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

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Abstract:	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 (Aequipecten opercularis) 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.

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<u>Corrections made</u>

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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17 **Abstract**

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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

22 models revealed this trend to be significantly related to the greater presence of macroalgae

23 and hydroids growing within the boundaries of the reserve. These results suggest that

24 structurally complex habitats growing within the reserve have substantially increased spat

25 settlement and / or survival. The density of adult king scallops declined 3-fold with increasing

26 distance from the boundaries of the reserve, indicating possible evidence of spillover or

27 reduced fishing effort directly outside and around the marine reserve. However, there was no

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.

Introduction

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

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

2

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 (Dinmoreet
84   al. 2003) and reduce profits through the loss of fishing grounds (Rassweileret 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^2 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^2 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 disproportionally 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) 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^2 (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) 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^2 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 glacial*),

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). 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 x 100 m^{-2}.

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

Density of king and queen scallops

Densities of king and queen scallops were compared between the two treatments and across the years using a two-way ANOVA as before. However, the density data had to be square root transformed to comply with the assumption of normality. Density data from 2013 was also split between individuals of sub-legal and legal size classes. For king scallops, this was any individual greater than 100 mm in length (Keltz and Bailey 2010). For queen scallops, a size of 50 mm was used as the cut-off point (see above). Differences in the density of these size 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 ±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, $\chi^2 = 0.78$,

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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 individuals x 100 m^{-2} (± 2.1 SE) within
369 the reserve compared to a value of 7.6 (±2.3 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 (±1.8 SE) and 6.0 (± 2.1 SE) x 100 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 x 100 m^{-2} (± 0.8 SE) inside the reserve and
382 2.3 (± 0.9 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 (± 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 (± 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_∞ = 151.01, T_0
446   = 0.13) compared to outside (k = 0.38, L_∞= 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_ω=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_ω=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

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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;

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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 disproportionally 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^2. In contrast, we estimated the densities of both scallop species

622 to be between 6-8 per 100 m^2 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^2. In

630 comparison, our study estimated king scallop density to be markedly higher at 6-7.5 individuals

631 per 100 m^2. 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.

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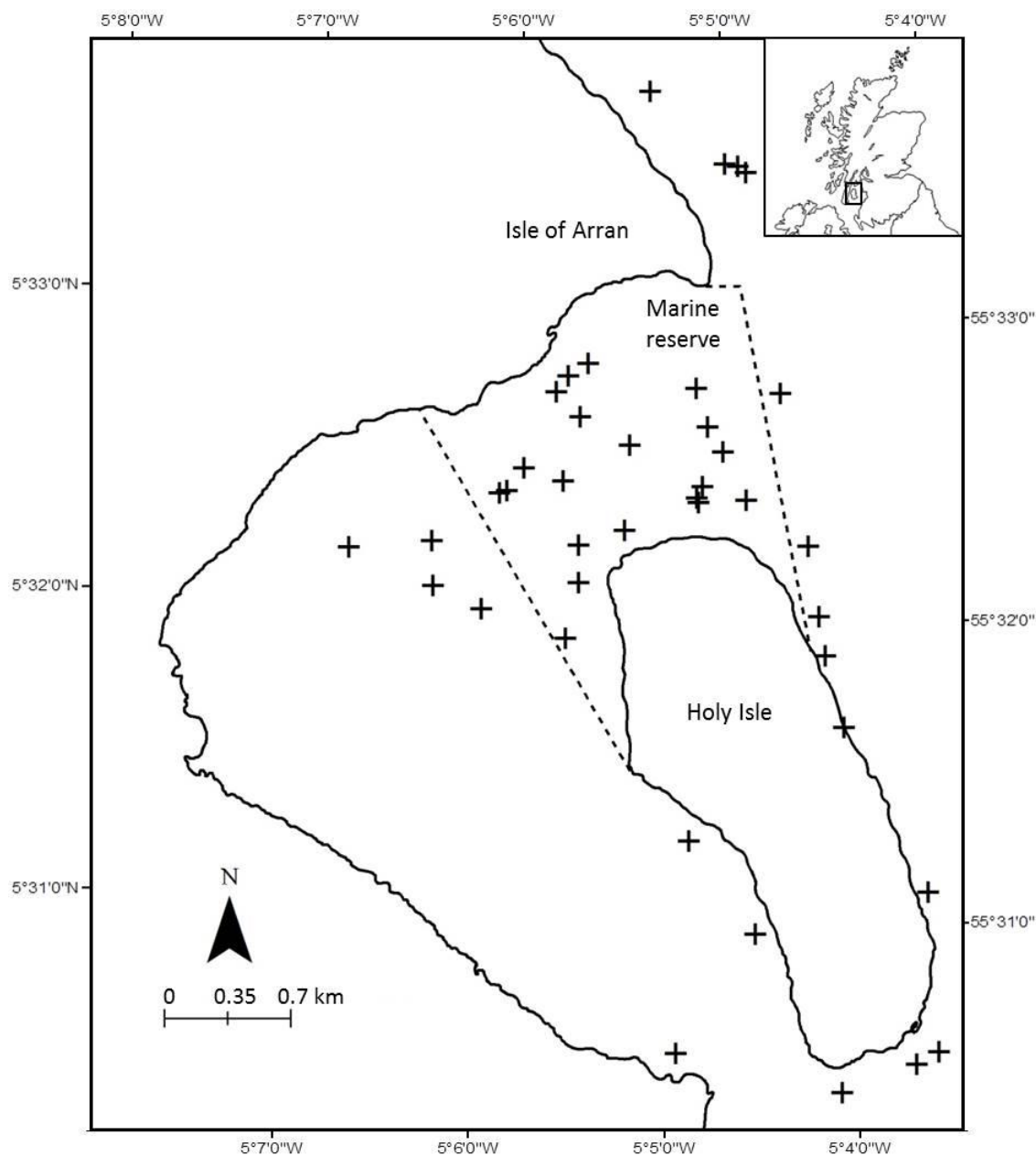
Fig. 1 Site locations of dive transects for all years. Also displayed are the boundaries of the
Lamlash Bay fully protected marine reserve. The inset shows the location of the Isle of Arran
off the west coast of Scotland, United Kingdom.

