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Complex habitat boosts scallop recruitment in a fully protected marine reserve

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Abstract This study investigated the effects of a fully protected marine reserve on commercially valuable scallops and benthic habitats in Lamlash Bay, Isle of Arran, United Kingdom. Dive surveys found the abundance of juvenile scallops to be greater within the marine reserve than outside. A novel multivariate approach, based upon neural networks and generalised linear models, revealed the greater abundance of juveniles to be related to the greater presence of macroalgae and maerl within the reserve boundaries. This complex habitat appeared to have positively encouraged spat settlement. In contrast, the density of adult scallops did not differ between the two treatments, possibly due to the short duration of protection. However, the age, size and biomass of adult scallops were significantly greater within the reserve. Overall, this study suggests that the newly created marine reserve is already providing benefits which are flowing back to species targeted by fisheries, emphasising the importance of marine reserves in ecosystem-based management of fisheries.

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Introduction

Closing areas to some or all types of fishing through the implementation of marine protected areas (MPAs) and marine reserves is becoming an increasingly utilised management tool to conserve marine biodiversity, ecosystem services and fisheries resources (Gell and Roberts 2002; Adams et al. 2010; Halpern et al. 2010; Unsworth et al. 2010). The rising interest in MPAs and marine reserves is supported by a growing number of scientific studies that have shown that closed area protection can increase the abundance and mean size of target species (Halpern and Warner 2002; Halpern 2003), enhance local reproductive output (Roberts and Hawkins 2000; 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 result in the greater production of larvae, juveniles and adults which then disperse to grounds outside the closed area and contribute to fishery landings (McClanahan and Mangi 2000; Gell and Roberts 2003).

The growing use of MPAs and marine reserves as a fisheries management tool has co-occurred with a paradigm shift in fisheries management; with perspectives shifting from traditional single-species management to more holistic approaches where management priorities begin with the ecosystem rather than the target species (Pikitch et al. 2004; Zhou et al. 2010). The aim of such 'ecosystem-based fishery management' is to sustain healthy marine ecosystems and the fisheries they support by addressing some of the unintended consequences of fishing, such as the mortality of non-target organisms and the physical impacts of fishing gears (Link 2002; Zhou et al. 2010, Stokesbury et al. 2011). Theory suggests that integrating ecosystem level concerns into fishery management will

result in the maintenance of more complete ecosystems, and in doing so, will generate numerous benefits that flow back to the species targeted by fisheries (Jennings and Kaiser 1998).

One way in which MPAs and marine reserves can achieve ecosystem and fishery benefits is by maintaining the integrity of benthic habitats through excluding the use of towed demersal fishing gears, such as dredges and trawls (Link 2002; Zhou et al. 2010). Trawl gear can be extremely heavy, requiring combinations of bobbins, rock hoppers, warps and chains, designed to prevent the net from becoming snagged on uneven surfaces and to maximise catch rates (Japp and Wilkinson 2007). Scallop dredges, such as the Newhaven dredge, are also heavy, and are equipped with spring-loaded teeth that dig into the seabed or scrape hard substratum to rake out scallops living in or on the surface layers of sediment (Eleftheriou and Robertson 1992; Jennings et al. 2001; Sewell and Hiscock 2005). 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). However, these organisms play a key function in marine ecosystems and their removal has been known to have severe consequences on the recruitment of target species and dramatically reduce an area's capacity to support other biodiversity (Roberts and Polunin 1991; Auster et al. 1996; Collie et al. 1997; Airoldi et al. 2008).

Benthic assemblages are important to marine ecosystems as they often provide an element of 3-dimensional structure to otherwise featureless seafloors (Beukers-Stewart and Beukers-Stewart 2009). They therefore supply important refuges for small/juvenile fish from predators and unfavourable environmental conditions (Monteiro et al. 2002; Ryer et al. 2004; Cacabelos et al. 2010), represent important feeding sites for fish (Bradshaw et al. 2003; Warren et al. 2010) and provide essential habitat for the settlement of scallop spat and a range of other invertebrates, including the settlement of further epifauna (Beukers-Stewart and Beukers-Stewart 2009). 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). Commonly cited nursery areas include maerl beds (Kamenos et al. 2004a, b; Hall-Spencer et al. 2006), seagrass beds (Warren et al. 2010) and areas of dense macrophytes/macroalgae (Christie et al. 2007; Cacabelos et al. 2010), all of which have been shown to harbour high densities of commercially exploited species

such as juvenile cod, *Gadus morhua*, edible crab, *Cancer pagurus* and edible sea urchins, *Echinus esculentus*. In particular, it has been well documented that scallop spat tend to primarily attach to coarse substratum and epifaunal structures (Paul 1981; Minchin 1992; Bradshaw et al. 2001; Kamenos et al. 2004a, b). It has therefore been argued that protecting settlement substratum from fishing damage should result in the enhanced recruitment of scallops and a range of other invertebrates and fish species (Bradshaw et al. 2001). Since closing areas to fishing is the surest way of protecting ecosystems from the physical impacts of fishing gear (Beukers-Stewart et al. 2005; Roberts et al. 2005), MPAs and marine reserves represent particularly useful tools for the ecosystem-based fishery management of scallops.

In addition to reducing the physical effects of fishing, MPAs and marine reserves can also benefit scallops stocks in many other ways. First, as scallops breed by releasing both male and female gametes into the water column during synchronised spawning events (Shumway and Parsons 2006), any increase in population density is likely to rapidly result in an increase in fertilisation success (Macleod et al. 1985; Peterson and Summerson 1992; Claereboudt 1999; Stoner and Ray-Culp 2000; Vause et al. 2007). Second, as younger/smaller scallops produce fewer offspring than older/larger individuals (Beukers-Stewart and Beukers-Stewart 2009), MPAs and marine reserves can enhance the productivity of scallop stocks by restoring more natural and extended age structures, which often become truncated in the presence of high levels of fishing (Berkeley et al. 2004; Beukers-Stewart et al. 2005; Roberts et al. 2005). Both responses may then contribute towards an increase in scallop density and reproductive output, thereby offering higher and less variable catches in surrounding areas (Bradshaw et al. 2001; Lewis et al. 2001; Gell and Roberts 2002; Rago and McSherry 2002; Beukers-Stewart et al. 2005; Kaiser et al. 2007; Beukers-Stewart and Beukers-Stewart 2009).

