recover, MPAs should offer higher and less variable catches in adjacent fishing grounds  
522 (Bradshaw et al. 2001; Roberts et al. 2001, 2005). The following lines of discussion support  
523 this.

524 When monitoring began in 2010 it was concluded that, despite providing apparent benefits to  
525 juvenile scallops, the reserve in Lamlash Bay was yet to have a significant effect on the density  
526 of adult scallops (Howarth et al. 2011). Likewise, in this extended study, neither time, nor level  
527 of protection (i.e. in or outside the reserve), nor the interaction between the two were found  
528 to be significantly affecting the density of adult king scallops. This result was surprising as the  
529 density of king scallops had been consistently greater within the reserve than outside for the  
530 past three years, and their density within the reserve had steadily increased over the four year  
531 study period. Even so, as scallops breed by releasing both male and female gametes into the  
532 water column during synchronised spawning events (Brand 2006), any increase in population  
533 density will likely result in a rapid increase in fertilisation success (Macleod et al. 1985; Stoner  
534 and Ray-Culp 2000; Vause et al. 2007).

535 Despite finding no significant difference in the density of adult scallops between the two  
536 treatments, we did find that scallop density significantly declined with increasing distance from  
537 the boundaries of the marine reserve. Many studies have detected similar gradients  
538 (McClanahan and Mangi 2000; Harmelin-Vivien et al. 2008; Halpern et al. 2010; Ludford et al.  
539 2012) and several possibilities could explain such a trend. Environmental gradients and spatial  
540 heterogeneity of habitats are known to result in gradients of abundance (Vandeperre et al.  
541 2011) but as our survey design was balanced (i.e. we surveyed an equal number of sites of  
542 similar habitat and depth) this is unlikely. It could be that spillover of larvae and juveniles from  
543 within the reserve to outside has occurred, and that its effects diminish with increasing  
544 distance from the reserve (Kellner et al. 2007). This is possible as the larvae of these two  
545 species typically spend 3–6 weeks in the water column where they can disperse over  
546 considerable distances (Brand et al. 1980; Macleod et al. 1985). Then again, it may be that  
547 fishers have been avoiding areas immediately outside and around the marine reserve since its  
548 establishment, meaning fishing pressure would consequently increase with distance from the  
549 reserve. This could be occurring as the marine reserve protects the north entrance to Lamlash  
550 Bay (see Fig. 1), meaning fishers may choose to bypass the general area. Otherwise they would  
551 have to haul their fishing gears whilst they passed over the reserve, or attempt to turn around

552 while fishing in the unprotected southern half of Lamlash Bay. As scallop densities were similar  
553 out to 1 km away from the reserve, but then suddenly dropped at 1.5 km and remained similar  
554 out to >2 km, this may be evidence of such a “halo effect” occurring. Furthermore, scallops  
555 from the wider Clyde were substantially smaller than those measured in the Lamlash Bay area,  
556 further supporting this idea.

557 We also found evidence that Lamlash Bay Marine Reserve was allowing the age and size  
558 structure of scallop populations within its boundaries to return to a more natural and  
559 extended state. The size and age of both scallop species were consistently greater within the  
560 reserve than surrounding areas over the study period. On average, we found king scallops to  
561 be 28 mm larger and 1.7 years older within the reserve than outside. Likewise, we found  
562 queen scallops to be 13 mm larger and 0.8 years older within the reserve. King scallops within  
563 Lamlash Bay Marine Reserve were also substantially larger than king scallops caught and  
564 landed by the wider Firth of Clyde scallop fishery, suggesting this was not just a localised  
565 phenomenon. By the end of our study, the exploitable biomass of king scallops within the  
566 reserve was twice than what was observed outside, and the reproductive biomass 2.5 times  
567 greater. As there was no significant interaction between protection and year, we could not  
568 definitively attribute this difference to protection. Nevertheless, the greater levels of  
569 reproductive biomass within the reserve should mean the reserve is contributing  
570 disproportionately to recruitment compared to the size of area it protects by exporting large  
571 amounts of larvae to surrounding areas (Beck et al. 2001; Gibb et al. 2007; Laurel et al. 2009;  
572 Harrison et al. 2012). Furthermore, because scallops are broadcast spawners, the high  
573 densities of scallops inside the reserve would have increased the proximity of individuals to  
574 one another, which will enhance rates of fertilisation success and further add to levels of larval  
575 export (Beukers-Stewart et al. 2005).

576 The greater abundance, age and size of scallops within the reserve are consistent with the  
577 hypothesis that closing areas to fishing can protect individuals within their boundaries from  
578 fishing-induced mortality. Although mortality rates were indeed lower within the reserve than  
579 outside, we expected it to be far lower than the 0.77 observed in this study. For instance, a  
580 study within a closed area off the Isle of Man estimated the natural mortality of king scallops  
581 to be just 0.22 (Beukers-Stewart et al. 2005). The difference between our study and the one in  
582 the Isle of Man can be explained by the relatively young age of the reserve in Lamlash Bay. This  
583 area only became protected in 2008, meaning any scallops older than 2 years old had been  
584 subject to fishing pressure, and still applies to any individuals greater than 5 years sampled in

585 2013 at the end of this study. Consequently, these older year classes remained at a low density  
586 throughout our study. Furthermore, due to poor fit of the catch curve, we were only able to  
587 plot the catch curve analysis on scallops older than 5 years, meaning all individuals within this  
588 bracket would have been subject to fishing prior to the reserve becoming established. In  
589 comparison, the Isle of Man closed area had been protected for over 14 years. It is therefore  
590 highly likely that in order to achieve results like those observed in the Isle of Man, Lamlash Bay  
591 marine reserve would have to be established for at least 10 to 15 years before it will give a  
592 true indication of the natural population and natural mortality. Still, the overall reduction in  
593 fishing pressure observed in this study should mean that scallops within the marine reserve are  
594 no longer being damaged by mobile fishing gears and having to divert energy into shell repair  
595 (Beukers-Stewart et al. 2005). One previous study off Devon, UK, found that this allowed  
596 scallops within the boundaries of protected area to invest a greater proportion of metabolic  
597 energy into body growth and gonad development (Kaiser et al. 2007). On the contrary, we  
598 observed no difference in the weight of adductor muscle or gonads per unit shell length  
599 between Lamlash Bay Marine Reserve and fishing grounds, in agreement with the study off the  
600 Isle of Man (Beukers-Stewart et al. 2005).

