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

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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

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.

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

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

For populations to benefit from the protection afforded by MPAs, it is necessary that a number of individuals spend a substantial part of their lives within their boundaries (Roberts et al. 2005). Thanks to their sedentary nature and relatively fast growth, scallops have been shown to be particularly responsive to closed area protection. In 1994, three areas totalling 17,000 km^2 were closed to fishing gears on Georges Bank in the Gulf of Maine, United States of America (USA). Ten years later, observations revealed that the reduction in fishing mortality was responsible for a 20-fold increase in scallop biomass within the closures, and increased catches in neighbouring fishing grounds (Murawski et al. 2000; Hart and Rago 2006; Hart et al. 2013). The scallop fishery on Georges Bank is now the most valuable of any fishery in the USA (Lowther 2013). On a smaller scale, 17 years of protection of within a 2 km^2 area off the Isle of Man resulted in scallop densities 30 times greater than those observed prior to protection (Beukers-Stewart et al. 2005; Beukers-Stewart and Brand 2007). The reduction in fishing mortality also allowed individuals within the closed area to become older and reach larger sizes, with exploitable and reproductive biomass of scallops becoming 20 and 33 times higher respectively, than on adjacent fishing grounds. In addition, there is growing evidence that export of larval scallops, generated from high rates of breeding within the closed area, have boosted surrounding populations and therefore the fishery (Beukers-Stewart et al. 2005, 2004; Beukers-Stewart and Brand 2007; Neill and Kaiser 2008).

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

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

MPAs can be implemented via top-down processes which are government led and enforced, or by bottom-up mechanisms, whereby local communities and stakeholders propose the establishment of an MPA and help with its management, enforcement and monitoring (Kelleher 1999; Jones 2012). There is growing evidence that community and stakeholder involvement in setting up and running MPAs builds greater support and reduces management costs due to lower infringements rates (Pollnac et al. 2012). Although community-led MPAs are relatively common in tropical waters (Johannes 2002), they are very rare in temperate areas and almost non-existent in the UK (Fenberg et al 2012). As an exception, a fully protected marine reserve was established in Lamlash Bay, Isle of Arran, UK, in September 2008 prohibiting all fishing within the reserve under the Inshore Fishing (Scotland) Act of 1984 (Axelsson et al. 2009). The Firth of Clyde, in which the Isle of Arran sits, is known to be one of the most degraded marine environments in the UK, primarily due to over a century of intensive fisheries exploitation (Thurstan and Roberts 2010; Howarth et al. 2013). The reserve was therefore passed by the Scottish parliament under the rationale that the reduction in fishing pressure should help regenerate the local marine environment and enhance commercial shellfish and fish populations in and around Lamlash Bay, particularly with regards to scallops. Lamlash Bay Marine Reserve came in effect after a decade of campaigning by local residents for better protection of their seas (Community of Arran Seabed Trust or "COAST"; www.arrancoast.com) and is the first and only fully protected marine reserve in Scotland, and the only statutory reserve in the UK that was originally proposed by a local community which bans all extractive activities (Prior 2011). Lamlash Bay is also unique in that the majority of MPAs in the UK were proposed either for conservation (e.g. Lundy Marine Nature reserve and Lyme Bay Marine Reserve) or fishery purposes (e.g. closed areas off the Isle of Man), not for both.

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

Materials and methods

Study area and scallop fishery

Lamlash Bay Marine Reserve encompasses an area of 2.67 km^2 (Fig. 1), with water depths ranging between 0 and 29 m below chart datum, but reaching as deep as 43 and 50 m outside to the east and the west of the reserve, respectively (Admiralty Chart 1864; Baxter et al. 2008). Previous surveys (Duncan 2003; Axelsson et al. 2009) indicated a seabed of mixed sediments (i.e. mud, sand and gravel with various proportions of shell) but that the central and southern regions of the bay tend to be characterised by softer sediment, mainly muddy sand. In addition, the area has long been identified as containing important maerl beds, although recent evidence points to deterioration in their health (Howarth et al. 2011).

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

Dive surveys

We began monitoring Lamlash Bay in 2010 (see Howarth et al. 2011). Initially, 40 sites were surveyed, half of which were located within the reserve and the other half outside. These surveys were then repeated and expanded in 2011, 2012 and 2013 by using a greater variety of survey techniques but reducing the number of study sites. Therefore we surveyed 28 sites in 2011, 31 sites in 2012, and 32 sites in 2013. Again, these sites were divided so that half fell within the boundaries of the marine reserve (Fig. 1). Sites were chosen so that each one within the reserve could be paired with at least one other suitable control outside, based on similar depth and predominant substrate type (S1-4). It must be noted that this matching of sites was based on visual inspection of the substrate. Ideally, data on several physical characteristics of these sites (e.g. particle size analysis, current speed, percentage cover of benthic habitats) would have been collected prior to protection to ensure these sites were statistically similar. However, no such data existed prior to protection and the collection of such physical data was beyond the scope of this study. Then again we did collect data on the percentage cover of benthic habitats but this only began two after the reserve had been established; at which point differences in seafloor habitats would be expected between sites protected and unprotected from fishing gears.

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

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

A SACFOR abundance scale was also used by the divers to estimate the abundance of different benthic taxa. These were live maerl (e.g. *Phymatolithon calcareum* and *Lithothamnion glacial*), dead maerl, macroalgae (e.g. *Laminaria* and *Ceramium* spp) sponges (e.g. *Pachymatisma* *johnstonia*), anemones (e.g. *Cerianthus lloydi*), tunicates (e.g. *Clavelina lepadiformis* and *Diazona violacea*), hydroids (e.g. *Obelia geniculata*), bryozoans (e.g. *Alcyonidium diaphanum* and *Flustra foliacea*) and soft corals (e.g. *Alcyonium digitatum*). The SACFOR method was chosen to provide quick underwater estimates of benthic cover.