In September 2008, a fully protected marine reserve was established in Lamlash Bay, Isle of Arran, United Kingdom (UK), thereby prohibiting all sea fishing within the reserve under the Inshore Fishing (Scotland) Act of 1984 (Axelsson et al. 2009). The reserve was passed by the Scottish parliament under the rationale that the reduction in fishing pressure will help regenerate the local marine environment and enhance commercial shellfish and fish populations in and around Lamlash Bay, particularly with regards to scallops (for the original marine reserve proposal see COAST 2005). 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). Since the 1960s, one of the main fisheries operating in the area (including where the reserve is now located) has been dredging for scallops (Thurstan and Roberts 2010). This fishery focuses on the larger, more valuable great scallop, *Pecten maximus*, but can also exploit the smaller queen scallop, *Aequipecten opercularis* (Howell et al. 2006). Stocks of both species have shown marked declines in abundance in the area in recent years (Howell et al. 2006). The Newhaven dredges and trawls employed in this fishery are also known to cause considerable damage and disturbance to benthic communities and associated nursery habitat (Eleftheriou and Robertson 1992; reviewed in Jennings et al. 2001; Kaiser et al. 2006). Marine species and habitats within Lamlash Bay were mapped using remote technology (photography and side-scan sonar) and day grabs, immediately after its designation as a marine reserve (Axelsson et al. 2009). This survey provided much useful information, but was largely descriptive or semi-quantitative in nature and acknowledged to be effected by certain methodological and logistical constraints (Axelsson et al. 2009).

The aim of our study was therefore to use quantitative and strategically designed diver surveys to look for any early evidence of the marine reserve promoting the recovery of nursery habitats from fishing disturbance and enhancing scallop recruitment. Other benefits potentially offered by the reserve were also explored by testing for differences in scallop density, age structure, body size and biomass in areas within and outside the reserve. Given the short duration of protection received to date, effects of the marine reserve were not expected to be substantial. The surveys described in this report were therefore also designed to become part of an annual monitoring scheme to provide a baseline for future, related studies in the area.

Materials and methods

Study area and species

Lamlash Bay is located on the south-eastern shore of the Isle of Arran, an island situated off the west coast of Scotland, UK, in the Firth of Clyde. The fully protected marine reserve encompasses an area of 2.67 km^2 (Thurstan and Roberts 2010) where water depths range between 0 and 29 m below chart datum, but can reach 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) indicate the seabed to consist mostly 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 (Duncan 2003; Kamenos et al. 2004c; COAST 2005) but recent evidence points to a deterioration in their health (Axelsson et al. 2009).

Our study focused on the great scallop, *Pecten maximus*, and the smaller-bodied queen scallop, *Aequipecten opercularis*. Both species represent natural resources of considerable economic importance to the UK fishing industry. The *P. maximus* fishery has grown steadily since the 1970s to the point where it has consistently ranked in the top five most valuable UK fisheries for at least the past 5 years (Beukers-Stewart and Beukers-Stewart 2009). In contrast, *A. opercularis* landings have fluctuated greatly and the fishery is worth considerably less, obtaining a first-sale value of £2.2 million in 2007 compared to £38.8 million for *P. maximus* (Beukers-Stewart and Beukers-Stewart 2009).

Pecten maximus becomes sexually mature after 2–3 years of age and at around 80–90 mm in shell length. When left undisturbed, *P. maximus* individuals can live for over 20 years and grow to over 200 mm in length (Beukers-Stewart and Beukers-Stewart 2009; Marshall and Wilson 2009). *A. opercularis*, on the other hand, becomes sexually mature after 1–2 years and at approximately 40 mm in length. Individuals rarely live for more than 5 or 6 years and grow to no more than 90 mm in length (Vause et al. 2007; Barnes 2009).

The pelagic life of these scallops begins with the release of gametes during spring/summer spawning events (Brand 2006a), followed by fertilisation and embryonic and larval stages (Le Pennec et al. 2003). The resulting free-swimming larvae typically spend 3–6 weeks in the water column, often dispersing over considerable distances (Brand et al. 1980; Macleod et al. 1985) before eventually settling on to the seabed and attaching to the substrata to undergo final metamorphosis into their free-swimming adult form (Brand 2006a). As a result, the reproductive success and recruitment of scallops are heavily influenced by availability of suitable settlement habitat, as well as many other factors including environmental conditions (Brand 2006a; Beukers-Stewart and Beukers-Stewart 2009) and biotic interactions such as predator density (Beukers-Stewart et al. 2003; Le Pennec et al. 2003). Once they reach adulthood, scallops are relatively static, rarely moving more than 30 m in 18 months (Howell and Fraser 1984) and characterised by predictable patterns of distribution (Brand et al. 1991). This means the entire post-settlement life of individuals can generally be protected within a defined area (Beukers-Stewart et al. 2005). Scallops have therefore been identified as particularly suitable candidates for managing via the use of areas closed to fishing (Bradshaw et al. 2001; Beukers-Stewart et al. 2005, 2006; Beukers-Stewart and Beukers-Stewart 2009).

Dive surveys

A total of 40 dive surveys were conducted between June and August 2010. Of these, 20 were inside the Lamlash Bay fully protected marine reserve and 20 were outside. Of the 20 conducted outside, 10 were to the west of the marine reserves' boundary and 10 were to the east (Fig. 1). The wide distribution of surveys was intended to provide a good representation of Lamlash Bay whilst being limited to areas of the seabed that were shallow enough to remain within no decompression limits. Surveys were also conducted parallel to relief contours to ensure the depth of a single survey did not change by more than 3 m.