601 The differences between the Lamlash Bay Marine Reserve and control areas observed in this  
602 study are less pronounced than those documented in other MPAs (Beukers-Stewart et al.  
603 2005; Hart et al. 2013). However, those studies were conducted over a decade after MPA  
604 implementation and in control areas subject to much greater fishing pressure. If anything,  
605 these studies suggest further improvements in scallop stocks are likely to occur within Lamlash  
606 Bay Marine Reserve in the future, since it had only been established for 2-5 years during the  
607 period of study (Roberts et al. 2001, 2005). Our findings also present an interesting  
608 comparison to a recent study conducted in Wales, which found no evidence of scallop recovery  
609 within an MPA (Sciberras et al. 2013). The lack of response in that case was attributed to high  
610 levels of natural disturbance. However, this study was conducted during just the first 23  
611 months of protection and high levels of illegal fishing within the MPA have since been detected  
612 (Milford and West Wales Mercury 2012; Misstear 2012; Morris 2014). In contrast, due to  
613 almost constant visual surveillance of Lamlash Bay Marine Reserve by COAST and its members,  
614 illegal fishing has been comparatively rare in Lamlash Bay (VMS data Marine Scotland 2014). It  
615 is therefore possible that the action and involvement of the local community in establishing  
616 and monitoring Lamlash Bay Marine Reserve has contributed to its success in improving  
617 scallop stocks.

618 It should be noted that several other scientists have performed scallop surveys in Lamlash Bay.  
619 The first of these was done just a month after the reserve was established in October 2008  
620 (Axelsson et al. 2009). These surveys estimated the density of both scallop species to be  
621 around 3 individuals per 100 m<sup>2</sup>. In contrast, we estimated the densities of both scallop species  
622 to be between 6-8 per 100 m<sup>2</sup> in 2010. This difference could be taken as evidence of the  
623 reserve allowing scallop densities to return to more natural levels over the preceding two  
624 years. However, those early surveys utilised drop-down cameras to record the abundance of  
625 scallops. Diver surveys, such as those employed in our study, are thought to produce more  
626 accurate and reliable estimates of scallop density (Mason et al. 1982; Beukers-Stewart et al.  
627 2001) meaning direct comparisons cannot be made. Emphasizing potential differences  
628 between these two methodologies, drop down cameras employed by Boulcott et al. (2012)  
629 estimated the density of king scallops in 2010 to be between 4-5 individuals per 100 m<sup>2</sup>. In  
630 comparison, our study estimated king scallop density to be markedly higher at 6-7.5 individuals  
631 per 100 m<sup>2</sup>. It should be noted that, in agreement with our work, neither of these previous  
632 studies found significant differences in the density of adult inside and outside of the reserve.  
633 However, given the lower densities they detected, this would have been less likely than using  
634 our methodology.

635 In summary, we have presented several lines of evidence that suggest Scotland's first and only  
636 fully protected marine reserve is benefitting two commercially important scallop species. The  
637 growing abundance of nursery habitats within the marine reserve appears to be substantially  
638 increasing the settlement juvenile scallops, suggesting that protecting areas from fishing can  
639 generate ecological benefits that flow back to species commercially targeted by fisheries. Then  
640 again, for fisheries to truly benefit from marine reserves, it is essential that larvae, juveniles  
641 and adults originating from within the reserve spillover into surrounding fishing grounds where  
642 they can then contribute to landings (McClanahan and Mangi 2000; Stelzenmüller et al. 2007).  
643 The greater size, age and reproductive biomass we observed within the reserve should  
644 translate to higher reproductive output and scallop recruitment both within the marine  
645 reserve and surrounding fishing grounds, especially if these trends continue to increase over  
646 time (Pelc et al. 2010). Overall, our results support an increasing number of other studies  
647 which suggest the implementation of MPAs can be a useful tool in ecosystem-based fishery  
648 management. This is important as studies into the effects of MPAs are far less common in  
649 temperate and cold waters, and are particularly limited in Europe and the UK (Lester et al.  
650 2009; Caveen et al. 2012; Fenberg et al. 2012). Lamlash Bay is the first and only fully protected  
651 marine reserve in Scotland, and the only statutory reserve in the UK that was originally

652 proposed by a local community which bans all extractive activities (Prior 2011). Researching  
653 the marine reserve in Lamlash Bay has therefore offered a vital insight into the benefits that  
654 highly protected marine reserves can provide. In particular, this study highlights that full  
655 protection and support from the local community is likely to be highly important in maximising  
656 the effectiveness of MPAs as any illegal extraction would have further weakened the  
657 differences between Lamlash Bay Marine Reserve and surrounding fishing grounds.