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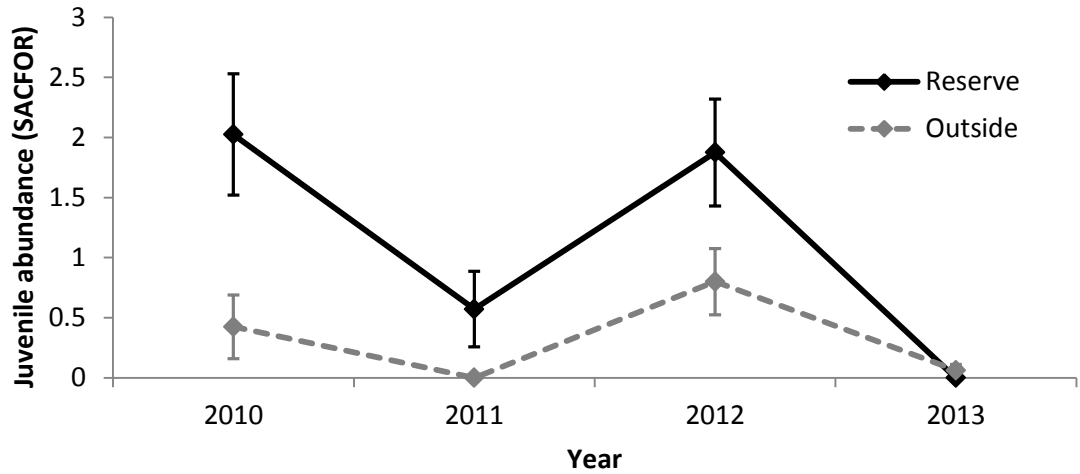
Fig. 2 The mean estimated abundance (SACFOR) of juvenile scallops within and outside the fully protected marine reserve across four years. Error bars represent ±1 SE.
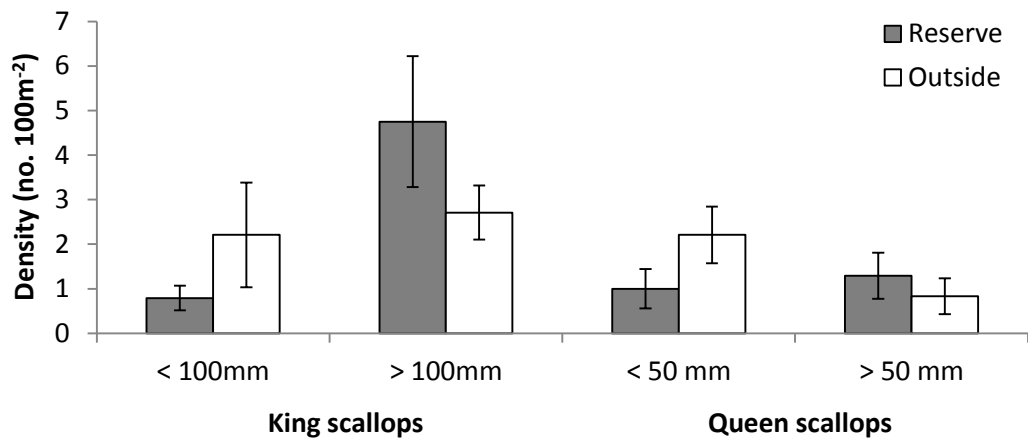