Laboratory analysis

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

Data analysis

Multivariate analyses of juvenile scallop distribution

All data were tested for normality using histograms, boxplots, QQ plots and the Shapiro–Wilk test. These basic exploratory measures were conducted within the statistical package R (www.r-project.org). The Shapiro–Wilk test was chosen as it is widely accepted to be the most suitable for small and medium-size samples (*N* up to 2000; Royston 1982, Conover 1999). For statistical analysis, the SACFOR scale used to estimate juvenile scallop abundance and benthic cover was converted into numerical categories ranging from 0 to 6, where a value of 0 would indicate the absence of a taxon and 6 would represent the superabundance of a taxon as denoted by the SACFOR scale. The counts of adult scallops collected by both divers were 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–

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

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

Population structure of king and queen scallops

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

Mortality and growth rates

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

Biomass data

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

Results

Juvenile scallop abundance and the relationship with benthic habitats

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

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

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

Comparisons of scallop density

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

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

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

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

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

Comparisons of population structure

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

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

In 2010, queen scallops differed from king scallops in that their size (Fig. 9) and age (Fig. 10) distributions were similar. However, as observed for king scallops, queen scallop abundance suddenly declined across all age and size classes outside the reserve. Queen scallops then began to recover in 2012 and 2013 to sizes and ages slightly lower than those observed within the reserve.

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

Comparisons of mortality rates

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

Comparisons of growth rates

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

Comparisons of exploitable and reproductive biomass

For the years in which scallop dissections were conducted, the exploitable (Fig. 13a) and reproductive (Fig. 13b) biomass of king scallops were substantially greater within the reserve than outside. In 2010, the average exploitable and reproductive biomass of king scallops was 18% and 39% greater within the reserve respectively. The following years saw the biomass of king scallops increase within the reserve but remain relatively static outside. By 2013, the exploitable and reproductive biomass of king scallops within the reserve had increased to become 2 and 2.5 times more than in the fished area. Two-way ANOVA found level of protection, but neither year nor the interaction between the two, to significantly affect king scallop biomass (Table 5).

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

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

Discussion

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

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

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

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

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

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

Despite finding no significant difference in the density of adult scallops between the two treatments, we did find that scallop density significantly declined with increasing distance from the boundaries of the marine reserve. Many studies have detected similar gradients (McClanahan and Mangi 2000; Harmelin-Vivien et al. 2008; Halpern et al. 2010; Ludford et al. 2012) and several possibilities could explain such a trend. Environmental gradients and spatial heterogeneity of habitats are known to result in gradients of abundance (Vandeperre et al. 2011) but as our survey design was balanced (i.e. we surveyed an equal number of sites of similar habitat and depth) this is unlikely. It could be that spillover of larvae and juveniles from within the reserve to outside has occurred, and that its effects diminish with increasing distance from the reserve (Kellner et al. 2007). This is possible as the larvae of these two species typically spend 3–6 weeks in the water column where they can disperse over considerable distances (Brand et al. 1980; Macleod et al. 1985). Then again, it may be that fishers have been avoiding areas immediately outside and around the marine reserve since its establishment, meaning fishing pressure would consequently increase with distance from the reserve. This could be occurring as the marine reserve protects the north entrance to Lamlash Bay (see Fig. 1), meaning fishers may choose to bypass the general area. Otherwise they would have to haul their fishing gears whilst they passed over the reserve, or attempt to turn around while fishing in the unprotected southern half of Lamlash Bay. As scallop densities were similar out to 1 km away from the reserve, but then suddenly dropped at 1.5 km and remained similar out to >2 km, this may be evidence of such a "halo effect" occurring. Furthermore, scallops from the wider Clyde were substantially smaller than those measured in the Lamlash Bay area, further supporting this idea.

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

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

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

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

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

In summary, we have presented several lines of evidence that suggest Scotland's first and only fully protected marine reserve is benefitting two commercially important scallop species. The growing abundance of nursery habitats within the marine reserve appears to be substantially increasing the settlement juvenile scallops, suggesting that protecting areas from fishing can generate ecological benefits that flow back to species commercially targeted by fisheries. Then again, for fisheries to truly benefit from marine reserves, it is essential that larvae, juveniles and adults originating from within the reserve spillover into surrounding fishing grounds where they can then contribute to landings (McClanahan and Mangi 2000; Stelzenmüller et al. 2007). The greater size, age and reproductive biomass we observed within the reserve should translate to higher reproductive output and scallop recruitment both within the marine reserve and surrounding fishing grounds, especially if these trends continue to increase over time (Pelc et al. 2010). Overall, our results support an increasing number of other studies which suggest the implementation of MPAs can be a useful tool in ecosystem-based fishery management. This is important as studies into the effects of MPAs are far less common in temperate and cold waters, and are particularly limited in Europe and the UK (Lester et al. 2009; Caveen et al. 2012; Fenberg et al. 2012). Lamlash Bay is the first and only fully protected marine reserve in Scotland, and the only statutory reserve in the UK that was originally proposed by a local community which bans all extractive activities (Prior 2011). Researching the marine reserve in Lamlash Bay has therefore offered a vital insight into the benefits that highly protected marine reserves can provide. In particular, this study highlights that full protection and support from the local community is likely to be highly important in maximising the effectiveness of MPAs as any illegal extraction would have further weakened the differences between Lamlash Bay Marine Reserve and surrounding fishing grounds.