658

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668

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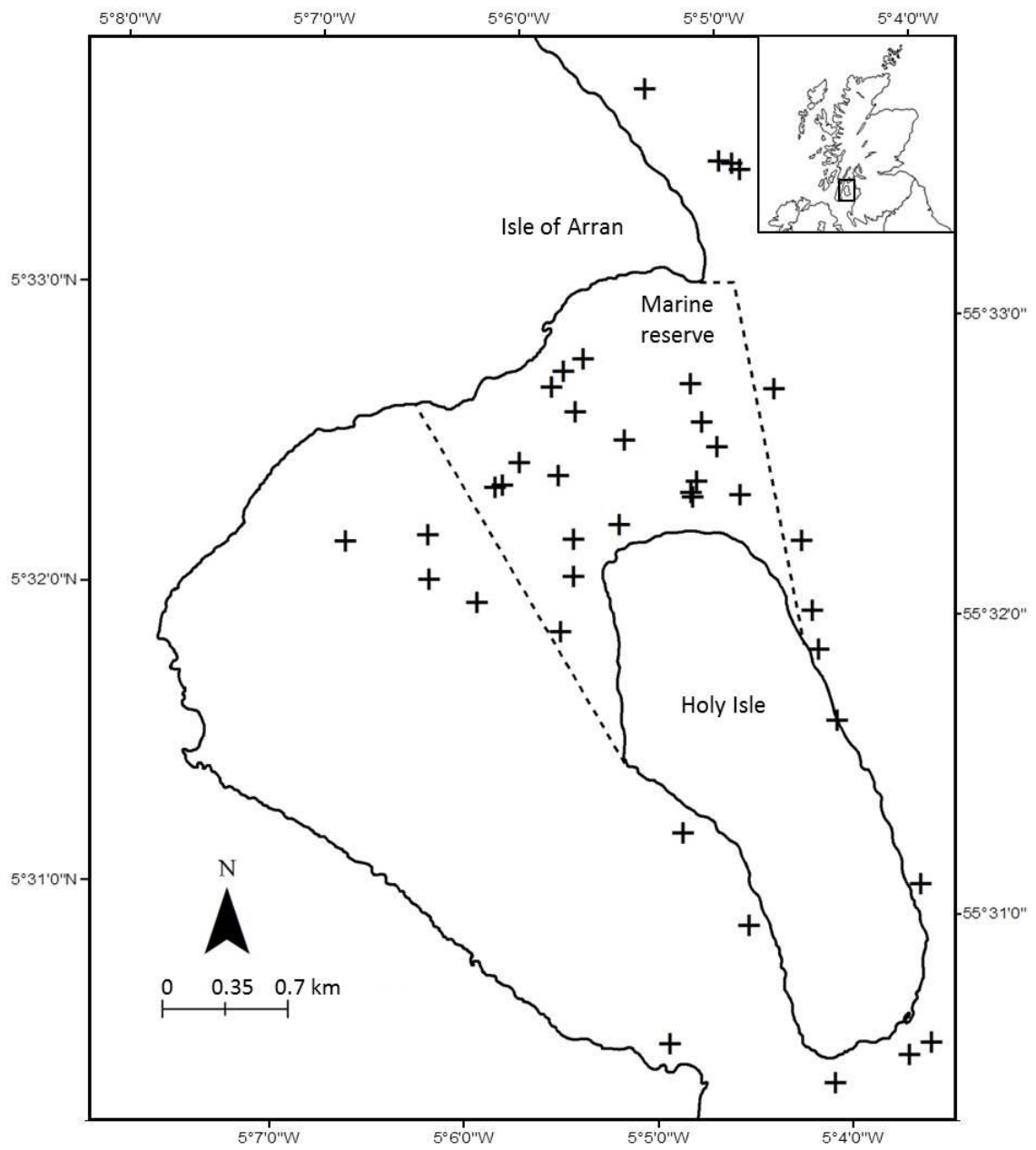
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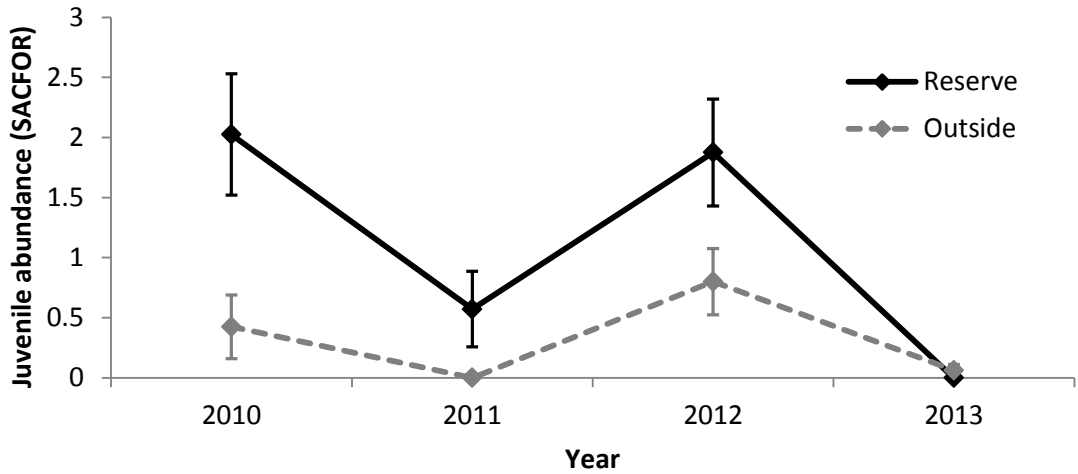


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2 **Fig. 1** Site locations of dive transects for all years. Also displayed are the boundaries of the  
3 Lamlash Bay fully protected marine reserve. The inset shows the location of the Isle of Arran  
4 off the west coast of Scotland, United Kingdom.

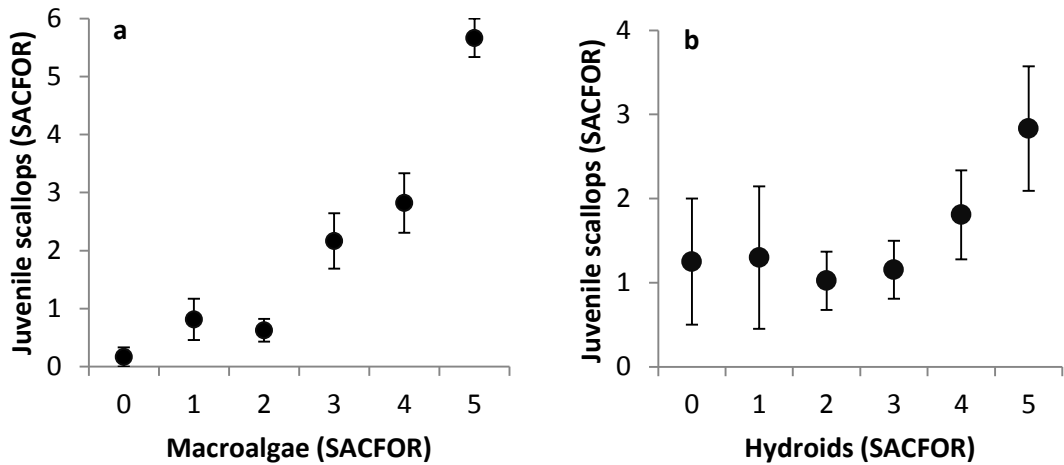
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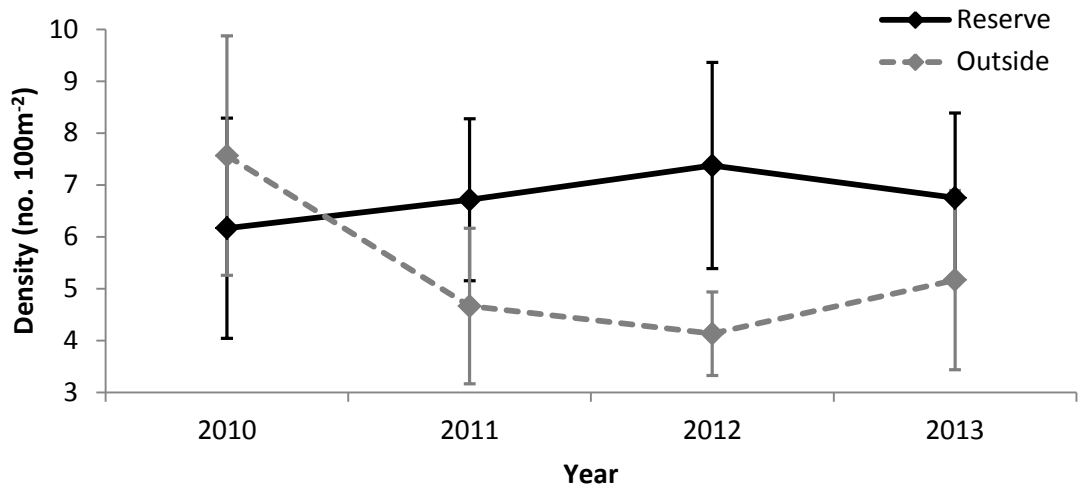
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7 **Fig. 2** The mean estimated abundance (SACFOR) of juvenile scallops within and outside the  
 8 fully protected marine reserve across four years. Error bars represent  $\pm 1$  SE.