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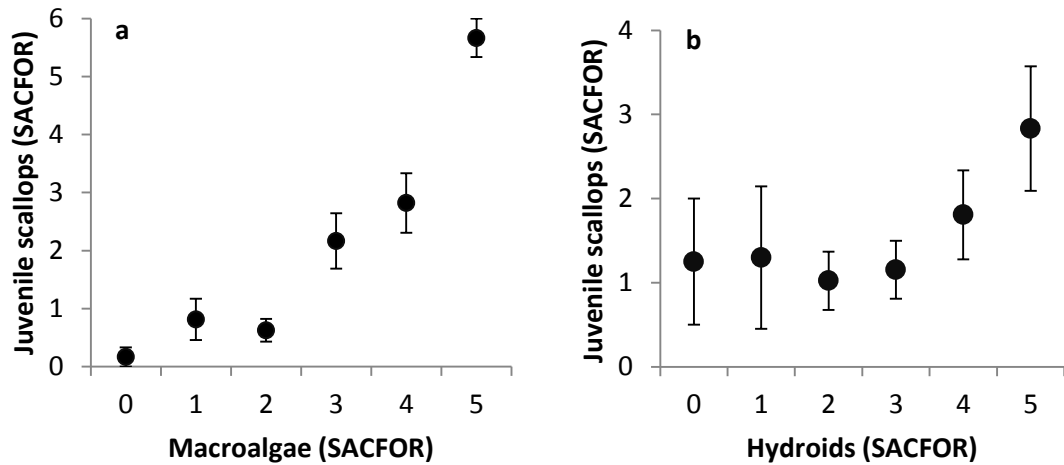
Fig. 3 Mean abundance of juvenile scallops in relation to the mean abundance of macroalgae (a) and hydroids (b). These trends were highlighted as significant by a GLM. Error bars represent ±1 SE.
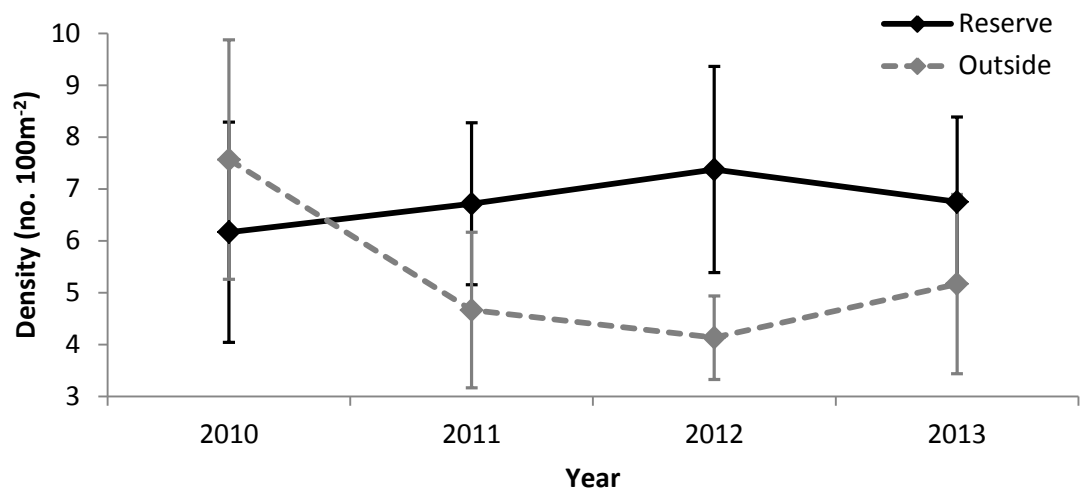
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14 **Fig. 4** The mean density of king scallops in and outside the fully protected marine reserve
15 across four years. Error bars represent ±1 SE.