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Figure

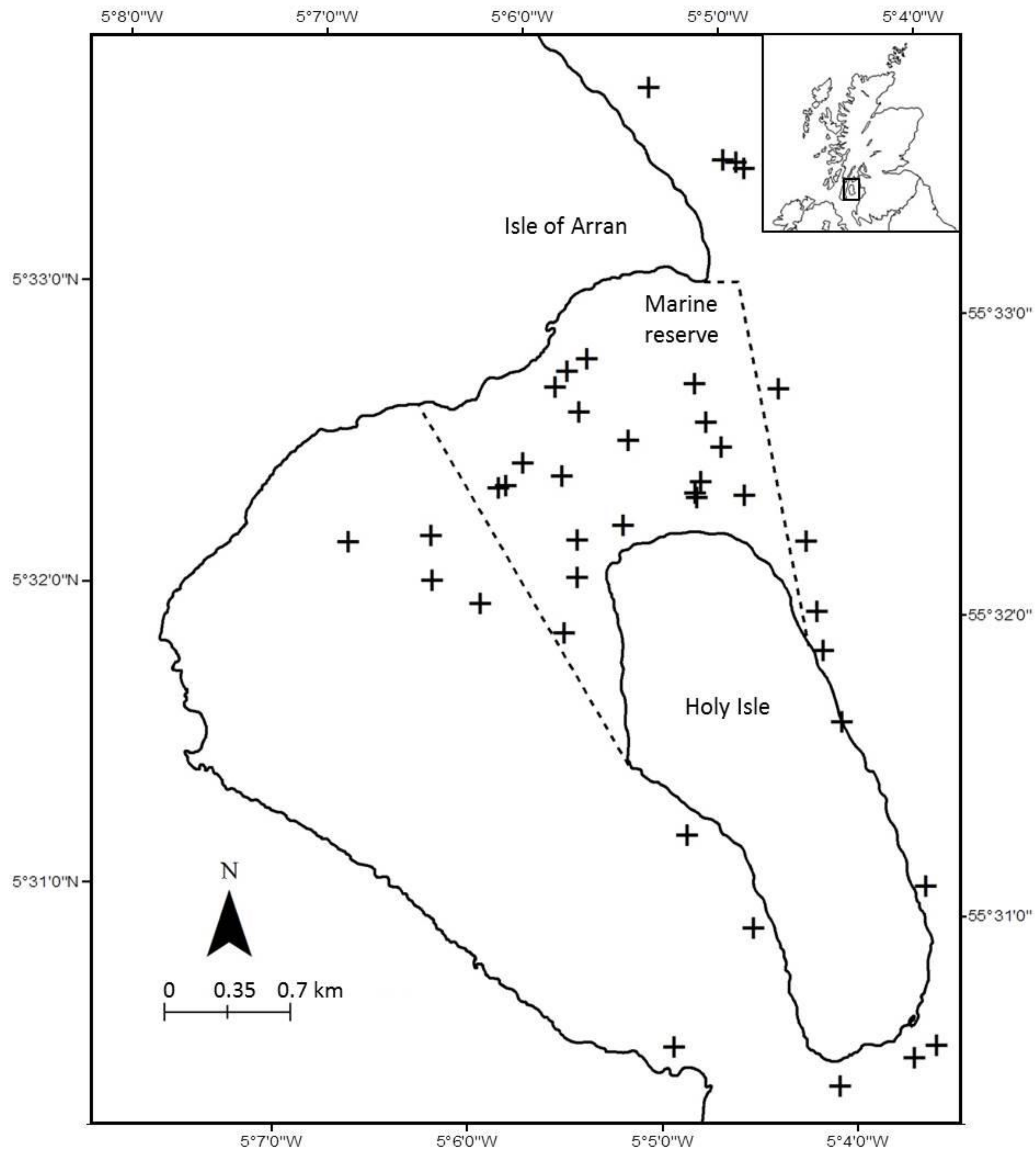

Fig. 1 Site locations of dive transects for all years. Also displayed are the boundaries of the Lamlash Bay fully protected marine reserve. The inset shows the location of the Isle of Arran off the west coast of Scotland, United Kingdom.

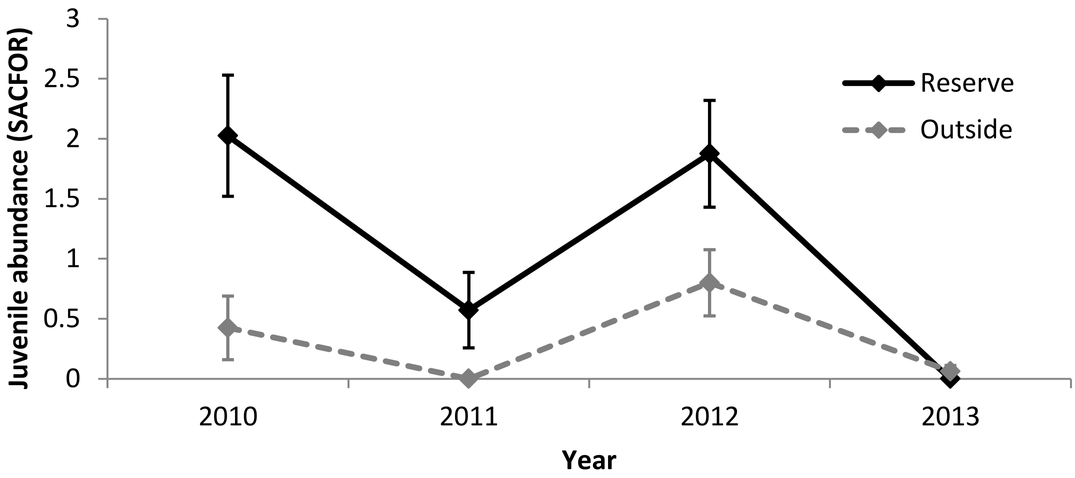

Fig. 2 The mean estimated abundance (SACFOR) of juvenile scallops within and outside the fully protected marine reserve across four years. Error bars represent ±1 SE.

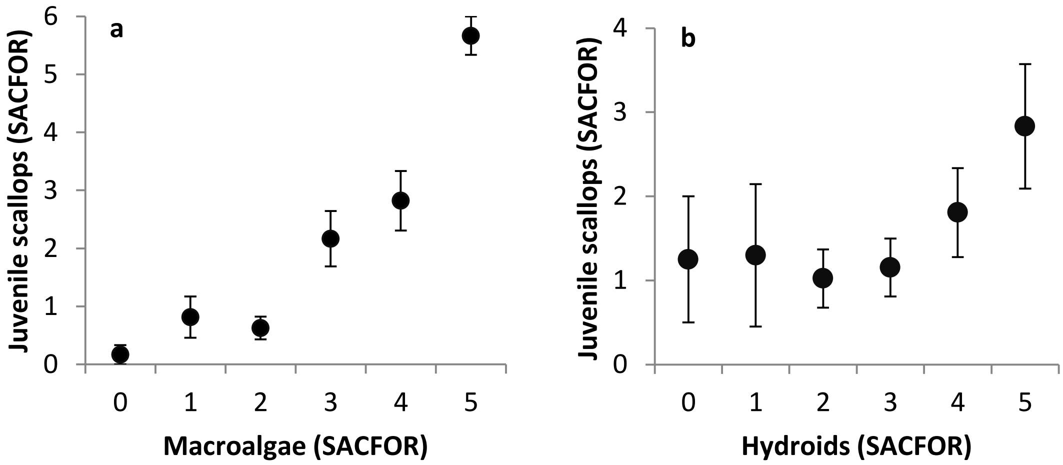

Fig. 3 Mean abundance of juvenile scallops in relation to the mean abundance of macroalgae (a) and hydroids (b). These trends were highlighted as significant by a GLM. Error bars represent ±1 SE.