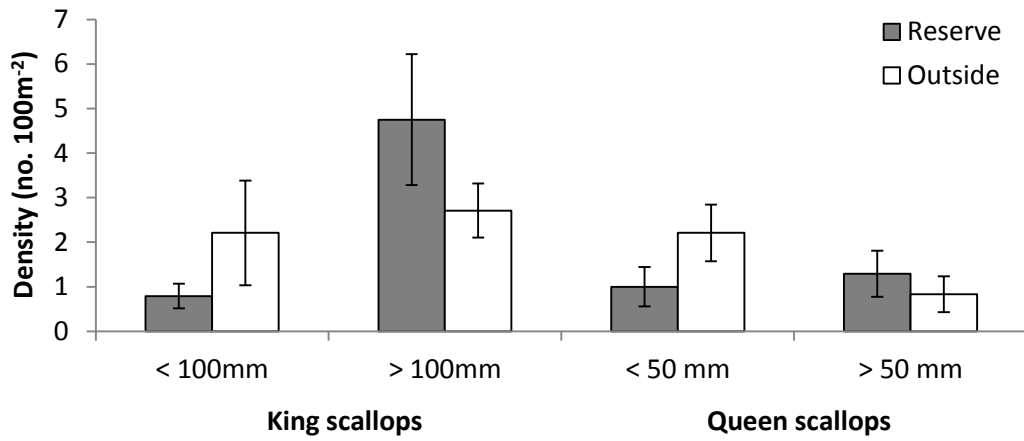
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10 **Fig. 3** Mean abundance of juvenile scallops in relation to the mean abundance of macroalgae  
 11 (a) and hydroids (b). These trends were highlighted as significant by a GLM. Error bars  
 12 represent  $\pm 1$  SE.



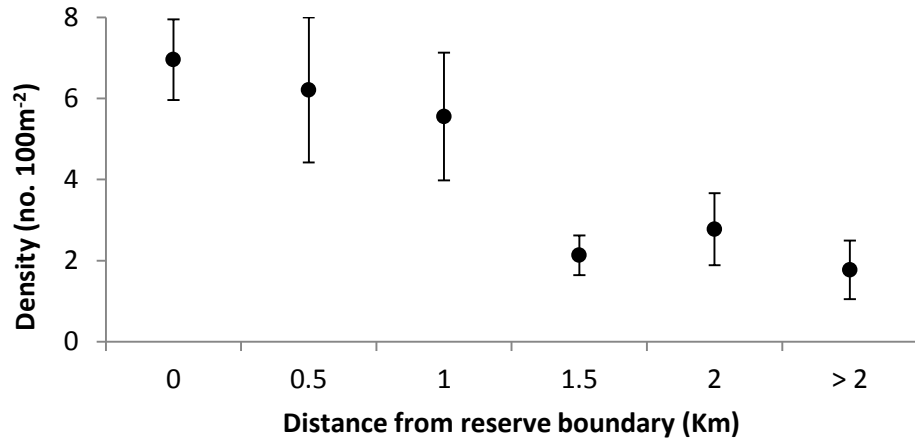
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**Fig. 4** The mean density of king scallops in and outside the fully protected marine reserve across four years. Error bars represent  $\pm 1$  SE.



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**Fig. 5** The density of different size classes of two scallop species sampled in 2013 within and outside a fully protected marine reserve. Error bars represent  $\pm 1$  SE.



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24 **Fig. 6** Mean density of king scallops for the years 2010-2013 plotted against distance from the  
 25 marine reserve. A distance of 0 represents those sites located within the marine reserve. Error  
 26 bars represent  $\pm 1$  SE.