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

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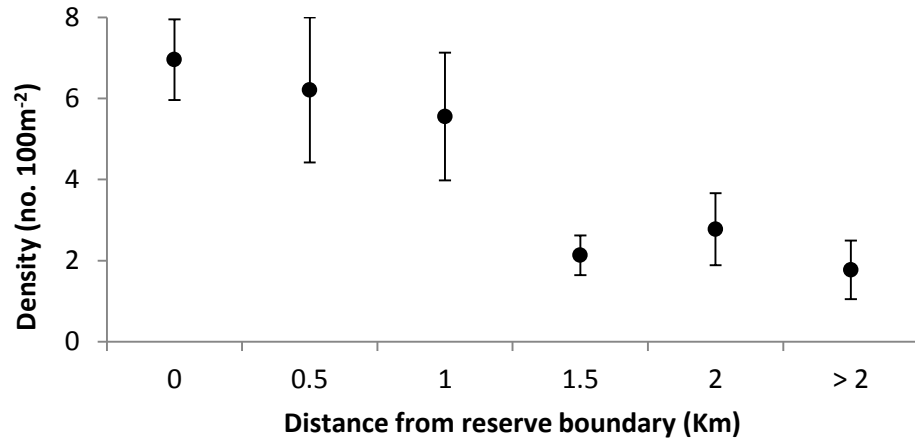
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24 **Fig. 6** Mean density of king scallops for the years 2010-2013 plotted against distance from the
25 marine reserve. A distance of 0 represents those sites located within the marine reserve. Error
26 bars represent ±1 SE.
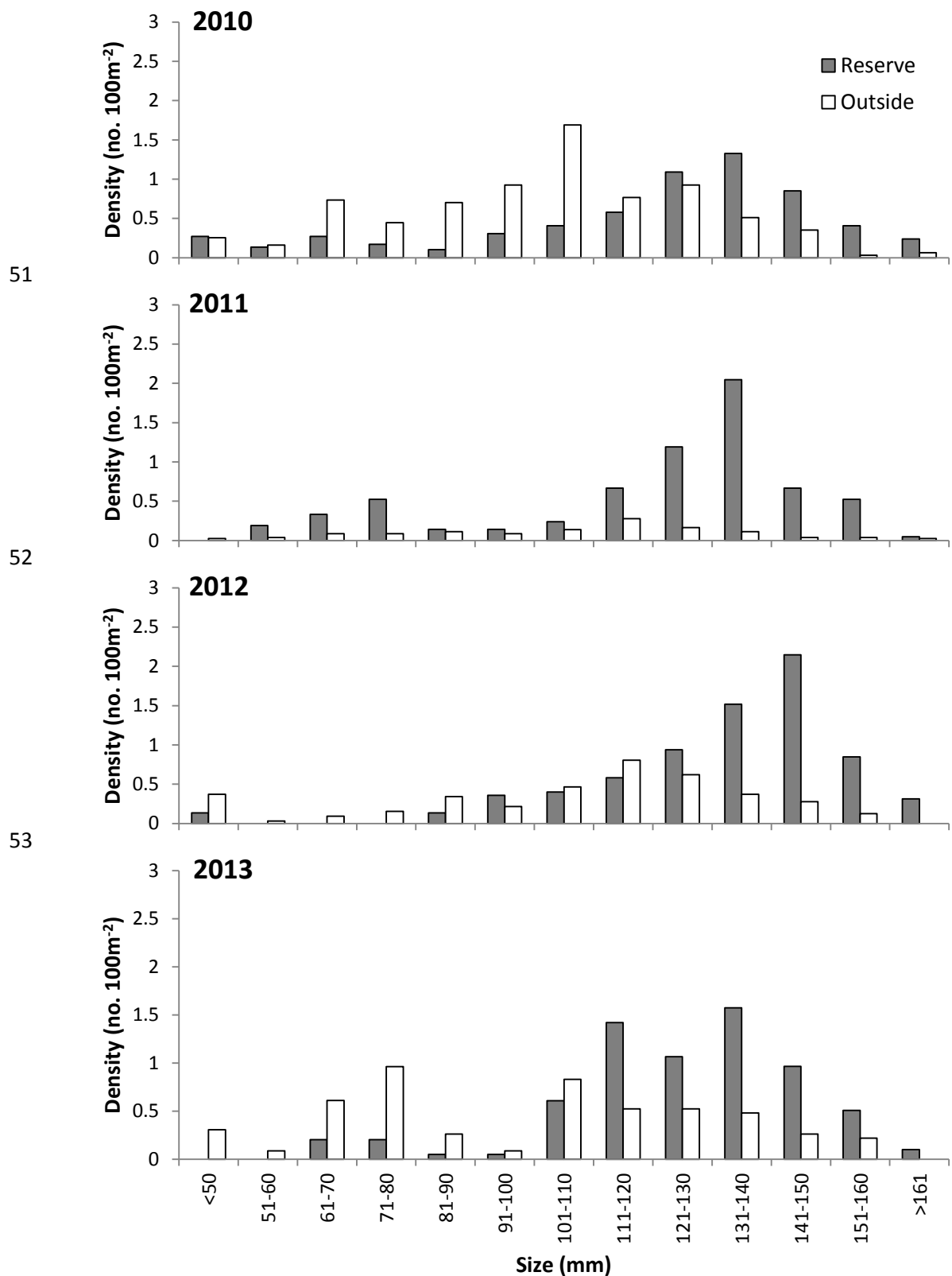
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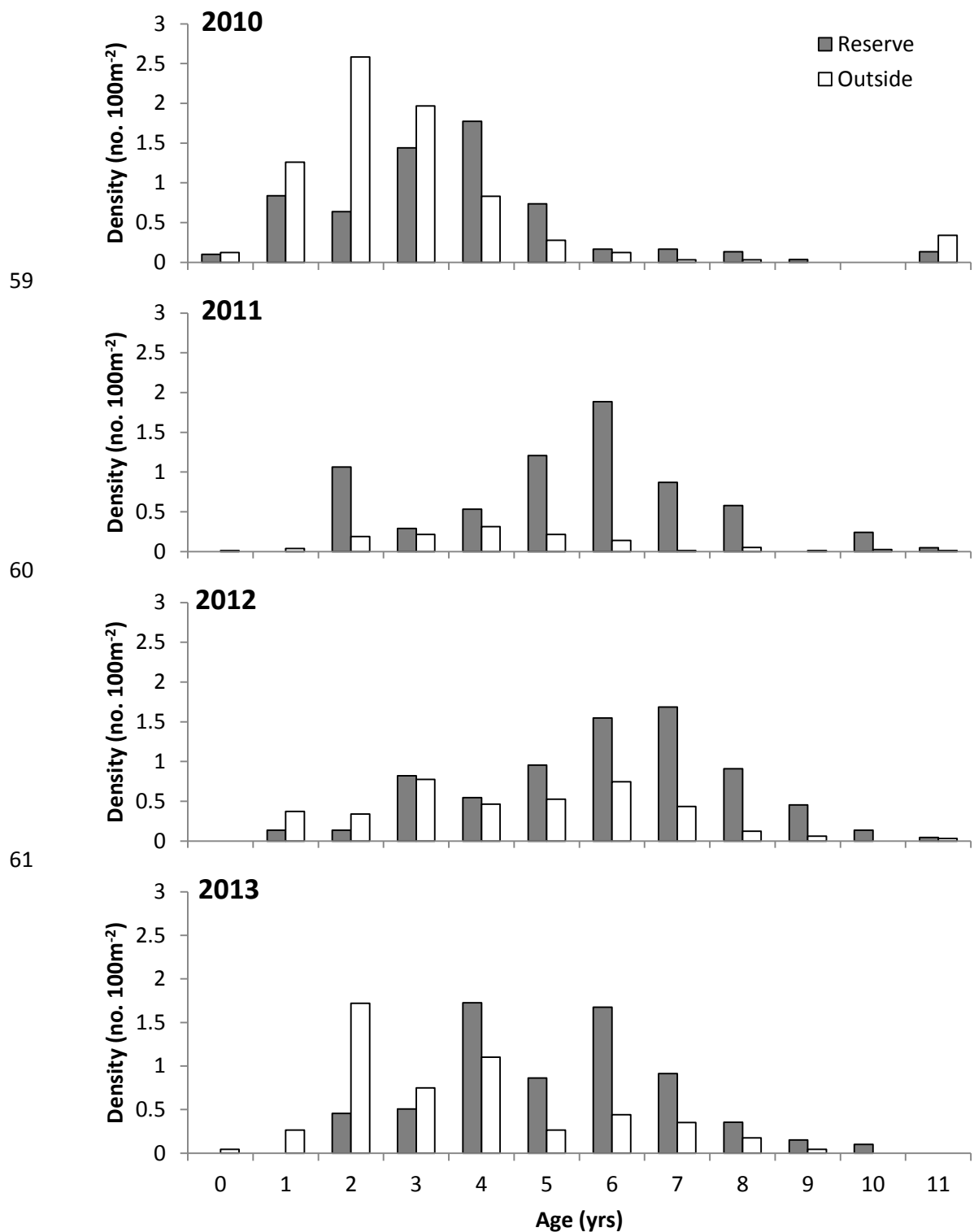28