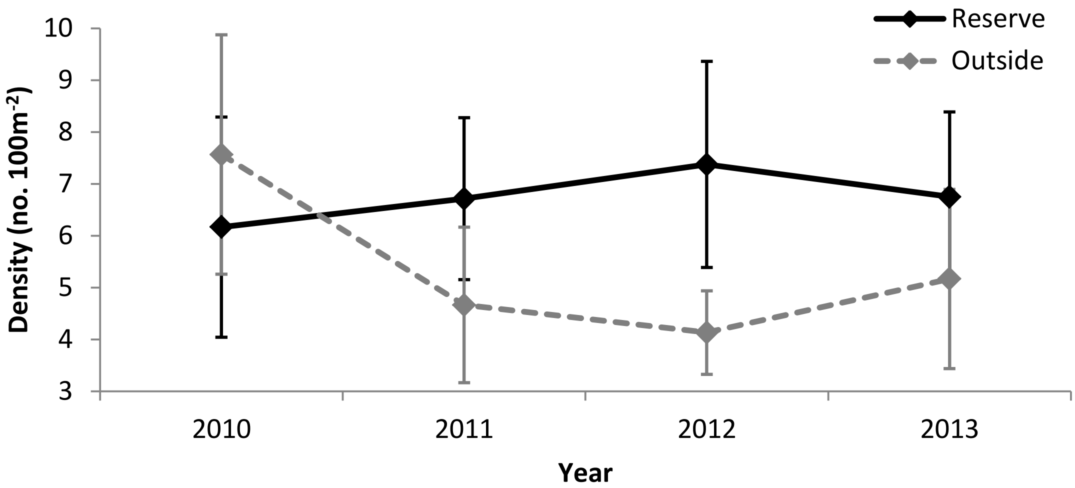

Fig. 4 The mean density of king scallops in and outside the fully protected marine reserve across four years. Error bars represent ±1 SE.

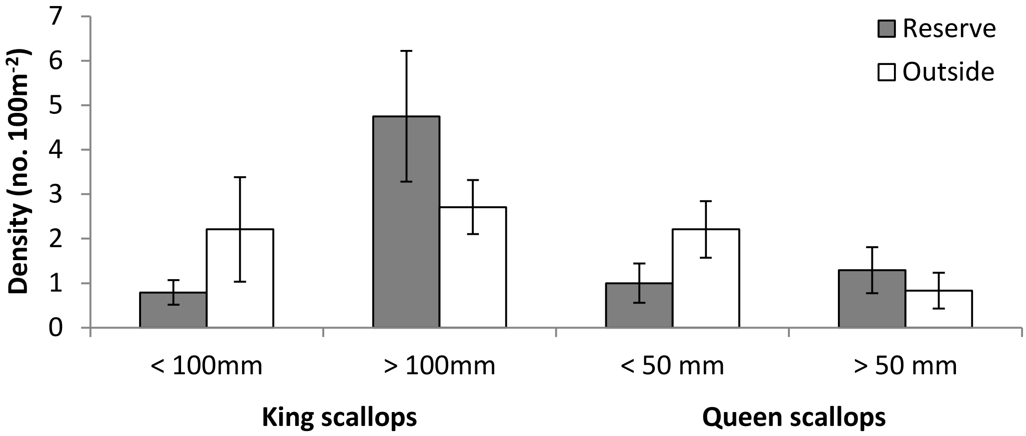

Fig. 5 The density of different size classes of two scallop species sampled in 2013 within and outside a fully protected marine reserve. Error bars represent ±1 SE.

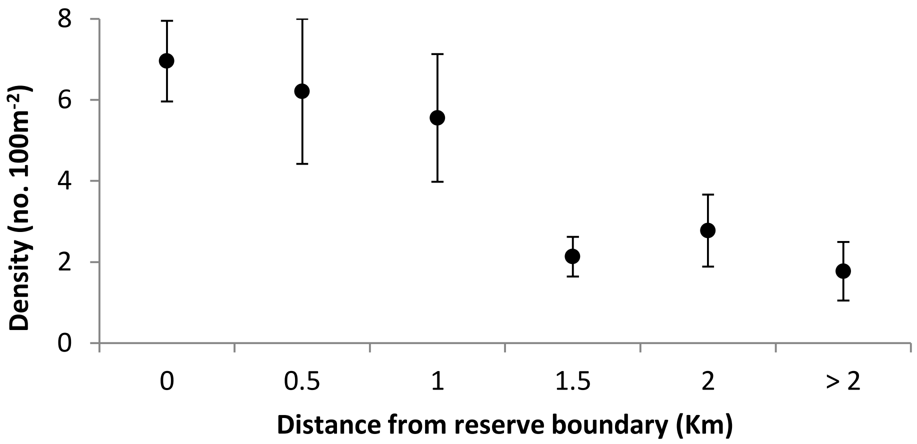

Fig. 6 Mean density of king scallops for the years 2010-2013 plotted against distance from the marine reserve. A distance of 0 represents those sites located within the marine reserve. Error bars represent ±1 SE.