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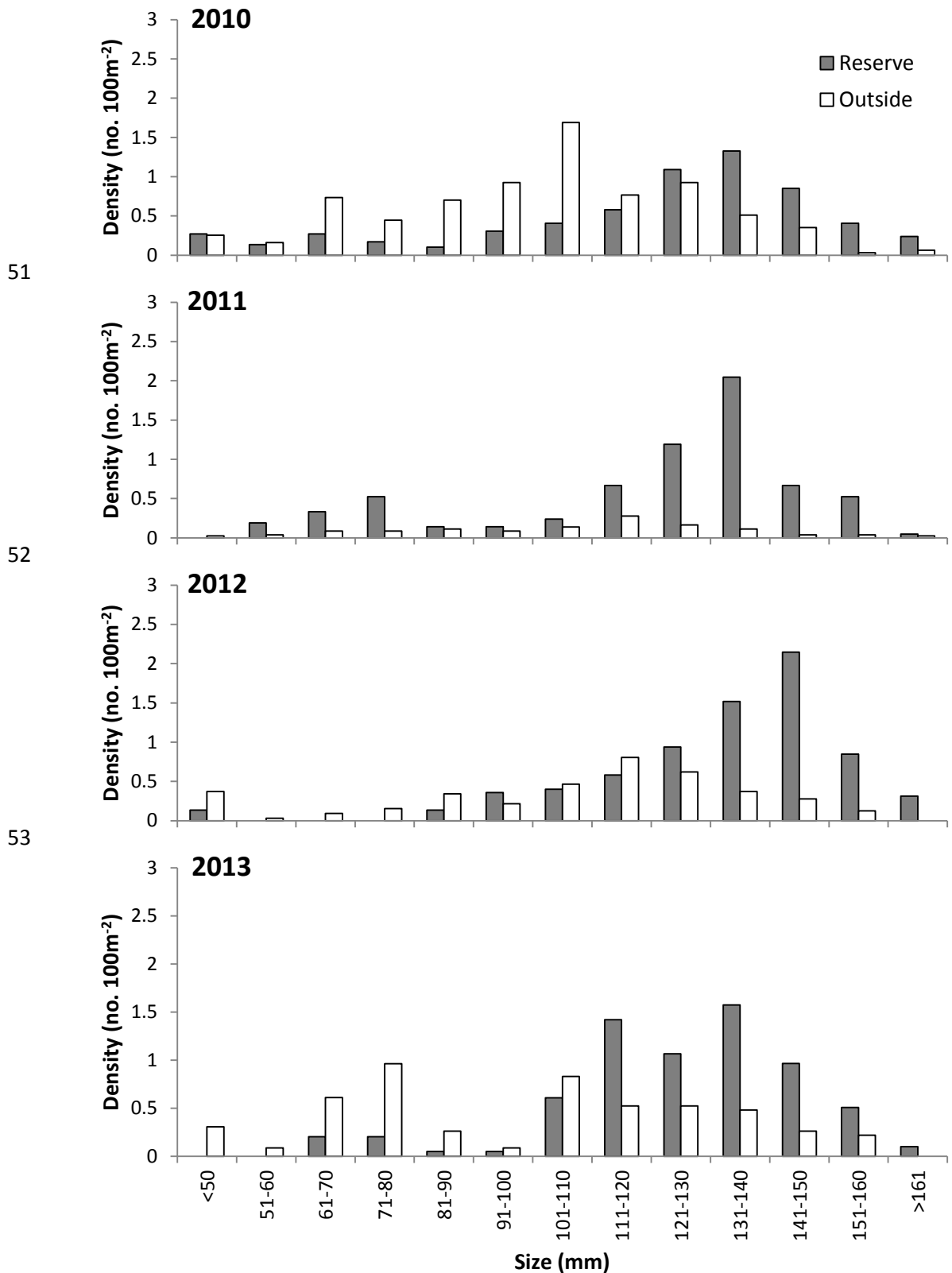
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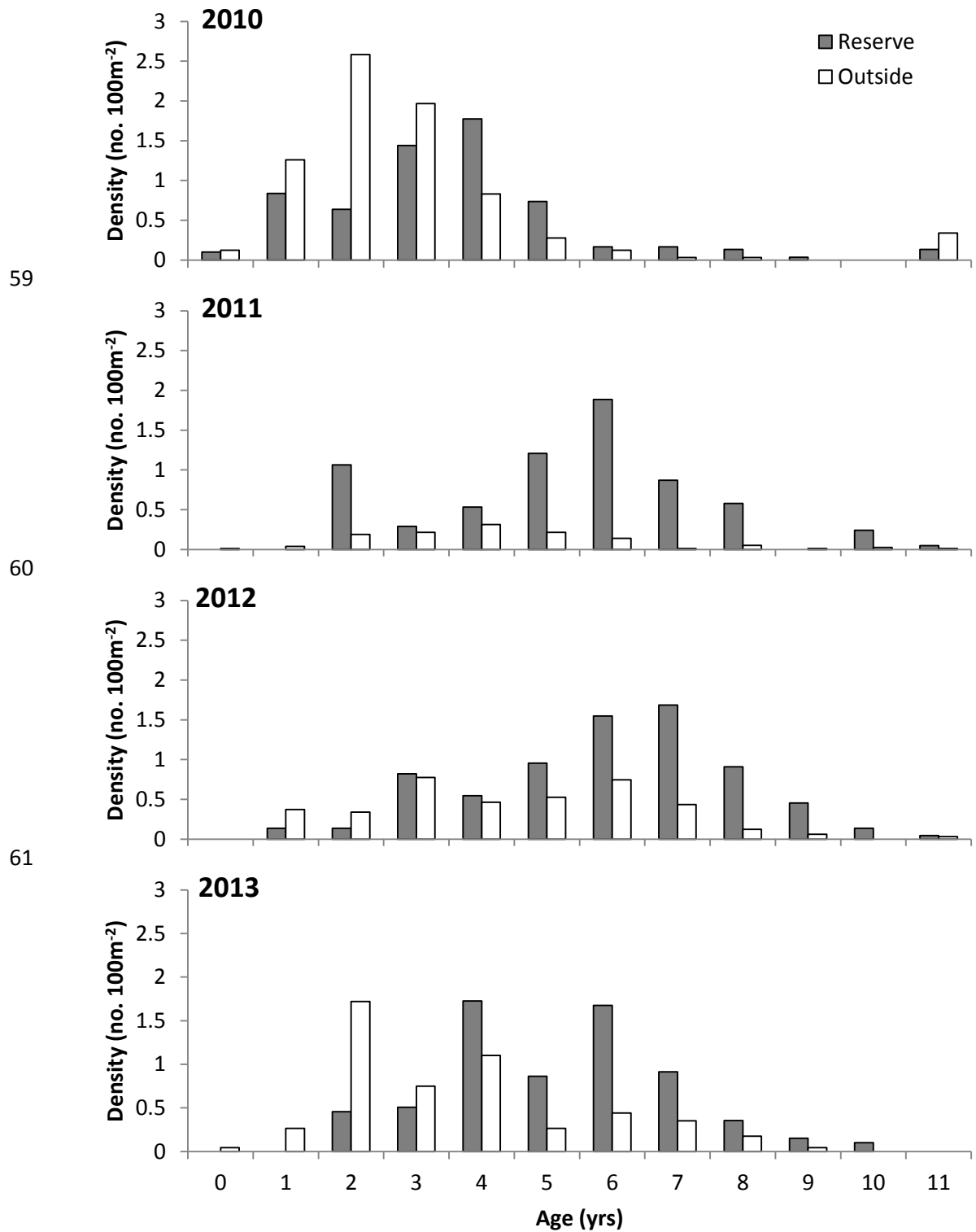
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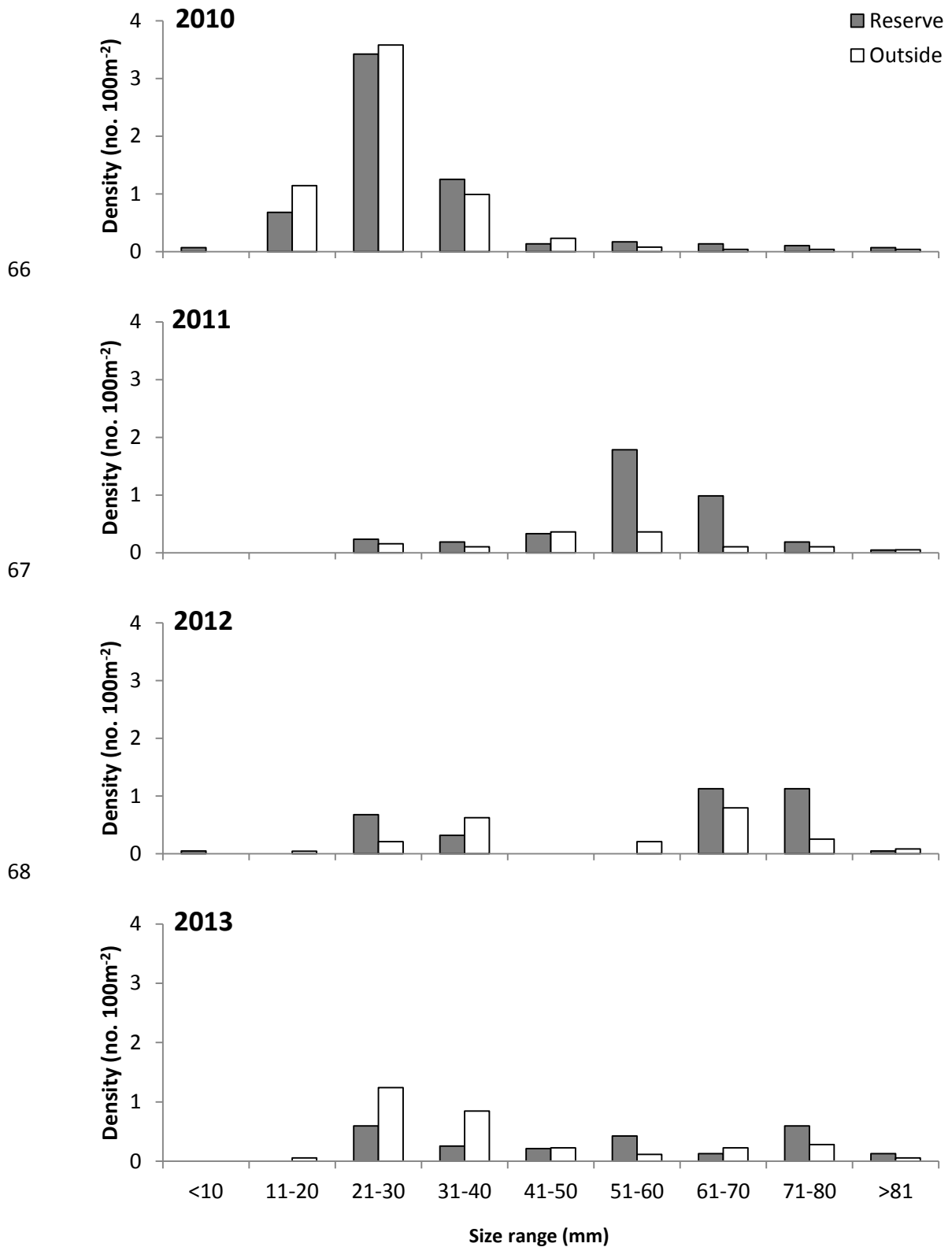