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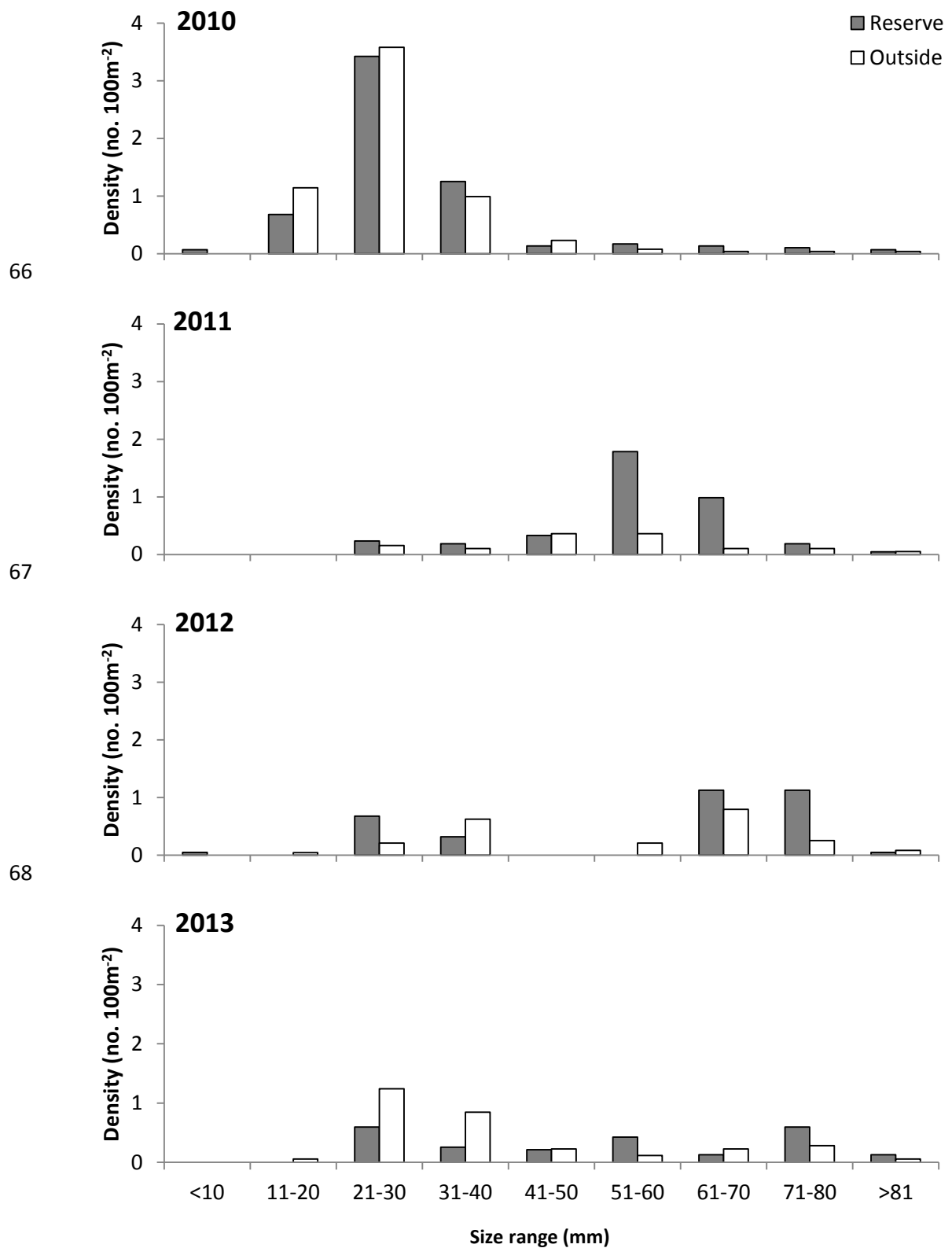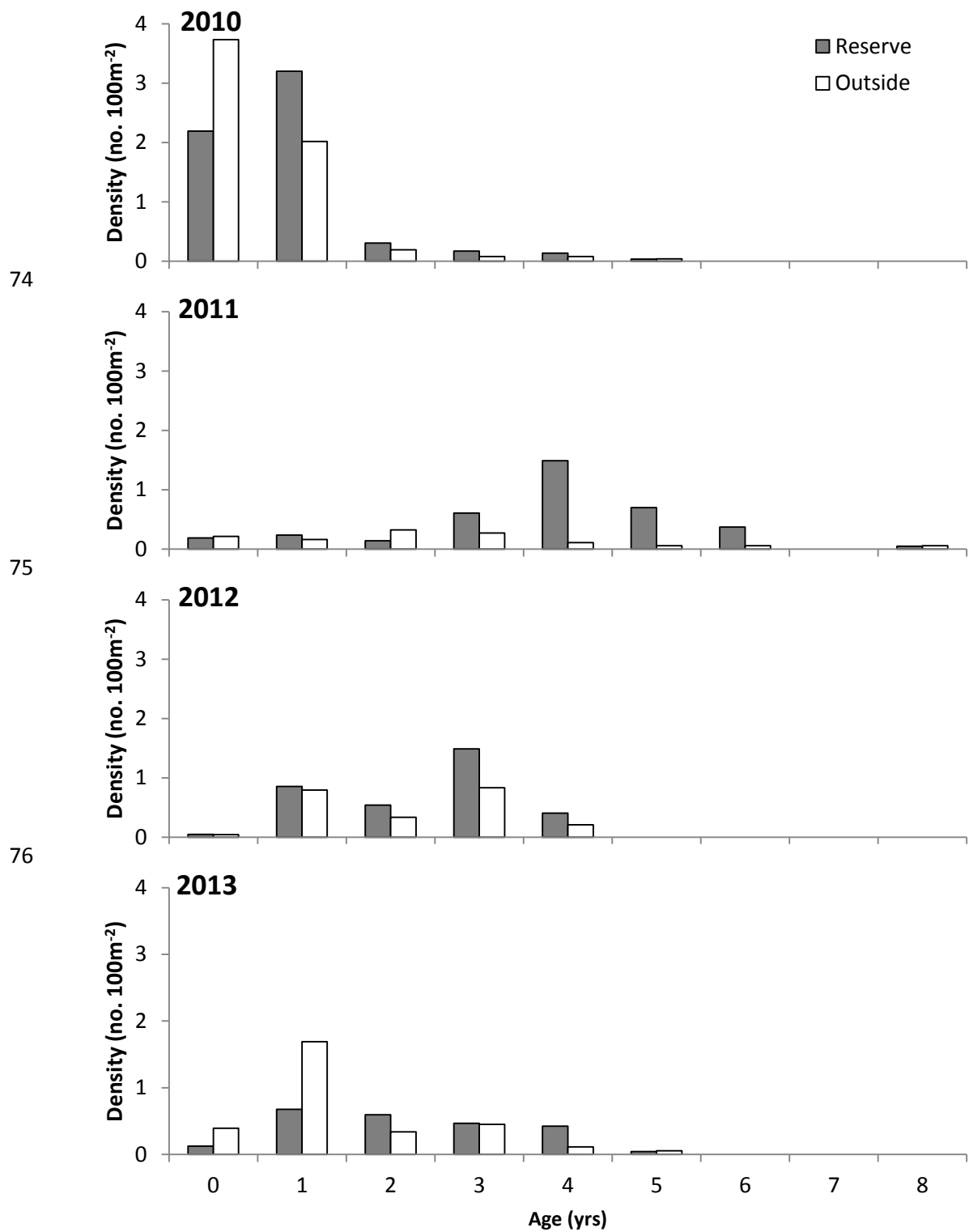
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55 **Fig. 7** The size structure of king scallops sampled within and outside the fully protected marine
56 reserve across four years. The number (N) of individuals sampled from each population is
57 available in Table 4.
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Fig. 8 The age structure of king scallops sampled within and outside the fully protected marine reserve across four years. The number (N) of individuals sampled from each population is available in Table 4.