Transects were surveyed along a 50 m leaded line that was laid out straight across the seabed. 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 would then work along each transect, recording the abundance of all free-swimming (subsequently described as adult) scallops (both *A. opercularis* and *P. maximus*) and other megafauna encountered 1.5 m either side of the transect, creating a total area surveyed of 150 m² for each transect. The width of the transect was marked by a 3-m long pipe that the divers pushed ahead of themselves. The data generated by
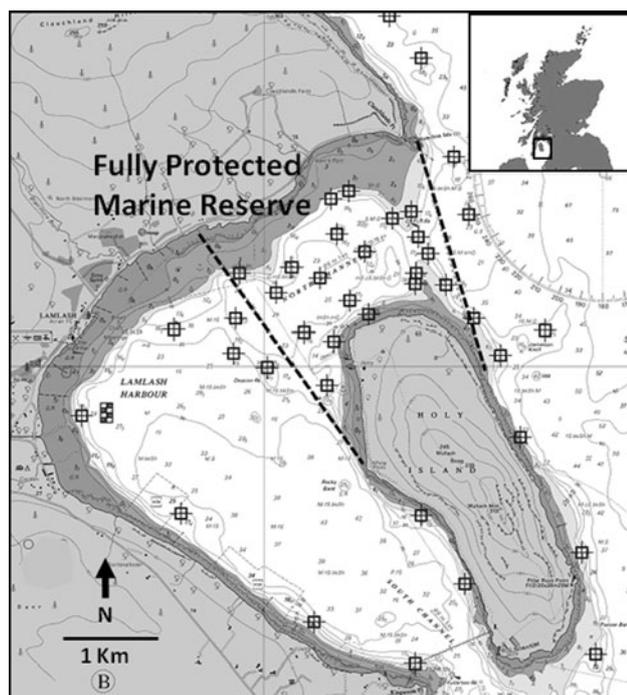

Fig. 1 The locations of the 2010 diver surveys as indicated by the crosshairs. Also displayed are the boundaries of the Lamlash Bay fully protected marine reserve (Adapted from Admiralty Chart 1864). The inset shows the location of the Isle of Arran off the west coast of Scotland, United Kingdom

both divers were later pooled to generate densities of organisms per 100 m².

In addition to density data, the shell length (see Jennings et al. 2001) of all adult scallops encountered underwater was recorded to the nearest millimetre. To generate semi-quantitative estimates of the abundance of juvenile scallops (taken to be any scallop < 10 mm in size and still attached to the substrata via byssal threads), a SACFOR abundance scale (**s**uperabundant, **a**bundant, **c**ommon, **f**requent, **o**ccasional, **r**are) was used (see Connor et al. 2004). Unfortunately, juvenile *P. maximus* and *A. opercularis* could not be distinguished apart underwater and had to be grouped as one category. Similarly, a SACFOR scale was also used to estimate the area covered by different epifaunal assemblages such as live and dead maerl (e.g. *Phymatolithon calcareum* and *Lithothamnion glacial*), seagrass (e.g. *Ruppia* and *Zostera* spp.), kelp (e.g. *Laminaria* spp.), macroalgae (e.g. *Ceramium* spp.) sponges (e.g. *Pachymatisma johnstonia*), anemones (e.g. *Metridium senile* and *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 the habitat types and structural complexity of the surrounding seabed, as well as to be compatible with methodologies currently adopted by SeaSearch (www.seasearch.org.uk), a volunteer-based project aimed at mapping out the various types of seabed found in the near-shore zone around the UK. For statistical analysis, the SACFOR scale 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. During surveys, environmental conditions such as depth and temperature were recorded at various intervals by both divers.

At the end of each survey, global positioning system (GPS) coordinates were taken from both ends of the transect to mark its location for future purposes. This was done by part hauling in one of the surface buoys until the boat lay directly atop of the transect end and then recording the GPS coordinates.

Laboratory analysis

A random sub-sample of adult *P. maximus* and *A. opercularis* scallops encountered during the dive surveys was collected from sites within and outside the marine reserve. These were then stored in seawater to be dissected within 24 h of their collection. Before dissection, scallops were cleaned of sediment and epibionts. Their shell length was then recorded along with their age, which was determined by counting the number of annual growth rings deposited

on the external surface of their shell (Macleod et al. 1985). The method of ageing *A. opercularis* individuals differed slightly from the ageing of *P. maximus*, as after dissection, the shells of *A. opercularis* individuals were subjected to immersion in a 5% bleach solution for 24 h prior to being aged. The readability and precision of their growth rings have been shown to increase after such treatment (Vause et al. 2006). Whole scallops were initially blotted dry and weighed whole to 1 decimal place using an electronic balance. All tissues were then dissected from the samples and blotted dry again. From these tissues, the wet weight of the total tissue biomass, reproductive biomass (gonad weight only) and exploitable biomass (gonad weight and adductor muscle weight combined) 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 part 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).

Data analysis: biometrics

Biomass data obtained from scallop dissections were used to explore relationships between shell length and age with exploitable and reproductive biomass, by plotting them in scatter charts and fitting a power trendline in Microsoft Excel 2007. Equations derived from the trendlines were then extrapolated for the entire sampled population, allowing for the age, exploitable biomass and reproductive biomass to be estimated for all scallops measured during the diver surveys. Any differences observed between sites in and outside the marine reserve were tested for significance through a one-way analysis of variance (ANOVA), after variables had been tested for normality using histograms, boxplots, normal QQ plots and the Shapiro–Wilk test. These basic exploratory measures were conducted on all variables within this study using 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).

Density and population structure of *P. maximus* and *A. opercularis*

Densities of adult *P. maximus* and *A. opercularis* were compared between the two treatments (i.e. 'reserve' and 'outside') using the Mann–Whitney–Wilcoxon test. This test was chosen as the two groups were independent and both variables were found to have a non-normal distribution, which could not be normalised by transformation. The Mann–Whitney–Wilcoxon test was also performed on the estimated abundance of juvenile scallops between both levels of protection. These data were then plotted in bar graphs using ± 1 standard error (SE) bars to illustrate any variation around the mean. The mean size and age of scallops in and outside the marine reserve were plotted in similar bar graphs and tested for significance using a one-way ANOVA. Lastly, the size and age (age being estimated from biometrics) of scallop populations in and outside the reserve were compared using bar charts and tested for significance using a Kolmogorov–Smirnov (K–S) analysis.