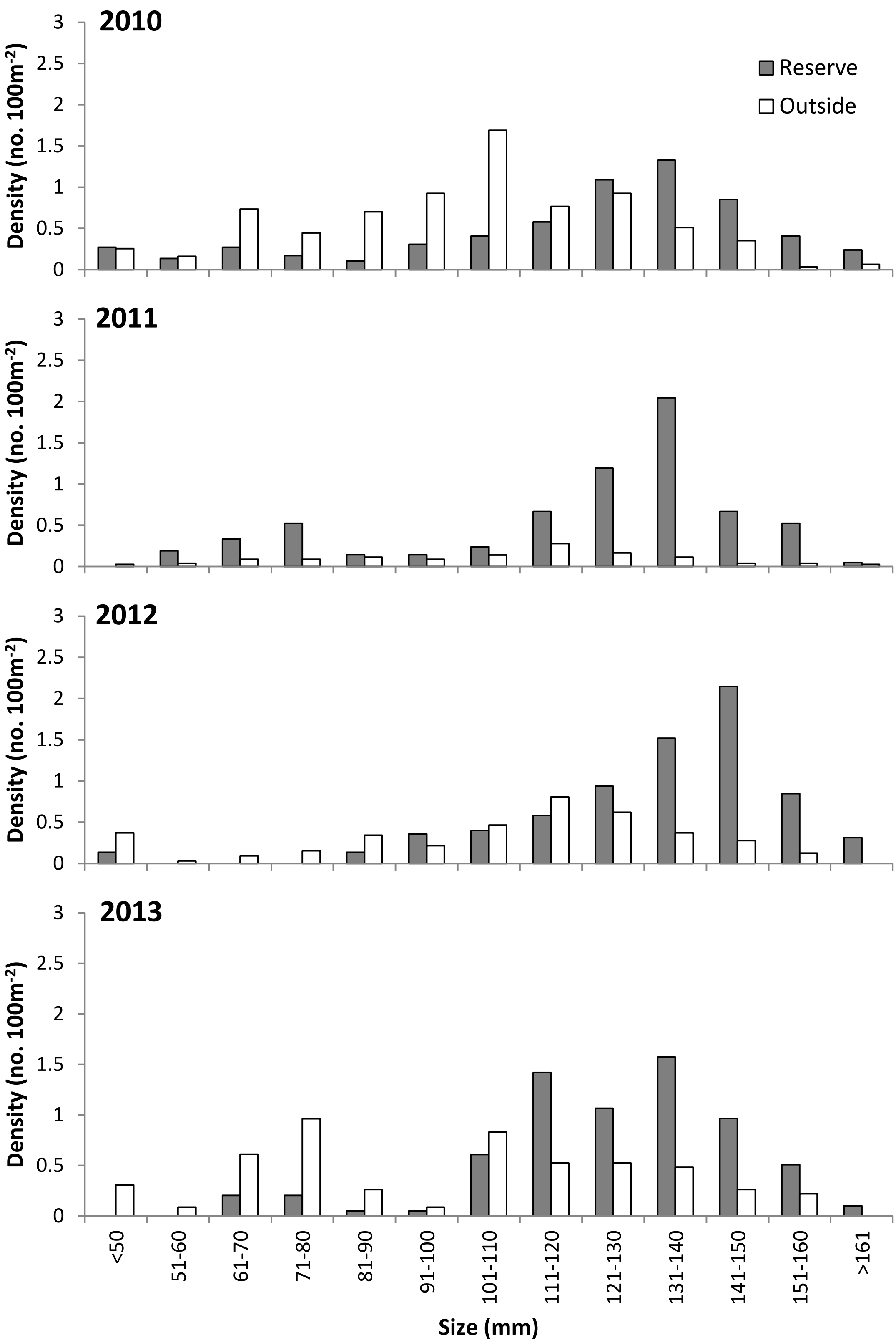

Fig. 7 The size structure of king scallops sampled within and outside the fully protected marine reserve across four years. The number (N) of individuals sampled from each population is available in Table 4.

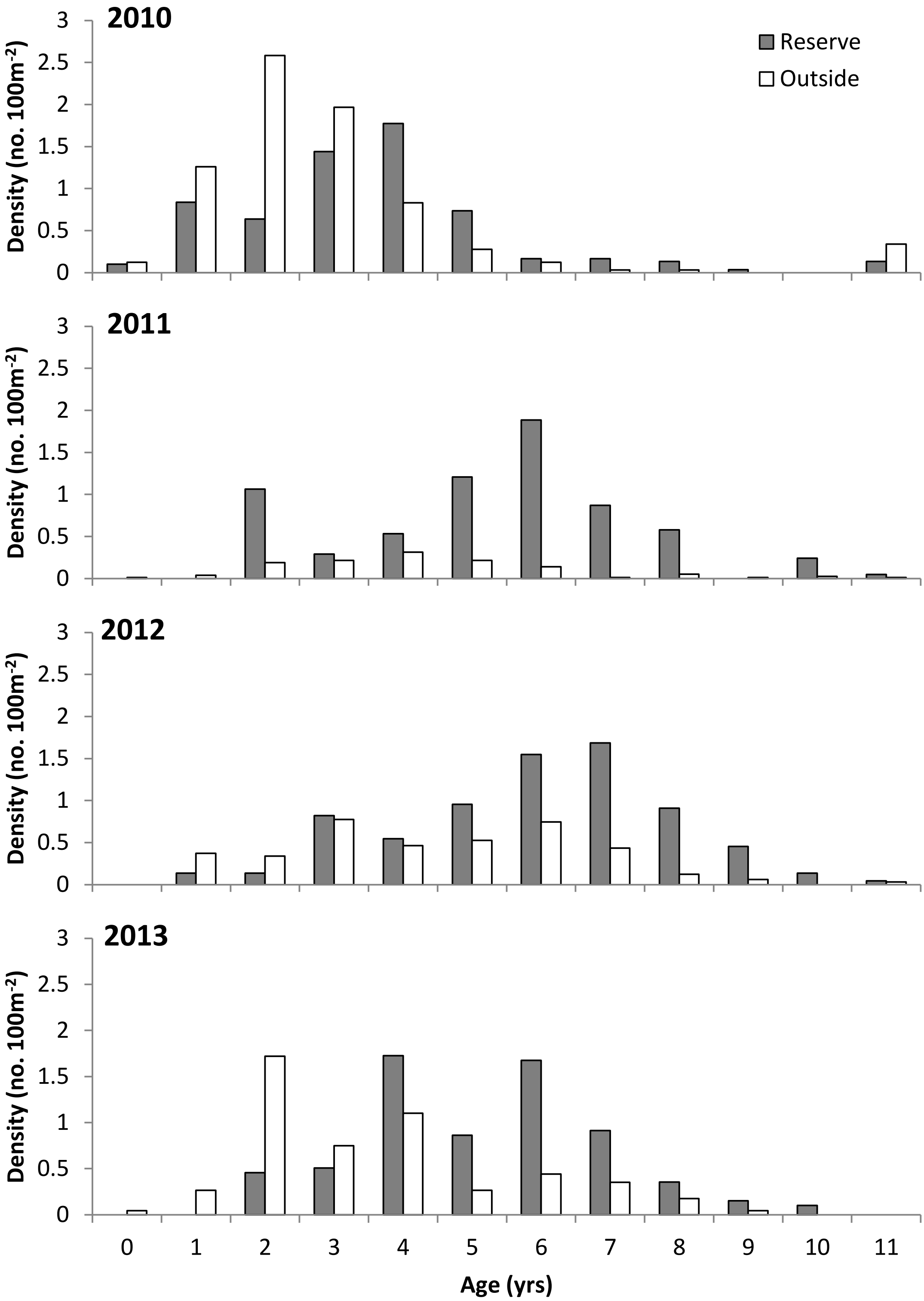

Fig. 8 The age structure of king scallops sampled within and outside the fully protected marine reserve across four years. The number (N) of individuals sampled from each population is available in Table 4.