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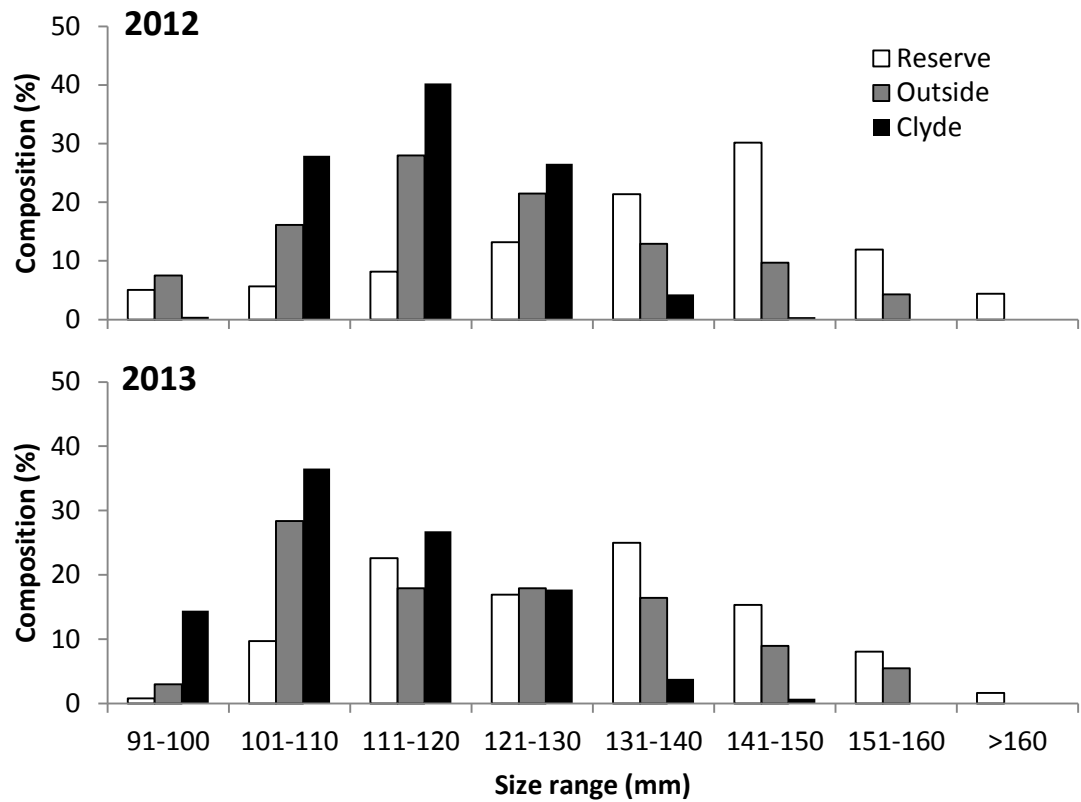
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78 **Fig. 10** The age structure of queen scallops sampled within and outside the fully protected
79 marine reserve across four years. The number (N) of individuals sampled from each population
80 is available in Table 4.