Multivariate analyses of scallop distribution

To determine whether environmental and ecological data recorded during diver surveys reflected the distribution and abundance of scallops, neural networks were created using the Neural Network Toolbox in MATLAB (Demuth and Beale 2001) testing the correlation between the environmental data gathered and the abundance of *P. maximus*, *A. opercularis* and juvenile scallops. These environmental variables included depth, a number of different habitat types and their estimated cover, predator density and level of protection (i.e. reserve or outside). Line graphs were then produced comparing the values predicted by the neural networks and the true values observed. Estimates of percentage error were then calculated to determine how well the environmental variables predicted the distribution of scallops using the equation below, where $Y' =$ the value predicted by the neural network and $Y =$ the value observed:

$$\% \text{ error} = \sum \frac{Y' - Y}{Y} \times 100$$

Neural networks were chosen as they are good at input output mapping and have an advantage over other multivariate analyses in that they can recognise patterns in the presence of noise (as is often the case with ecological data), predict future events based on past experience, predict latent variables that are not easily measured and can deal with non-linear regression problems (reviewed in Haykin 2009). Essentially, they are a very efficient way of determining if there is a relationship between independent and dependent variables without any prior knowledge about the data. In addition, due to the way in which neural networks are trained, it is possible to generate an error term for each network that directly relates to the predictability of the data and the strength of the relationship between the independent and dependant variables. However, due to the structure of neural networks, it is inherently complicated to ascertain exactly how much emphasis the neural network

classifier is placing on a given variable. For this, further analysis utilising generalised linear models (GLM) was required.

Before construction of a GLM, scatter plot and inter-correlation matrices (based upon Spearman's rank correlation) were created to explore basic relationships and determine whether any variables were strongly intercorrelated (i.e. $-0.7 \geq r \geq 0.7$) as such variables would not be allowed together in a GLM (Crawley 2005). Several GLMs were then constructed using SPSS v 17.0. These GLMs were originally intended to be based upon a Poisson error family as the response variables (i.e. scallop abundance) were based on count data and the explanatory variable representing protection was binary. However, due to over dispersion of the models, a negative binomial error function was used instead. Goodness of fit tests based upon deviance and Pearson chi-square were used to indicate how well the models fitted the data.

Results

Juvenile scallop abundance and the relationship with benthic habitats

The difference between the abundance values predicted by the neural networks and those actually observed for adult *P. maximus*, *A. opercularis* and juveniles are illustrated in Fig. 2. From the populations sampled, these models produced an estimation of scallop abundance to a 38% accuracy level for *P. maximus*, a 64% accuracy level for *A. opercularis* and an 86% accuracy level for juvenile scallops. Due to there being relatively poor correlation between the explanatory variables and the abundance of adult *P. maximus* and *A. opercularis* (i.e. the accuracy of the models was low), only one GLM was created using the abundance of juvenile scallops as the response variable.

The deviance and Pearson chi-square tests were non-significant, indicating that other covariates and/or other error distributions did not need to be considered (Table 1). Of the explanatory variables tested, the estimated cover of dead maerl and macroalgae was found to significantly influence the abundance of juvenile scallops, as did level of protection. As shown in Fig. 3, the relationship between protection and juvenile abundance was positive. Similarly, when plotted in simple scatter graphs, the relationship between the abundance of juveniles and cover of macroalgae and dead maerl also appeared to be positive and were confirmed to be significant (Spearman's rank correlation, $r_s = 0.4$, $N = 40$, $P < 0.05$). Personal observations made during the dive surveys also confirmed the positive relationship between macroalgae and juvenile abundance, as those sites found to contain dense patches of macroalgae
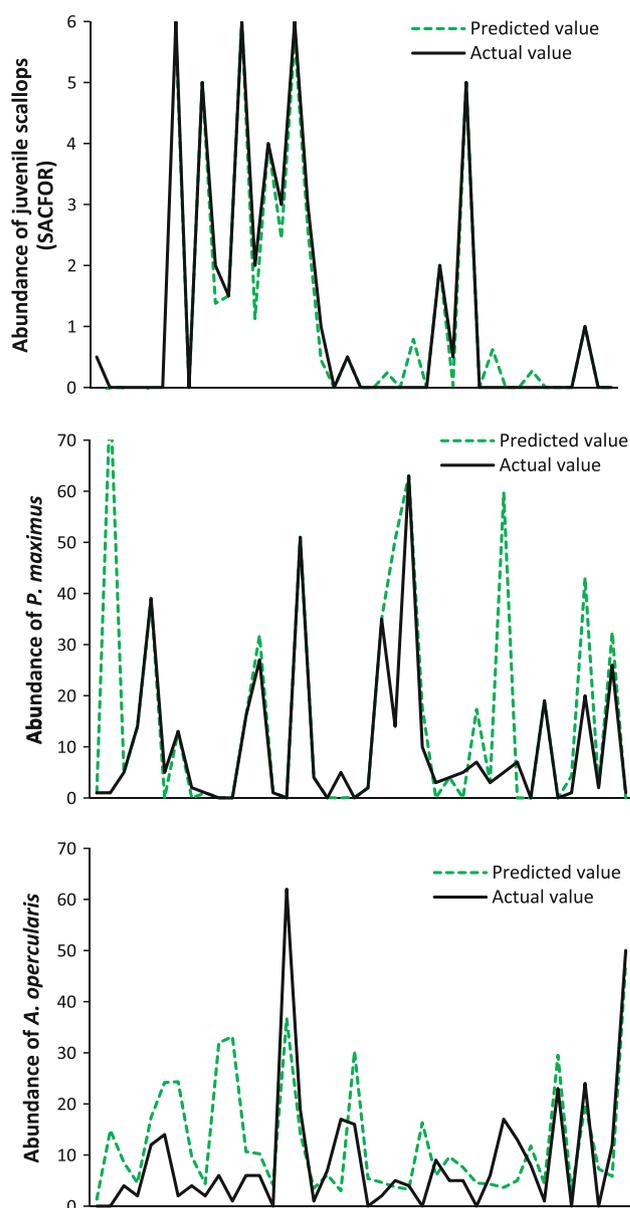

Fig. 2 Line graphs showing the abundance values predicted by the neural networks and those actually observed during the 40 dive surveys undertaken (represented by the *x*-axis) for juvenile scallops (*top*), *P. maximus* (*middle*) and *A. opercularis* (*bottom*)

also contained substantial quantities of juvenile scallops (Fig. 4). The abundance of dead maerl was higher in the reserve than outside (Fig. 5), but this difference was not significant (Mann–Whitney U test, $U = 152$, $N = 40$, $P > 0.05$). However, the abundance of macroalgae was significantly higher inside the reserve (Fig. 5; Mann–Whitney U test; $U = 112$, $N = 40$, $P < 0.05$). It should be noted that these statistical tests are very conservative as they treated differences between abundance categories as proportional, whereas measures of abundance on the SACFOR scale actually differ on an exponential scale.