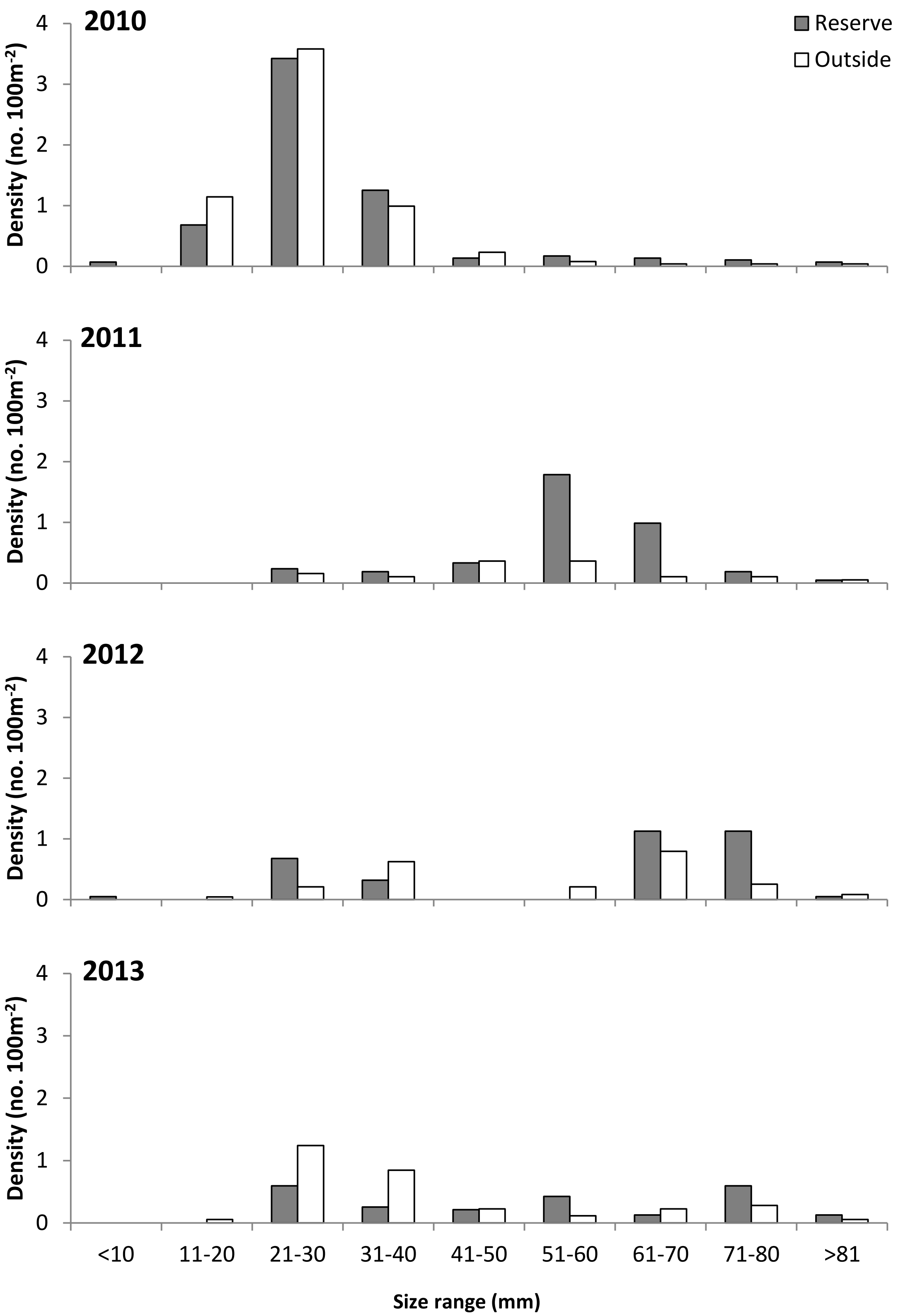

Fig. 9 The size structure of queen scallops sampled within and outside the fully protected marine reserve across four years. The number (N) of individuals sampled from each population is available in Tables 4.