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

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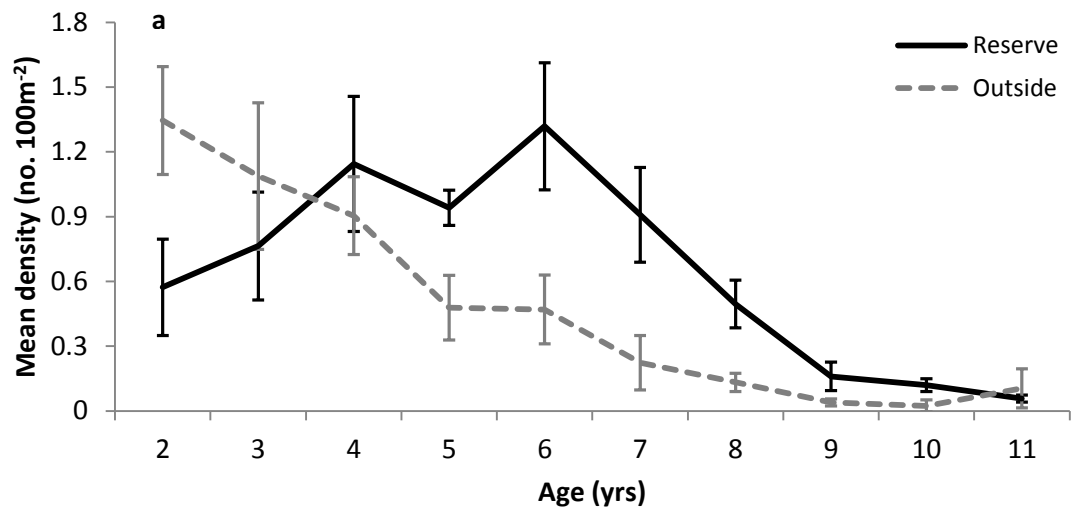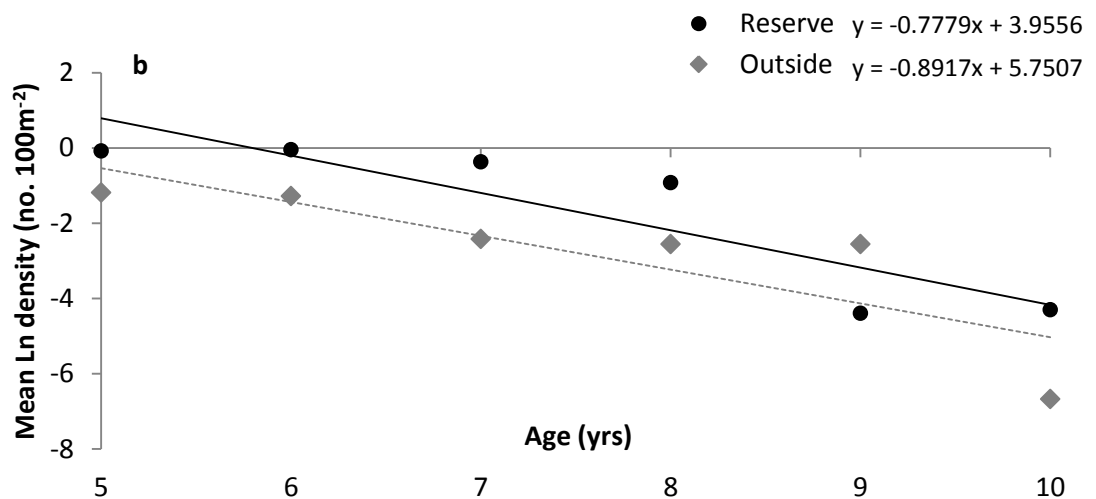
Fig. 12 (a) The density per age-class of king scallops within and outside the reserve across the years 2010-2013. (b) Catch curve analysis (total mortality estimates) of king scallops within and outside the reserve across the years 2010-2013.