Table 1 Goodness of fit tests obtained from the GLM

	Value	df	P
Goodness of fit			
Test			
Deviance	16.680	24	0.695
Pearson chi-Square	11.757	24	0.490
Wald chi-square			
Source			
Level of protection	5.154	1	0.023*
Dead maerl	4.110	1	0.043*
Live maerl	2.088	1	0.148
Macroalgae	6.824	1	0.009*
Kelp	0.287	1	0.592
Sponge	0.202	1	0.654
Anemones	0.270	1	0.603
Soft coral	0.785	1	0.376
Tunicates	0.656	1	0.418
Hydroids	0.512	1	0.474
Bryozoans	1.669	1	0.196
A. rubens density	0.060	1	0.806
Predator density	0.100	1	0.604

Their non-significance suggested the model fitted the data well. Also displayed are the variables entered into the GLM and their associated *P* values. Significant terms are denoted by (*)
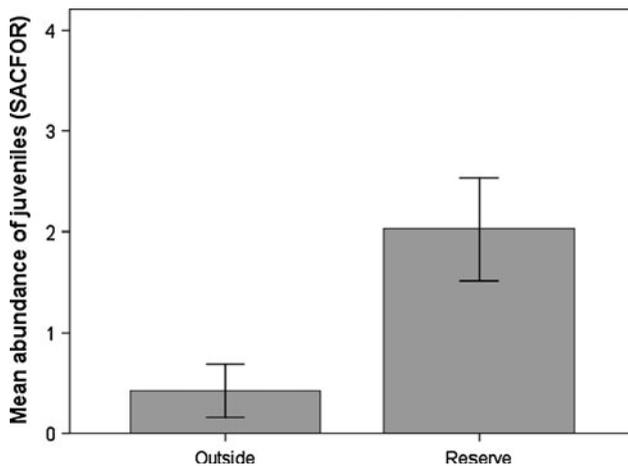
Fig. 3 The mean estimated abundance (SACFOR) of juvenile scallops within and outside the fully protected marine reserve. *Error bars* represent ±1 SE

Comparisons of scallop density and abundance

The mean density of adult *P. maximus* per 100 m^2 in and outside the marine reserve was 6.16 ($\pm$SE = 2.12, $N = 146$) and 7.56 ($\pm$SE = 2.30, $N = 217$), respectively, a difference found to not be significant (Mann–Whitney U test, $U = 160.0$, $N = 40$, $P > 0.05$). Similarly, the mean density of adult *A. opercularis* in and outside the reserve was 6.03 ($\pm$SE = 2.06, $N = 169$) and 6.13 ($\pm$SE = 1.81, $N = 184$) per 100 m^2, respectively, and was again found to not significantly differ (Mann–Whitney U test, $U = 199.5$, $N = 40$, $P > 0.05$). These relationships are illustrated in Fig. 6. Conversely, the estimated abundance of juvenile scallops was found to be significantly greater inside the reserve compared to outside (see again Fig. 3; Mann–Whitney U test, $U = 102$, $N = 40$, $P < 0.01$).

Comparisons of scallop population structure

Comparisons of age structure between treatments suggested that scallop populations within the reserve were composed of larger and older individuals (Fig. 7). These differences in age and size structure between the sites within and outside the reserve were found to be significant for both scallop species (Table 2). In fact, the mean age of *P. maximus* was 1.3 times higher inside the reserve and 1.2 times higher in size. Similarly, the mean age of *A. opercularis* was 1.5 times higher inside the reserve and 1.1 times higher in size.

Biometrics

Confidence could be expressed in all the biometric trends produced (i.e. $R^2 \geq 0.7$, see Table 3). Through extrapolating the biometrics to the entire sampled population, the mean exploitable biomass of *P. maximus* per 100 m^2 in and outside the marine reserve was found to be 36.8 g ($\pm$SE = 1.54, $N = 181$) and 25.5 g ($\pm$SE = 0.26, $N = 237$), respectively. The exploitable biomass of *P. maximus* was therefore 1.44 times higher inside the reserve, a relationship found to be significant (ANOVA, $F_{(1,39)} = 36.529$, $P < 0.05$). Similarly, the mean reproductive biomass of *P. maximus* per 100 m^2 was 8.1 g ($\pm$0.37 SE, $N = 181$) and 4.6 g ($\pm$SE = 1.7, $N = 237$), respectively, meaning reproductive biomass inside the reserve was 1.76 times higher than outside and was again found to be significant (ANOVA, $F_{(1,39)} = 58.864$, $P < 0.05$). In contrast, the mean exploitable biomass of *A. opercularis* per 100 m^2 in and outside the reserve was 1.1 g ($\pm$SE = 0.16, $N = 179$) and 1.0 g, respectively ($\pm$SE = 0.18, $N = 161$), a difference found to be non-significant (ANOVA, $F_{(1,39)} = 0.3$, $P > 0.05$). Likewise, the mean reproductive biomass of *A. opercularis* per 100 m^2 in and outside the reserve was 0.17 g ($\pm$SE = 0.02, $N = 179$) and 0.18 g ($\pm$SE = 0.002, $N = 161$), respectively, and again was found to be non-significant (ANOVA, $F_{(1,39)} = 0.44$, $P > 0.05$).