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 55 **Fig. 7** The size structure of king scallops sampled within and outside the fully protected marine  
 56 reserve across four years. The number (N) of individuals sampled from each population is  
 57 available in Table 4.  
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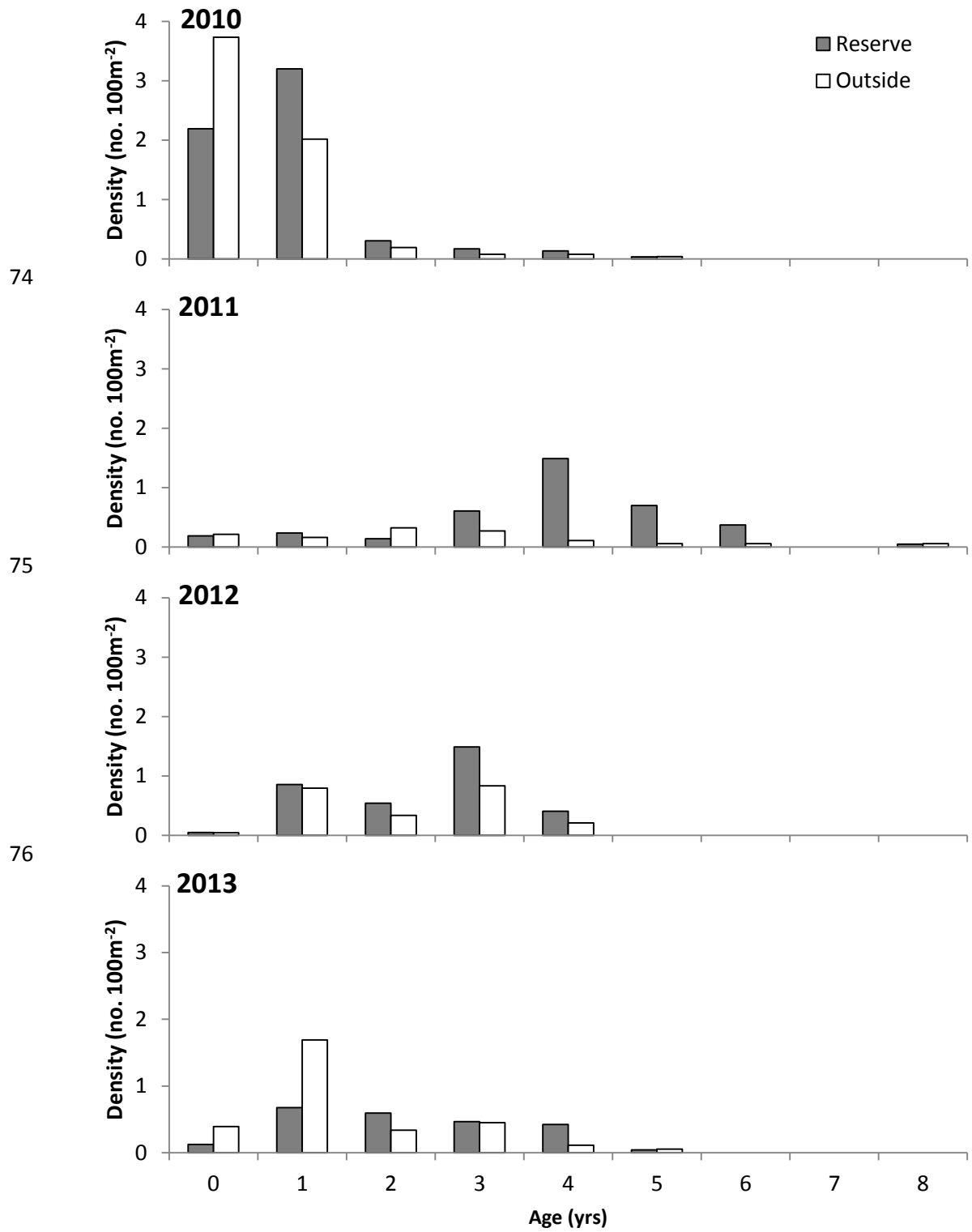