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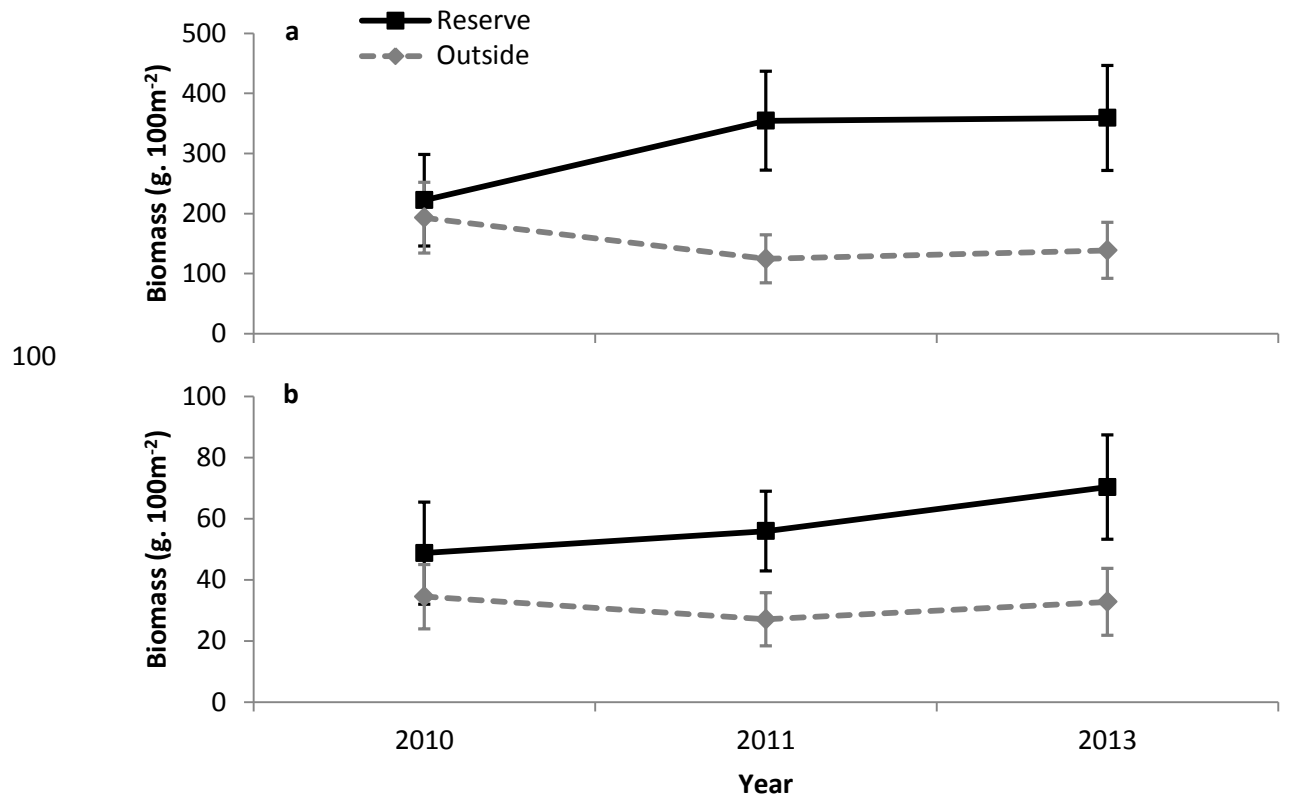
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102 **Fig. 13** The mean exploitable (a) and reproductive (b) biomass of king scallops within and
103 outside the fully protected marine reserve for the years when scallop dissections were
104 conducted. Error bars represent ±1 SE.

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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
Bryzozoans	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.

				Size		Age	
	Year	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

Click here to download Electronic Supplementary Material (Tables, Figures, Video, Movie, Audio, etc.): Supplementry material.docx