Fig. 4 The presence of 3-D mesh-like structures created by macroalgae often contained large numbers of juvenile scallops. This concurs with our analysis that juvenile scallop abundance could be predicted from the presence of complex habitat. Photo by Angus Robson
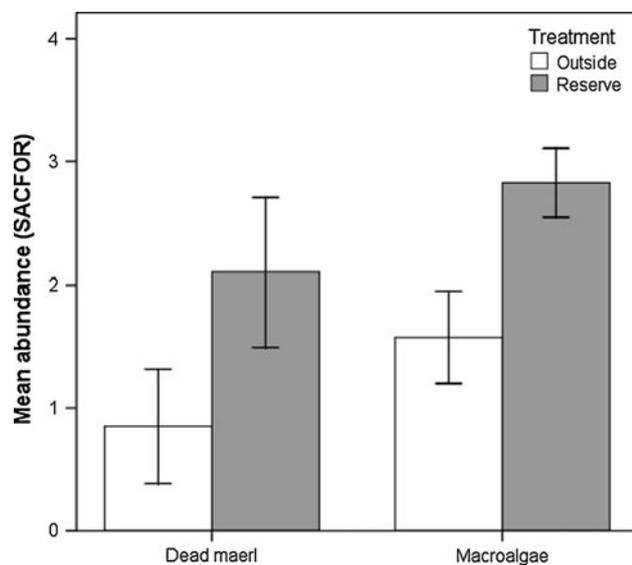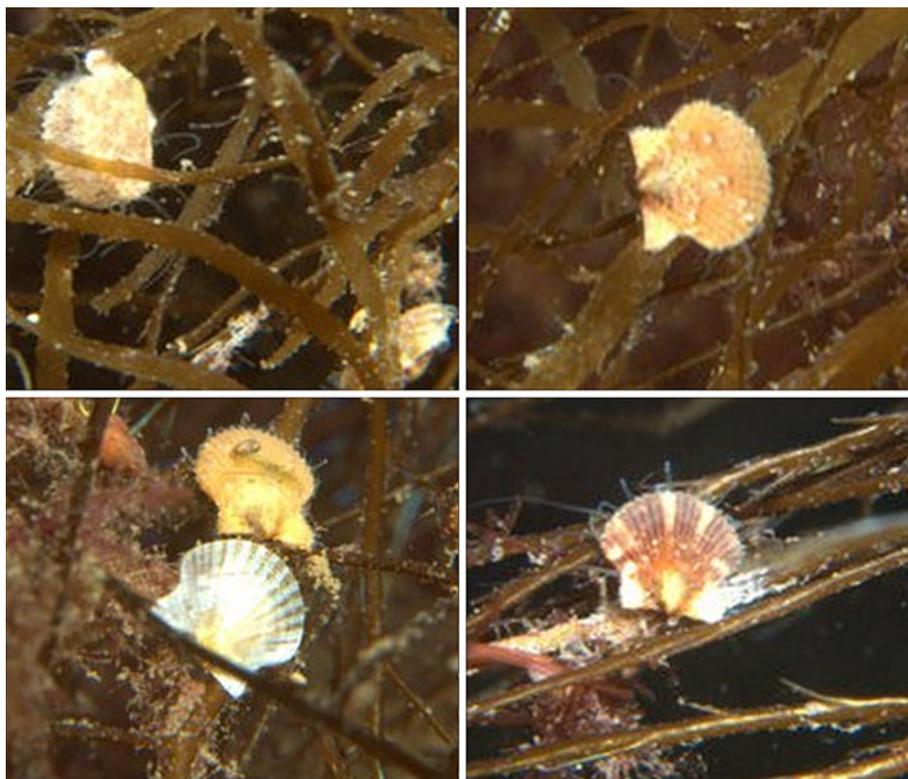
Fig. 5 The mean estimated abundance (based upon the SACFOR scale) of dead maerl and macroalgae within and outside the fully protected marine reserve. *Error bars* represent ±1 SE
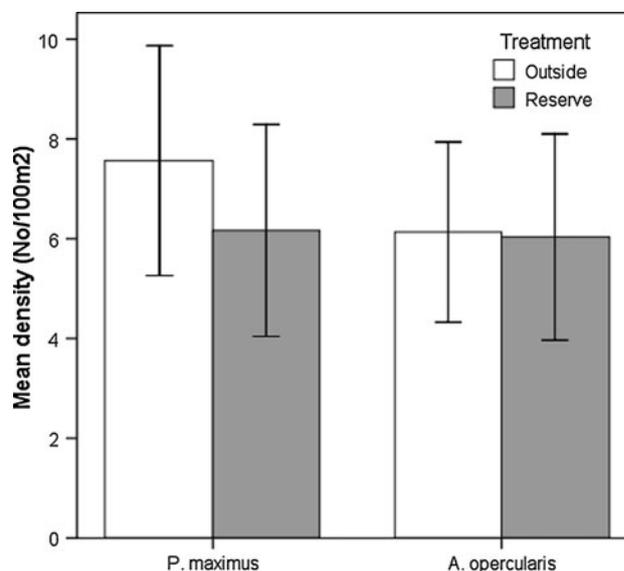
Fig. 6 The mean density of adult *P. maximus* and *A. opercularis* within and outside the fully protected marine reserve. *Error bars* represent ±1 SE

Discussion

This study provides evidence that after less than 2 years of protection, the Lamlash Bay marine reserve contains a higher density of juvenile scallops compared to surrounding areas. These findings are consistent with the hypothesis that marine reserves can enhance the recruitment of commercially exploited species. Unfortunately, this improvement cannot be conclusively related to the protection afforded by the fully protected marine reserve, due to the lack of comparable past data, especially prior to protection. However, our study does demonstrate the important role that complex habitats are thought to play in the settlement of juvenile scallops.
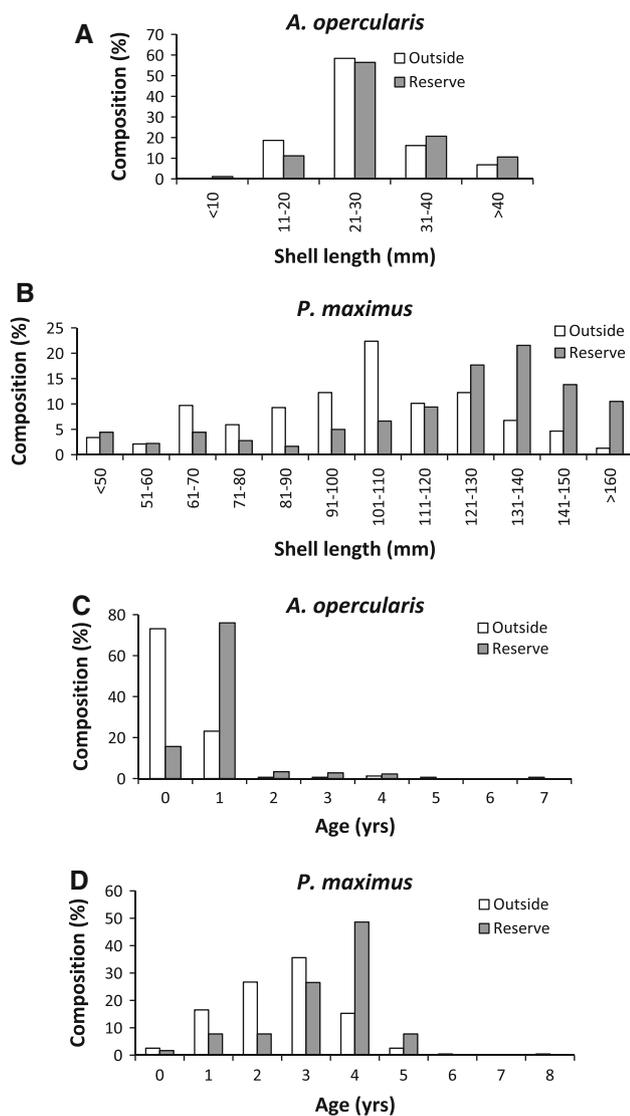
Fig. 7 The size structure of *A. opercularis* (**a**) and *P. maximus* (**b**) populations within and outside the fully protected marine reserve. Also shown are the age structures (estimated from biometrics) of *A. opercularis* (**c**) and *P. maximus* (**d**) within and outside the fully protected marine reserve. The number (*N*) of individuals sampled from each population is available in Tables 1 and 2