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 63 **Fig. 8** The age structure of king scallops sampled within and outside the fully protected marine  
 64 reserve across four years. The number (N) of individuals sampled from each population is  
 65 available in Table 4.

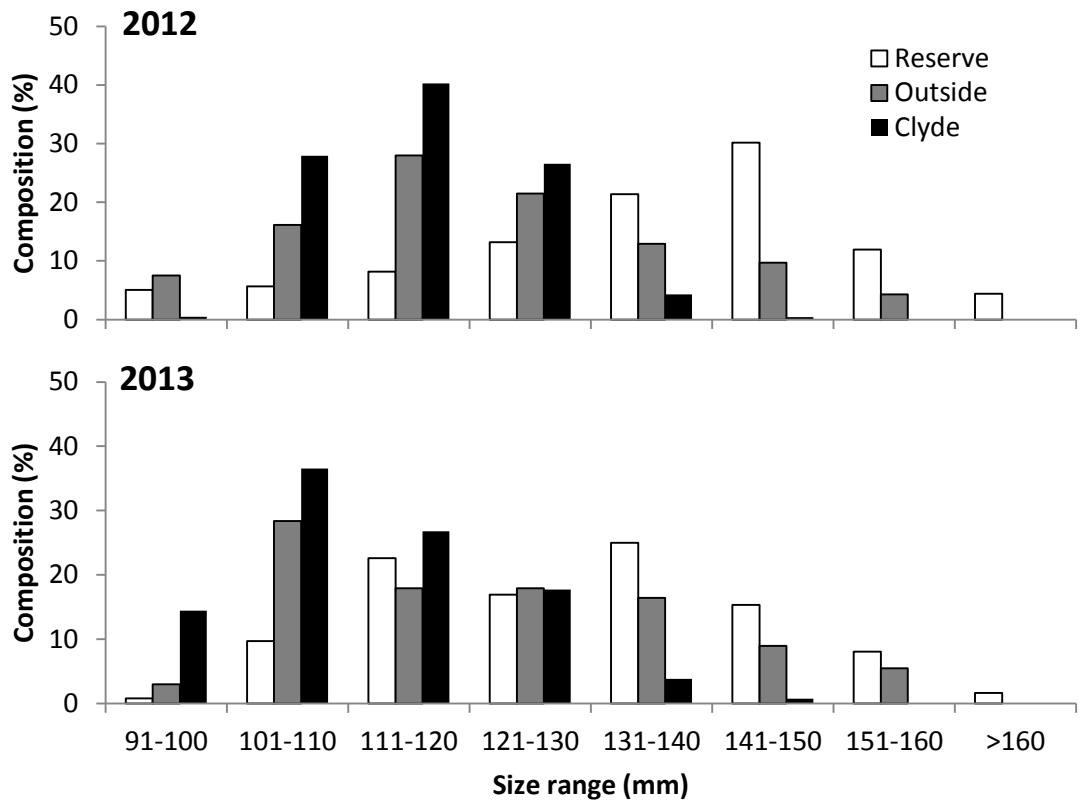


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70 **Fig. 9** The size structure of queen scallops sampled within and outside the fully protected  
 71 marine reserve across four years. The number (N) of individuals sampled from each population  
 72 is available in Tables 4.  
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77  
 78 **Fig. 10** The age structure of queen scallops sampled within and outside the fully protected  
 79 marine reserve across four years. The number (N) of individuals sampled from each population  
 80 is available in Table 4.



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83 **Fig. 11** The size composition of king scallops above legal landing size sampled within and  
 84 outside the fully protected marine reserve across two years. Also displayed is the size  
 85 composition of king scallops caught and landed within the Firth of Clyde region. Data provided  
 86 by Shona Kinnear of Marine Scotland - Science.

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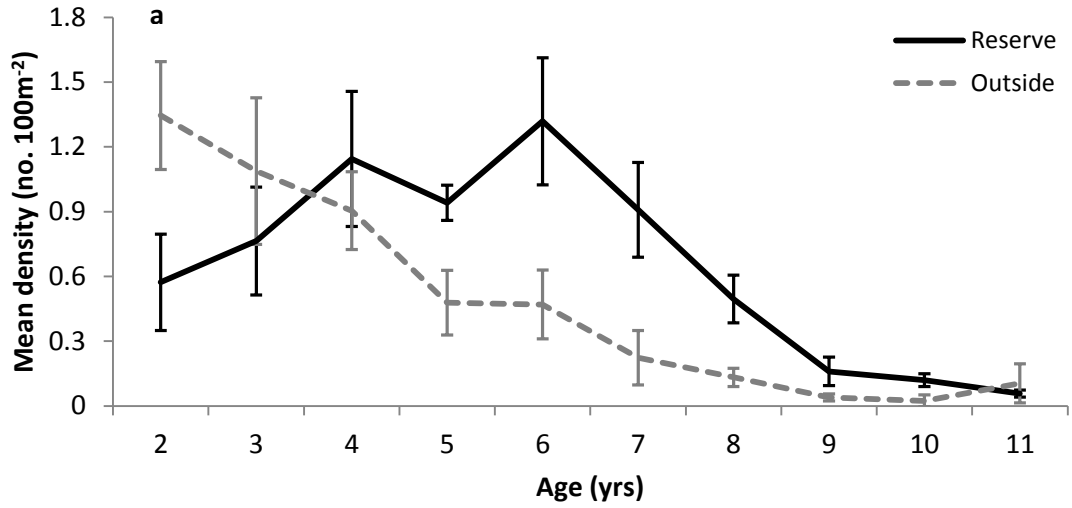
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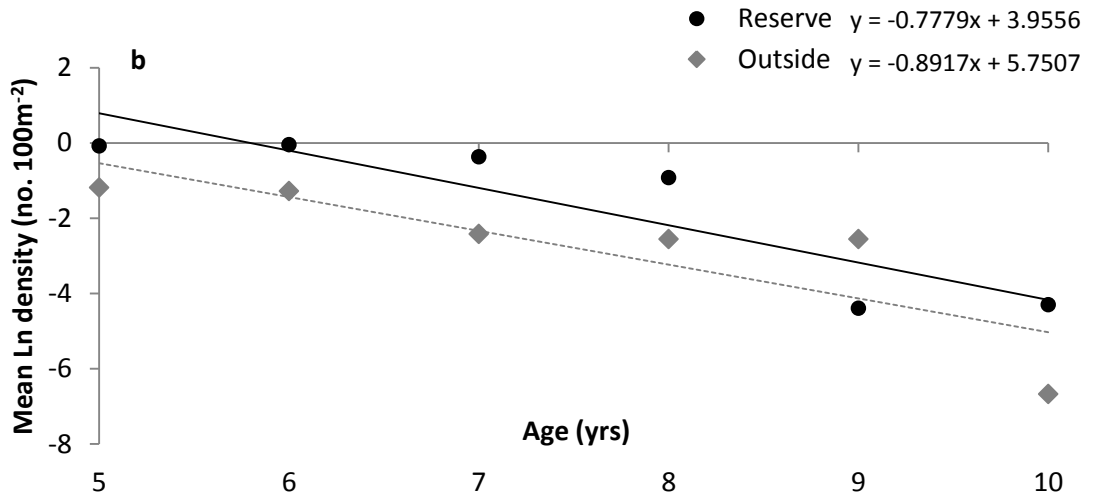
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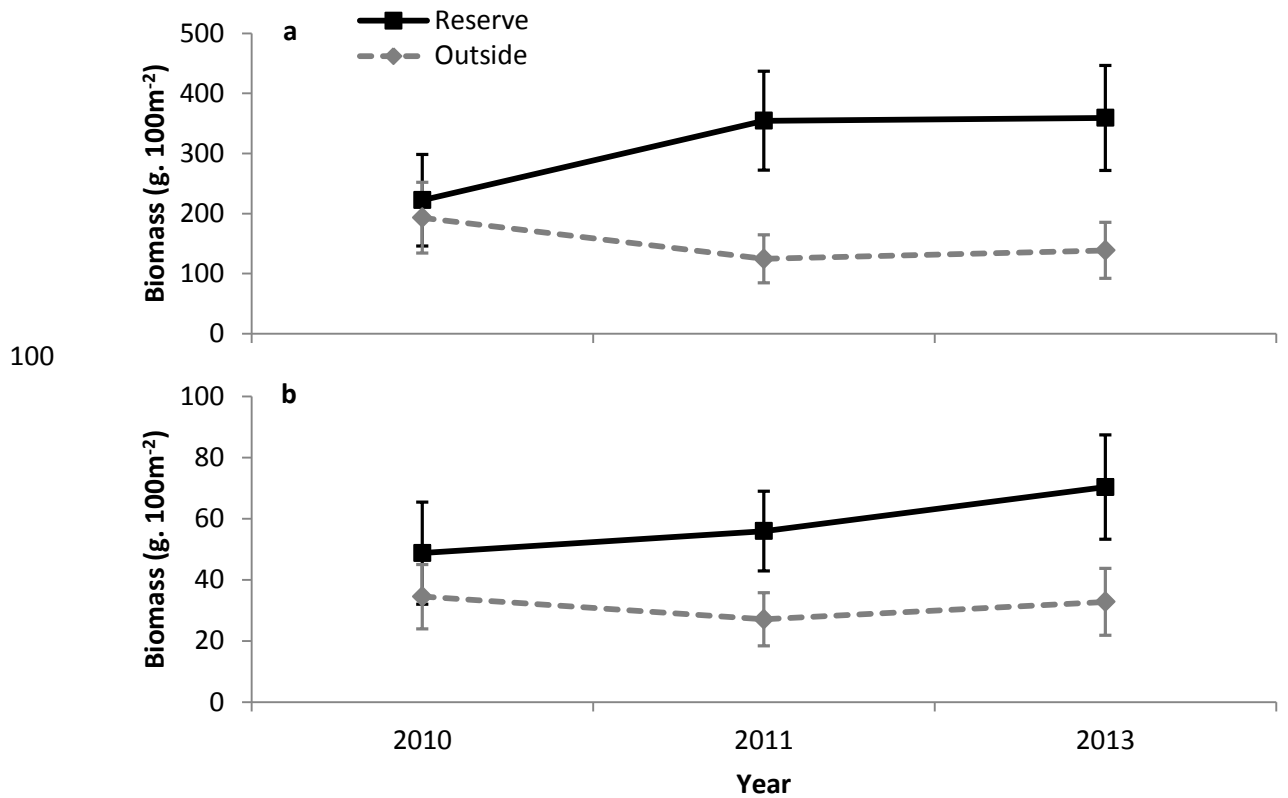