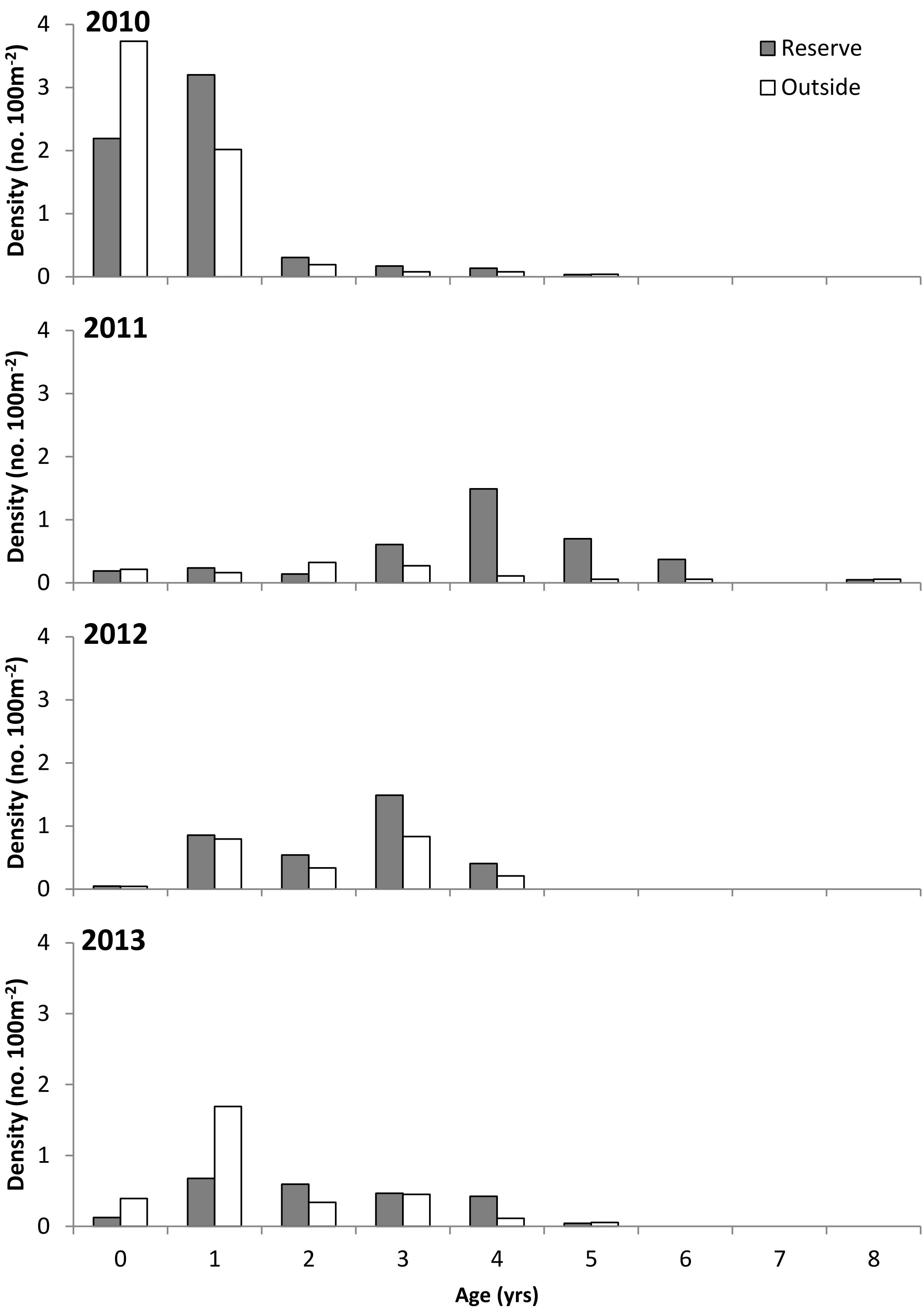

Fig. 10 The age structure of queen scallops sampled within and outside the fully protected marine reserve across four years. The number (N) of individuals sampled from each population is available in Table 4.

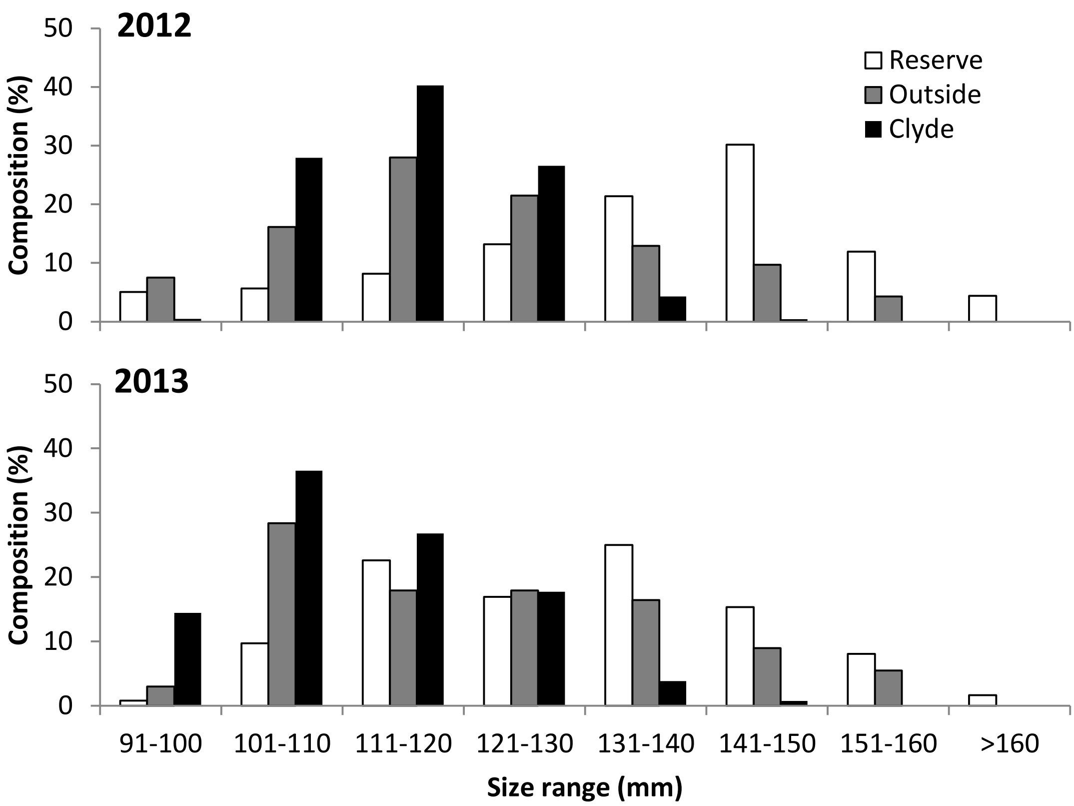

Fig. 11 The size composition of king scallops above legal landing size sampled within and outside the fully protected marine reserve across two years. Also displayed is the size composition of king scallops caught and landed within the Firth of Clyde region. Data provided by Shona Kinnear of Marine Scotland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