Table 2 Outputs from the Kolmogorov–Smirnov (K–S) 2 sample tests used to compare the size and age structure (age structure estimated from biometrics) of populations in and outside the fully protected marine reserve for both *P. maximus* and *A. opercularis*

Test variable	Reserve (*N*)	Outside (*N*)	K–S *Z*	*P*
Size—*P. Maximus*	237	181	4.121	<0.001*
Age—*P. Maximus*	237	181	3.785	<0.001*
Size—*A. Opercularis*	161	179	1.644	0.009*
Age—*A. Opercularis*	161	179	5.25	<0.001*

Significant comparisons are denoted by (*)

The GLM found that out of the many environmental variables tested, only 3 were shown to be significantly influencing the abundance of juvenile scallops. These were as follows: (1) the estimated cover of dead maerl, (2) the estimated cover of macroalgae and (3) the level of protection (i.e. whether sites were within or outside the boundaries of the marine reserve). Correlation analysis confirmed the relationships between juvenile scallop abundance and the cover of dead maerl and macroalgae to be positive. It has been well documented that scallop spat tend to attach primarily to 3-dimensional structures such as dead shells and gravel, as well as upright taxa including macroalgae, bryozoans, hydroids and live and dead maerl (Paul 1981; Minchin 1992; Bradshaw et al. 2001; Kamenos et al. 2004c). Therefore, the positive relationship observed between the abundance of juveniles and the presence of dead maerl and macroalgae supports the notion that scallop spat tend to settle in structurally more complex habitats (Paul 1981; Kamenos et al. 2004a, b). In addition, sites within the reserve contained a higher abundance of macroalgae than sites outside the reserve. Whether the protection afforded by the reserve is actively promoting the recovery of macroalgae within the reserve and consequently enhancing scallop recruitment could not be ascertained. However, although the mechanism behind this relationship is uncertain, if the reserve is protecting both juveniles and their habitats from fishing disturbance, then survival and growth during this critical life history phase will increase (Myers et al. 2000; Beukers-Stewart et al. 2005). In the long term, this would likely increase the number of juveniles entering the adult stock as a greater proportion of juveniles survive to reach maturity.

It is interesting that the cover of dead maerl was considered to be more important in influencing juvenile distribution than pristine live maerl, as this is contrary to observations made in a series of laboratory-based experiments (Kamenos et al. 2004a, b). However, the maerl beds encountered in Lamlash Bay were severely degraded, often containing only 0–10% live maerl, an observation identified in the past to be the likely result of scallop dredging and trawling (Hall-Spencer and Moore 2000; Kamenos et al. 2004c). Such small concentrations of live maerl would therefore be unlikely to greatly influence the distribution of juvenile scallops. If the marine reserve is protecting benthic habitats from fishing damage, the recovery of live maerl will take considerably longer than the recovery of macroalgae due to its slow growth (Hall-Spencer and Moore 2000; Sewell and Hiscock 2005).

The neural networks analysis found the environmental and ecological data collected during dive surveys to be able to predict juvenile scallop abundance to a relatively high level (86%), but not for the abundance of adult *P. maximus* and *A. opercularis*. This may be because when juvenile

Table 3 The equations and R^2 values derived from the biometric graphs, which were fitted with power trendlines

Species	Variable	Equation	R^2
P. maximus (Reserve, $N = 28$)	Reproductive biomass	$y = 2\text{E}{-}07x^{3.6055}$	0.901
	Exploitable biomass	$y = 1\text{E}{-}05x^{3.1181}$	0.981
	Age	$y = 0.0058x^{1.3218}$	0.787
P. maximus (Outside, $N = 28$)	Reproductive biomass	$y = 8\text{E}{-}11x^{5.2228}$	0.875
	Exploitable biomass	$y = 4\text{E}{-}05x^{2.8529}$	0.897
	Age	$y = 0.0008x^{1.7344}$	0.833
A. opercularis (Reserve, $N = 20$)	Reproductive biomass	$y = 2\text{E}{-}05x^{3.0514}$	0.933
	Exploitable biomass	$y = 2\text{E}{-}05x^{2.5683}$	0.799
	Age	$y = 0.0039x^{1.5767}$	0.711
A. opercularis (Outside, $N = 20$)	Reproductive biomass	$y = 4\text{E}{-}05x^{2.9031}$	0.945
	Exploitable biomass	$y = 0.0004x^{1.8225}$	0.758
	Age	$y = 0.0002x^{2.3467}$	0.748

These data were then extrapolated to the sampled population to estimate the age, reproductive biomass and exploitable biomass of all scallops measured underwater. Also shown are the sizes of each sample (N)

scallops attach to suitable substratum they become almost completely immobile. The distribution of juvenile scallops would therefore be much easier to predict than for adult scallops, requiring just the presence of suitable substrata at a suitable depth (with hydrographic features permitting) and may be why the environmental and ecological data recorded were much more important in determining the distribution and abundance of juvenile scallops compared to adults.