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97 **Fig. 12** (a) The density per age-class of king scallops within and outside the reserve across the  
 98 years 2010-2013. (b) Catch curve analysis (total mortality estimates) of king scallops within and  
 99 outside the reserve across the years 2010-2013.



101  
 102 **Fig. 13** The mean exploitable (a) and reproductive (b) biomass of king scallops within and  
 103 outside the fully protected marine reserve for the years when scallop dissections were  
 104 conducted. Error bars represent  $\pm 1$  SE.

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1 **Table 1.**Two-way ANOVA comparing juvenile scallop abundance between the marine reserve  
 2 and outside across the years 2010-2013. Significant results are denoted by (\*).

Test variable	SS	df	MS	F	P
Year	55.89	3	18.63	13.96	*<0.001
Protection	23.33	1	23.33	17.48	*<0.001
Year x Protection	18.57	3	6.19	4.63	*0.004
Residual	206.82	155	1.33		

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5 **Table 2** The reduced and full models were created from a Poisson GLM to test whether  
 6 environmental and ecological data reflected the distribution and abundance of juvenile  
 7 scallops. Significant terms are denoted by (\*).

Variables retained by reduced model			
Variable	SE	Z	P
Macroalgae	0.07	7.98	*<0.001
Hydroids	0.12	3.91	*<0.001
Sponge	0.16	-1.7	* 0.043
Protection	0.22	1.7	* 0.046
Variables removed from model			
Variable	SE	Z	P
Depth	0.04	-0.75	0.449
Dead maerl	0.06	-0.47	0.635
Live maerl	0.2	-0.8	4.432
Anemones	0.11	0.72	0.474
Soft coral	0.19	-1.78	0.076
Tunicates	0.1	-0.01	0.994
Bryozoans	0.11	-0.41	0.68

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17 **Table 3.** Two-way ANOVA comparing scallop densities (sqrt transformed) between the marine  
 18 reserve and outside across the years 2010-2013. Significant results are denoted by (\*).

Species	Test variable	SS	df	MS	F	P
King scallops	Year	0.14	3	0.05	0.02	0.99
	Protection	0.79	1	0.8	0.38	0.54
	Year x Protection	4.61	3	1.54	0.74	0.53
	Residual	254.3	123	2.1		
Queen scallops	Year	18.45	3	6.15	3.506	*0.01
	Protection	0.07	1	0.07	0.04	0.84
	Year x Protection	1.9	3	0.62	0.36	0.79
	Residual	215.78	123	1.75		

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22 **Table 4** Outputs from the Kolmogorov–Smirnov (K–S) 2 sample tests used to compare the size  
 23 and age distributions (% composition) of two commercially important species of scallop  
 24 located in and outside the fully protected marine reserve.

	Year	Size				Age	
		Reserve (N)	Outside (N)	KS-Z	P	K-S Z	P
King scallops	2010	181	237	4.12	* <0.001	3.38	* <0.01
	2011	139	98	2.83	* <0.001	2.59	* <0.01
	2012	162	125	3.97	* <0.001	2.42	* <0.01
	2013	133	118	3.65	* <0.001	3.09	* <0.01
Queen scallops	2010	179	161	1.64	* 0.009	2.26	* <0.01
	2011	81	24	1.39	* 0.041	1.39	* 0.04
	2012	74	53	1.4	* 0.04	5.17	* <0.01
	2013	133	54	5.77	* <0.001	3.77	* <0.01

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32 **Table 5** Two-way ANOVAs comparing the exploitable and reproductive biomass of two species  
 33 of scallop between the marine reserve and outside. Significant results are denoted by an (\*).

Source	Test variable	SS	df	MS	F	P
King scallops (exploitable biomass)	Year	2235.37	2	1117.68	0.36	0.69
	Protection	17447.68	1	17447.68	5.61	*0.02
	Year x Protection	2613.66	2	1306.83	0.42	0.66
	Residual	8343594.12	94	78655.26		
King scallops (reproductive biomass)	Year	34078.71	2	17039.35	0.22	0.81
	Protection	625559.91	1	625559.91	7.95	*<0.01
	Year x Protection	229638.67	2	114819.33	1.46	0.24
	Residual	7393594.64	94	78655.26		
Queen scallops (exploitable biomass)	Year	1508.74	2	754.37	2.42	0.1
	Protection	1138.27	1	1138.27	3.65	*0.05
	Year x Protection	884.79	2	442.39	1.42	0.25
	Residual	29332.83	94	312.05		
Queen scallops (reproductive biomass)	Year	766.83	2	383.42	7.76	*<0.01
	Protection	298.31	1	298.31	6.04	*0.02
	Year x Protection	306.65	2	153.33	3.10	*0.05
	Residual	4645.80	94	49.42		

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Supplementary material

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