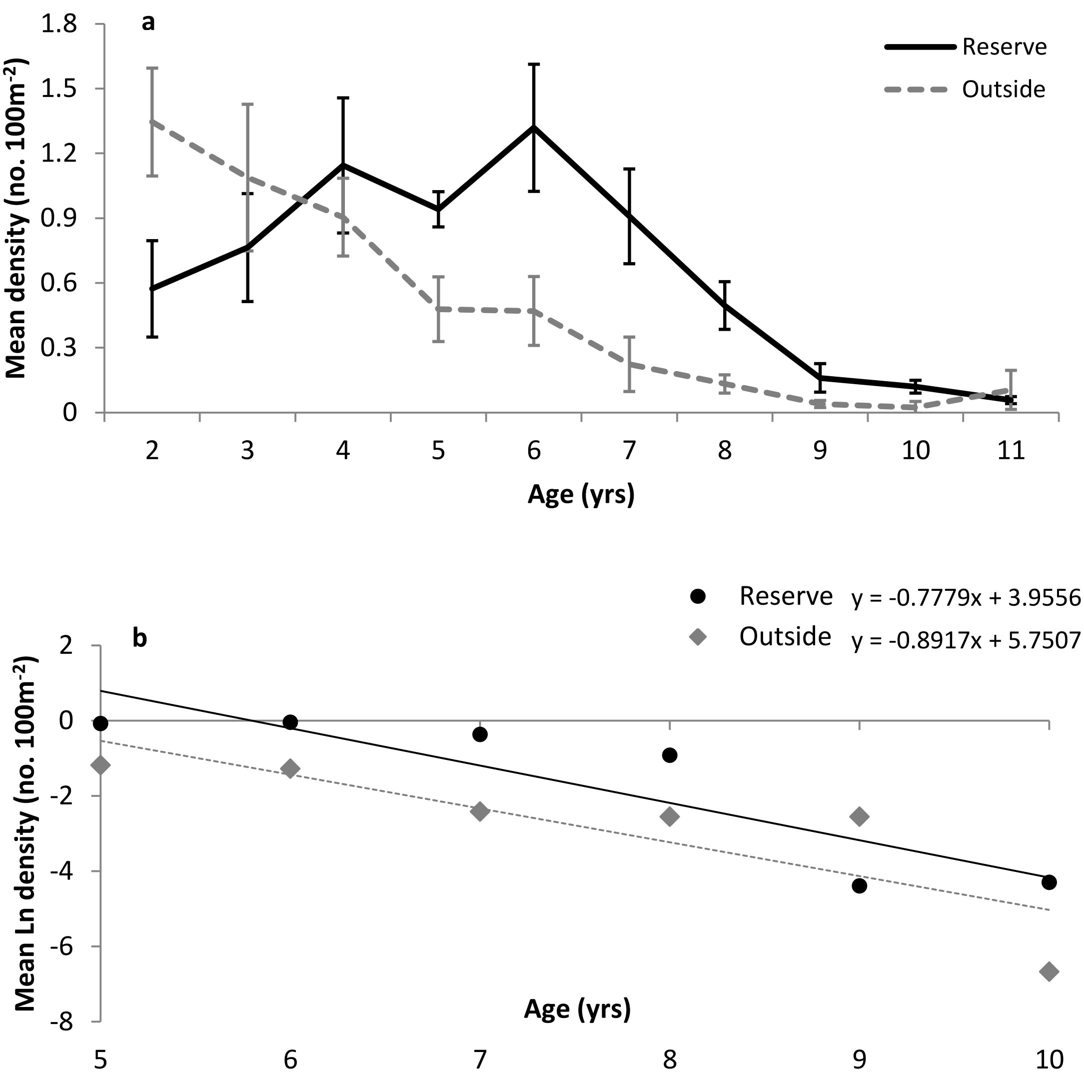

Fig. 12 (a) The density per age-class of king scallops within and outside the reserve across the years 2010-2013. (b) Catch curve analysis (total mortality estimates) of king scallops within and outside the reserve across the years 2010-2013.

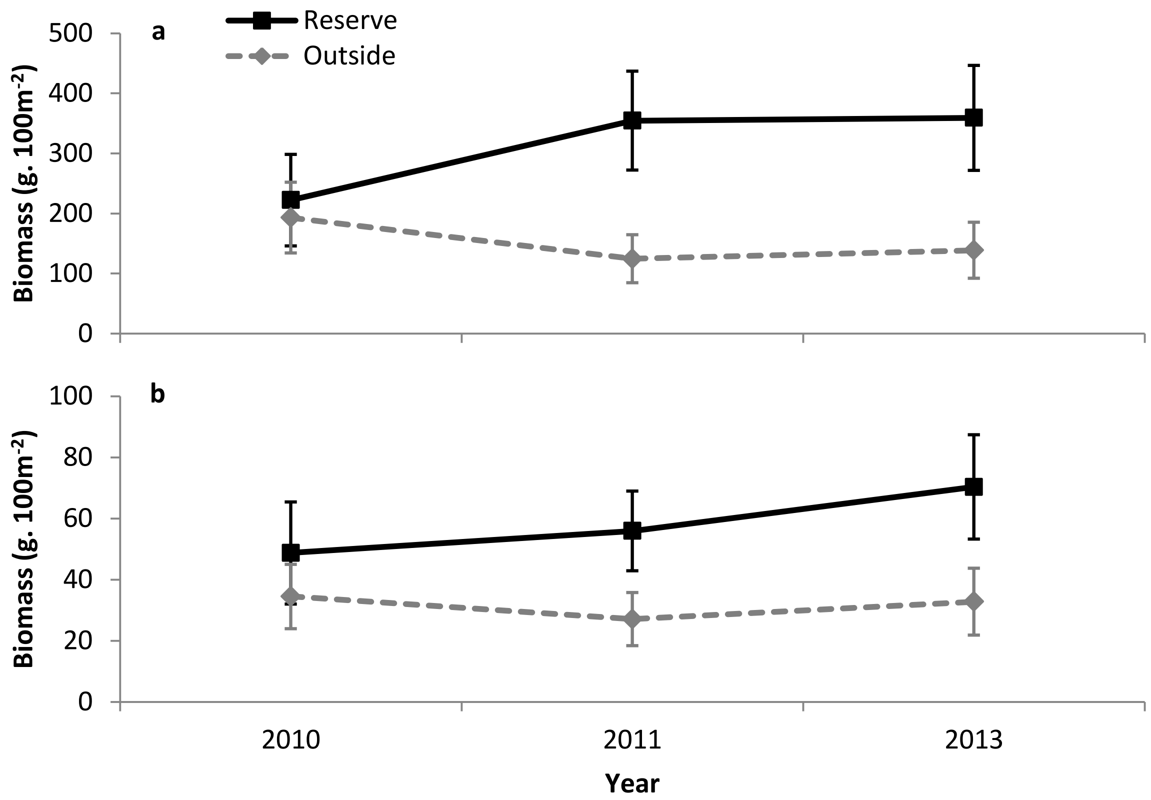

Fig. 13 The mean exploitable (a) and reproductive (b) biomass of king scallops within and outside the fully protected marine reserve for the years when scallop dissections were conducted. Error bars represent ±1 SE.

Table 1. Two-way ANOVA comparing juvenile scallop abundance between the marine reserve 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		

Table 2 The reduced and full models were created from a Poisson GLM to test whether environmental and ecological data reflected the distribution and abundance of juvenile 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

Table 3. Two-way ANOVA comparing scallop densities (sqrt transformed) between the marine 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		

Table 4 Outputs from the Kolmogorov–Smirnov (K–S) 2 sample tests used to compare the size and age distributions (% composition) of two commercially important species of scallop 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

Table 5 Two-way ANOVAs comparing the exploitable and reproductive biomass of two species 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		