The use of neural networks in determining how well environmental and ecological factors were influencing scallop abundance and distribution was a particularly novel aspect of this study, and therefore requires further discussion. External validity considers the level in which the results from these experiments can be generalised to other scenarios (reviewed in Haykin 2009). It must therefore be said that the models and the results achieved in this study can only be thought to be as strong as the data they were based upon and their sample size. Because of this, the results cannot be confidently justified in terms of global populations (Haykin 1994). Nonetheless, the models managed to predict the abundance of juvenile scallops to a high accuracy level. So, from the data that was gleaned and from the models developed, it can be considered that the results are highly promising for predicting juvenile abundance given the resources available. One possible future application of this type of analysis is as a planning tool for the setting up further marine reserves—i.e. by entering environmental and ecological information based upon the benthic habitats of an area, we may be able to predict the level of fishery benefits that could be received by protecting that site from fishing pressure.

In contrast to the relationships observed for juvenile scallops, it appears that the reserve is yet to have a significant effect on the abundance of adult *P. maximus* and *A. opercularis* as there was no difference in their densities between the two treatments. Previous surveys of Lamlash Bay, conducted in October 2008, estimated the density of both scallop species to be around 3 individuals per 100 m² (Axelsson et al. 2009). In contrast, this study estimated densities closer to 6–8 individuals per 100 m² for *A. opercularis* and *P. maximus*. This difference may be the evidence of the reserve providing scallop fishery benefits. However, previous surveys utilised drop-down cameras to record the abundance and composition of benthic megafauna, which generally underestimates abundance. Diver surveys, such as those employed in this 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 could not be made. Another feature observed in the data were that the density of scallops within treatments, and even within transects, was hugely variable. This was because scallops were often encountered in large, distinct aggregations. Aggregated distributions are a common feature in scallop populations (Macleod et al. 1985; Brand 2006b) and are thought to be the result of a combination of factors including hydrographic features, larval survival and suitability of substrata types (Charlotte and Wilson 2009).

Despite there being no difference in the density of adult scallops between sites in and outside the marine reserve, the size and age of scallops within the reserve were found to be significantly greater. In fact, individuals of *P. maximus* were on average 18 mm larger and 1.3 times older within the reserve than outside, whilst individuals of *A. opercularis* were 3 mm larger and 1.5 times older. These differences may be slight but they could be early evidence of the marine reserve protecting stocks from fishery-induced mortality, and thereby encouraging a return of their age structures to a more natural and extended state.

This trend has also been observed in scallops in marine reserves by Murawski et al. (2000), Bradshaw et al. (2001) and Beukers-Stewart et al. (2005), as well as for other shellfish species (e.g. Rice et al. 1989; Edgar and Barrett 1999). The differences we observed are also consistent with the expected effects of the scallop fisheries operating in the Firth of Clyde. The minimum legal landing size for *P. maximus* in this area is 100 mm, a size which is generally attained at 3–5 years of age (Howell et al. 2006). Furthermore, the Newhaven scallop dredges used in the fishery are highly selective for scallops above 90–100 mm (Beukers-Stewart et al. 2001). Individuals of *P. maximus* above these sizes and ages were of higher abundance inside the reserve. Likewise, the minimum legal landing size for *A. opercularis* is 40 mm and individuals above this size were also more common in the reserve. If these differences in scallop population structure are due to the protection afforded by the marine reserve, more substantial improvements in scallop stocks are likely to occur in the future, since the reserve has only been established for short period to date (Gell and Roberts 2003; Roberts et al. 2005).

In addition to scallops being both older and larger within the marine reserve, the exploitable biomass of *P. maximus* was 1.44 times higher inside than outside the reserve, and the reproductive biomass was 1.76 times higher. This trend may be a result of the older and larger scallops within the marine reserve naturally containing a higher biomass of tissues (Beukers-Stewart and Beukers-Stewart 2009). On the other hand, the protection afforded by the reserve may also be allowing individuals to invest a greater proportion of metabolic energy into body growth and gonad development, as scallops within the reserve would no longer be required to divert energy into repairing shell damage induced from mobile fishing gears (e.g. Beukers-Stewart et al. 2005; Kaiser et al. 2007). Either way, the higher levels of reproductive biomass of *P. maximus* within the reserve should translate to higher reproductive output and potentially higher scallop recruitment both within the reserve and to surrounding areas (Pelc et al. 2010). However, detailed studies of larval behaviour, settlement and local hydrodynamics (e.g. Tian et al. 2009) would be needed to predict and quantify where these benefits might accrue.

Unlike the larger-bodied *P. maximus*, the greater size and age of *A. opercularis* observed within the reserve did not translate into greater exploitable and reproductive biomass. This may partly be because the biomass data were recorded at too a low resolution (to the nearest 0.1 g) to detect any differences in the smaller-bodied *A. opercularis*. Increasing the number of scallops dissected may also have improved our ability to distinguish between areas. Nonetheless, the R^2 values obtained from extrapolating the biometrics to the entire sampled population indicated a good fit, and therefore relative confidence can be expressed in them. In general, *P. maximus* is much more heavily exploited in the Firth of Clyde than *A. opercularis* (Howell et al. 2006). Therefore, it is perhaps not surprising that differences between inside and outside the marine reserve were more pronounced for *P. maximus*.

In summary, this study has provided several lines of evidence that the fully protected marine reserve in Lamlash Bay may already be benefiting scallop populations and benthic habitats. Firstly, the greater presence of nursery habitat within the marine reserve appears to have substantially increased the settlement levels for two key commercial scallop species. Whether the greater presence of nursery habitat was due to the protection afforded by the marine reserve is unknown, but its continued protection should come to further enhance scallop recruitment. Secondly, through protecting a proportion of the population from fishing, a greater number of individuals appear to be reaching larger, older sizes. Moreover, due to the short period since the establishment of the marine reserve, more substantial improvements in scallop stocks are likely to occur in the future (Gell and Roberts 2003; Roberts et al. 2005). Overall, these results suggest that the presence of a fully protected marine reserve is generating several ecosystem benefits which are flowing back to species targeted by fisheries, emphasising the importance marine reserves can play in the ecosystem-based management of fisheries.

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